

Bears

—Their Biology and Management

Papers of the Third
International Conference on Bear Research
and Management

BINGHAMTON, NEW YORK, U.S.A.

and

MOSCOW, U.S.S.R.

June 1974



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The projects cover a very wide range from environmental policy and planning, environmental law, education, ecological studies and surveys, to the establishment and management of areas as national parks and reserves and emergency programmes for the safeguarding of animal and plant species threatened with extinction as well as support for certain key international conservation bodies.

WWF fund-raising and publicity activities are mainly carried out by National Appeals in a number of countries, and its international governing body is made up of prominent personalities in many fields.



Grizzly mother and cubs

(Photo Frank C. Craighead, Jr.)

bears
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and management

A selection
of papers from the
**Third International Conference
on Bear Research and Management**
held at the
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Edited by
**Michael R. Pelton
Jack W. Lentfer
G. Edgar Folk**

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Preface

In August 1968, Art M. Pearson, Canadian Wildlife Service, chaired a gathering of bear biologists in Whitehorse, Yukon, Canada. This 'bear workshop' represented a first attempt to bring together biologists interested in bears on more than a regional scale. The meeting consisted of a series of informal reports and discussions regarding ongoing research programs and was published by the Canadian Wildlife Service.

Interest did not wane and in 1970, a second meeting was held in Calgary, Alberta, Canada, chaired by Steve Herrero, University of Calgary. The result of this meeting are represented by a compilation of 29 formal presentations published by IUCN and entitled 'Bears—Their Biology and Management,' IUCN Publication New Series No. 23, 1972. At this time the meeting took on more of an international flavor with six of the presentations representing Russia, Japan and Norway and a status report on the brown bears in Europe (K. Curry-Lindahl). A highlight of the meeting was a presentation by I. McTaggart Cowan, University of British Columbia, on the status and conservation of bears of the world. A unanimous desire to hold another similar meeting three to four years hence was expressed by the group in attendance.

The coincidental meetings of the American Society of Mammalogists in Binghamton, New York and the First International Theriological Congress in Moscow, U.S.S.R., in June, 1974, four years post-Calgary, presented an opportunity for bear biologists to meet in both North America and Eurasia. These two meetings and some additional input afterwards resulted in the 33 North American and 12 Eurasian papers presented in this volume.

Besides the formal proceedings of the three symposia in 1968, 1970, and 1974, valuable spinoff has resulted in the formation of more specialized interest groups including the Border Grizzly Steering Committee, the Eastern U.S. Workshops on black bear management and research, and other smaller informal groups.

We would express the desirability of continuing periodic symposia of an international scope not only to serve as a focal point for biologists to report on research results, but for all resource managers and administrators to discuss current problems regarding the conservation of bears of the world. Such international gatherings might also function as a common meeting ground for the smaller, more specialized interest groups.

Finally, we wish to acknowledge with thanks the assistance given in the sponsorship, organization and financial support of the Conference and of the publication of these Proceedings by-

Alaska Arctic Gas Study Company
American Society of Mammalogists
American Petroleum Institute
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University of Iowa
University of Tennessee
Wildlife Management Institute
World Wildlife Fund

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Contents

Page

PART I. BEAR BEHAVIOR

1. Ingestive behaviors of the American black bear. Ellis S. Bacon and Gordon M. Burghardt 13
2. Learning and color discrimination in the American black bear. Ellis S. Bacon and Gordon M. Burghardt 27
3. Behavioral aspects of the polar bear, *Ursus maritimus*. S. E. Belikov 37
4. The social behaviour of brown bears on an Alaskan salmon stream. Allen L. Egbert and Allen W. Stokes 41
5. Threat behavior of the black bear, *Ursus americanus*. Robert H. Jordan 57
6. Observations on the breeding of captive black bears, *Ursus americanus*. Jeanne C. Ludlow 65
7. Fishing behavior of Alaska brown bear. Michael H. Luque and Allen W. Stokes 71
8. Play and agonistic behavior in captive black bears. Cheryl H. Pruitt 79

PART II. BEARS IN NATIONAL PARKS

9. Homing of black bears in the Great Smoky Mountains National Park. Larry E. Beeman and Michael R. Pelton 87
10. Grizzly bear ranges and movement as determined by radiotracking. Frank C. Craighead, Jr. 97
11. Aspects of grizzly bear population ecology in Mount McKinley National Park. Frederick C. Dean 111
12. Conflicts between man and grizzly bears in the national parks of North America. Stephen Herrero 121
13. Ecological role and management of grizzly bears in Glacier National Park, Montana. Clifford J. Martinka 147
14. Attitudes and opinions of persons experiencing property damage and/or injury by black bears in the Great Smoky Mountains National Park. Michael R. Pelton, Charles D. Scott and Gordon M. Burghardt 157
15. Characteristics and management of black bears that feed in garbage dumps, campgrounds or residential areas. Lynn L. Rogers, David W. Kuehn, Albert W. Erickson, Elsworth M. Harger, Louis J. Verme and John J. Ozoga 169

PART III. MANAGEMENT OF BEARS AND TECHNIQUES

16. Managing Montana's grizzlies for the grizzlies. Kenneth R. Greer 177

	<i>Page</i>
17. The dynamics and regulation of black bear, <i>Ursus americanus</i> , populations in Northern Alberta. Gerald A. Kemp	191
18. Polar bear den surveys in Svalbard, 1972 and 1973. Thor Larsen	199
19. Polar bear management in Alaska. Jack W. Lentfer	209
20. The black bear in Pennsylvania—status, movements, values, and management. James S. Lindzey, Walter S. Kordek, George J. Matula and William P. Piekielek	215
21. Use of M99 etorphine and antagonists to immobilize and handle black bears. Robert L. Miller and Gary B. Will	225
22. Preliminary management implications for black bears, <i>Ursus americanus</i> , in the Catskill region of New York state as the result of an ecological study. Eugene R. McCaffrey, Gary B. Will and Andrea S. Bergstrom	235
23. Population characteristics of the Arctic mountain grizzly bear. Art M. Pearson	247
24. An evaluation of the use of ERTS-1 satellite imagery for grizzly bear habitat analysis. Joel R. Varney, John J. Craighead and Jay S. Sumner	261
25. The use of the skull in age determination of brown bears. B. P. Zavatsky	275
 PART IV. STATUS OF BEARS	
26. A remnant brown bear population in southern Norway and problems of its conservation. Kåre Elgmork	281
27. Distribution and quantity of brown bears in Kazakhstan. Y.A. Grachev	299
28. The polar bears of Cape Churchill (abstract). Charles Jonkel, Ian Stirling and Richard Robertson	301
29. Ecology, protection and prospect of utilization of the brown bear in the Estonian S.S.R. Mati Kaal	303
30. Status of the last brown bears of the Alps in the Trentino, Italy (abstract). Hans U. Roth	307
31. On the ecology of brown bear in the southern Urals. I. V. Sharafutdinov and A. M. Korotkov	309
32. The European brown bear in the Carpathians. A. A. Slobodyan	313
33. Research on the polar bear in the U.S.S.R. S. M. Uspensky and S. E. Belikov	321
34. The brown bear on Baikal: a few features of vital activities. S.K. Ustinov	325

35. The brown bear in Eurasia, particularly the Soviet Union. N. K. Vereschagin 327

PART V. BIOLOGY OF BEARS

36. Reproductive cycles and rates in the grizzly bear, *Ursus arctos horribilis*, of the Yellowstone ecosystem. John J. Craighead, Frank C. Craighead, Jr. and Jay Sumner 337
37. Telemetry experiments with a hibernating black bear. John J. Craighead, J. R. Varney, Frank C. Craighead, Jr. and Jay S. Sumner 357
38. Physiology of hibernating bears. G. Edgar Folk, Anna Larson, and Mary A. Folk 373
39. Reproductive biology of female brown bears, *Ursus arctos*, McNeil River, Alaska. Leland P. Glenn, Jack W. Lentfer, James B. Faro and Leo H. Miller 381
40. Clinical, epidemiological and parasitological features of the *Trichinella* strain (ATS). N. N. Ozeretskorskaya and Ye. V. Pereverzeva 391
41. Denning ecology of grizzly bears in northeastern Alaska. Harry V. Reynolds, James A. Curatolo and Roland Quimby. 403
42. Parasites of bears: a review. Lynn L. Rogers and S.M. Rogers 411
43. Succinylcholine chloride immobilization of black bears. Lynn L. Rogers, Clarence M. Stowe and Albert W. Erickson 431
44. Cranial variation in polar bears. Don E. Wilson 447
45. Helminth and arthropod parasites of grizzly and black bears in Montana and adjacent areas. David E. Worley, J. Carl Fox, John B. Winters, Richard H. Jacobson and Kenneth R. Greer 455

ADDRESS LIST OF SENIOR AUTHORS 465

INDEX OF AUTHORS 467

PART I : BEAR BEHAVIOR

Paper 1

Ingestive Behaviors of the American Black Bear

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INTRODUCTION

This paper describes the behaviors associated with procurement and consumption of food by captive black bears. The few prior studies are largely anecdotal and associated with food habit studies. Murie (1937) briefly describes the foraging of an adult female for grasshoppers. He notes that the bear frequently overturned bison chips in search of food. Cottam *et al.* (1939 — p. 314) state that in Virginia 'the black bear is much more of a clean feeder than might be expected.' He reports finding little debris (leaves and twigs) of the plants from which fruits or seeds are consumed. Chatelain (1950) reports that black bears on the Kenai Peninsula of Alaska consume considerable debris and Frame (unpublished) notes fishing behavior along a river.

Three major categories of behavior will be discussed; foraging, predation, and consumption. Data for all three categories were obtained using various techniques of observation; written notes, super-8 ciné film, and video-tape. Most observations involved the same captive female bears studied by Burghardt & Burghardt (1972), Burghardt (1975), Jordan (this volume) and Pruitt (this volume). Details may be found in Bacon (1973).

FORAGING

Although particular behavioral sequences of foraging, including searching for and orientation to selected food items, depend upon the situations encountered, the components of the observed behaviors are relatively consistent and uncomplicated. Such consistency occurring in semi-natural conditions indicates that the behaviors described here are representative of patterns involved in the attainment of food by black bears in natural conditions. Although stereotypy may seem unusual for a member of the order Carnivora, it is understandable in view of the black bear's largely vegetarian diet. Predation upon other than sessile invertebrates and social insects was seldom observed and was not considered a component of foraging.

Olfactory Scanning

Bears use their noses in two ways: to sniff the air and to sniff (smell) objects within the enclosure, including the fence and the ground. When the bear sniffs



Fig. 1 Non-directional olfactory scanning, sniffing the air.



Fig. 2 Olfactory orientation, sniff close (Sc).

the air (S air), it is orienting toward a relatively distant odor. During this behavior, it generally does not move. Regardless of body position, the head is raised with the nose extended upward. This type of orientation is observed when the bears are in a variety of body postures including sitting on the haunches, standing on all fours, and standing on the back legs while resting against a tree or fence. The mouth is either open or closed depending upon the intensity of the orientation. If the bear is sniffing intently, the mouth is open and exhalations may be heard from a few m distance. The inhalation appears to be slow but becomes faster with greater arousal of interest. The S air is illustrated in Figure 1.

Sniffing or smelling objects within the enclosure involves several levels of intensity. At the lowest intensity the bears usually hold their noses close to the ground or objects being smelled and there is little actual contact. Depending upon the distance, this is called sniff medium (Sm) or sniff close (Sc). Figure 2 illustrates the Sc. With Sc the bear would place the upper lip within two cm of the object. Further distances, from approximately two to ten cm, are labeled Sm. A higher intensity is the sniff mash (Smh) where the bear pushes the front of its nose firmly onto the object being smelled. The Smh occurs as the bear smells the ground, logs, and the pockets of the investigators. It is generally associated with the presence of food. Sniffing objects within the enclosure also occurs with a variety of body postures. In addition to the postures in which the S air occurred, Sc and Sm were observed when the bears were lying down.

The inhalation rates during Sc and Sm are 1.2 to 1.6 inhalations per second. This appeared to be a consistent rate. Inhalation when the bear sniffs the air is much slower. As the bear inhales, the lower portions of the upper lip extend; the lip is drawn back as the animal exhales. Contact with objects being smelled is frequently accomplished with the upper lip as it extends. During foraging the upper lip is often used to move forest litter. The ears seldom move during the olfactory scanning and are maintained in an outward position known as the lateral 45° position (Pruitt 1974).

Ambulatory Movements

Two major patterns of movement were observed, apparent random walking and direct movement toward a food object. The predominant pattern that differentiated appetitive ambulation from other forms of movement such as pacing, running play and fright reactions, is the general Orientation of the bear toward the ground. As the bear wanders in search of food, the body line along the back and top of the head form an arc. The difference in angle of the head relative to the ground between food searching and other types of walking is subtle, but it can be distinguished by the experienced observer. When the bear is not searching for food, the head is held more upward than that of the foraging bear, whose head is closer to the ground.

A more obvious indication of foraging is the random breaking of stride to orient toward or sniff the ground and various objects. In this apparently random walking, the bears walk in a *Left-front, Right-rear, Right-front, Left-rear* pace frequently broken by olfactory orientation. The speed of forward movement in random walking varies greatly. In a fifteen minute video tape sequence of foraging behaviors, the maximum speed recorded was one m per second. The frequency of orientation toward objects varies according to the food available. When raisins are scattered in the enclosure, the bears seldom orient away from the ground. The ear position during the apparent random walking is the lateral 45° position with infrequent ear movements.



Fig. 3 One of the subjects foraging.

In direct movement toward food, the bear moves deliberately with no breaking of stride or olfactory orientation. The primary orientation appears to be visual as the head is not oriented toward the ground but rather toward the food being approached. Thus, the movement is similar to non-food walking. Although the direct movement sometimes involves running, the bear generally walks briskly and slightly more rapidly than the maximum speed of the apparent random walking. Again the ears are maintained in the lateral 45° position and do not move.

Use of the Front Paws

The front paws are frequently used during foraging; in digging, raking, turning over objects, lifting and pulling. Digging resulted in actual movement of earth. Limited digging in an area generally consists of small, shallow holes which are often enlarged over a period of time. Digging usually occurs adjacent to rocks, root systems of trees, and the concrete in which the fence was embedded. Figure 4 illustrates the results of long-term digging around the roots of a large pine. This would presumably be rarely, if ever, as localized under natural conditions.

As the bear digs, it stands on all fours with the nose near the ground. The hind feet are together and the paws are used one at a time. While a bear digs, it is always smelling the ground. The front claws are used to move the earth. A front leg is extended, lowered to the ground, and pulled back along the ground in a single motion. The front leg motion is always parallel to the body line, and the earth is always pulled toward, never away from the body (Fig. 5).



Fig. 4 Results of digging around roots of large pine.

Video tape analysis illustrated that the speed approximated 0.8 seconds per digging movement. After three to four digging movements, the bear would stop and Sc or Smh the ground. In a 10-minute recording, an average of 27 digging movements per minute occurred.

Raking is identical to digging except that only the litter on the ground was moved. Raking is used to move the surface litter, draw objects toward the animal, or move specific objects such as rocks and branches. Figure 6 illustrates a bear raking straw toward the den for use as bedding material.

The bears are adept at lifting and turning over rocks, logs and other objects on the ground. When bent downward, the claws of the front foot could almost touch the front pad of the foot. In this way the animals could partially grasp objects. To lift and turn over objects the bear would grasp the side of the object farthest away and pull it upward and back toward its body. Although a bear may turn the bottom of the front paws perpendicular to the ground, it



Fig. 5 Typical digging posture.



Fig. 6 Kit raking straw toward the den.

never seemed to flip objects by a rotation of the foreleg. Also, the bears never lifted an object with the pads of the front foot turned upward. Instead, all lifting was a continuation of the raking motion with the claws turned downward and back.

The front paws are also used to pull at objects such as the bark of a tree. In debarking logs the bears would hook the claws of one paw under the bark and pull toward the body. The other front foot was used for support against the log.

PREDATION

Both bears used a forepaw for initial contact with prey animals, usually via slapping. The bears would quickly snap up an insect in their mouth, but generally they trapped it beneath the paw. Often they used both front paws in apparent attempts to cover and crush the prey. The reaction to an introduced uninjured mouse (*Peromyscus* sp.) was similar to that toward insects. Both bears chased the mouse with a series of front paw slaps. The bears' approach to a water snake (*Natrix sipedon*) was similar in that the forepaws were used to initiate contact with the snake. Unlike the insects and mouse, however, the snake exhibited an aggressive defense. During the interaction with the snake, the bears cautiously raked and pulled the animal toward them but made no crushing slap. The sequence of approach and paw slap of a butterfly is shown in Figure 7 traced from a super-8 ciné sequence. The orientation appears to

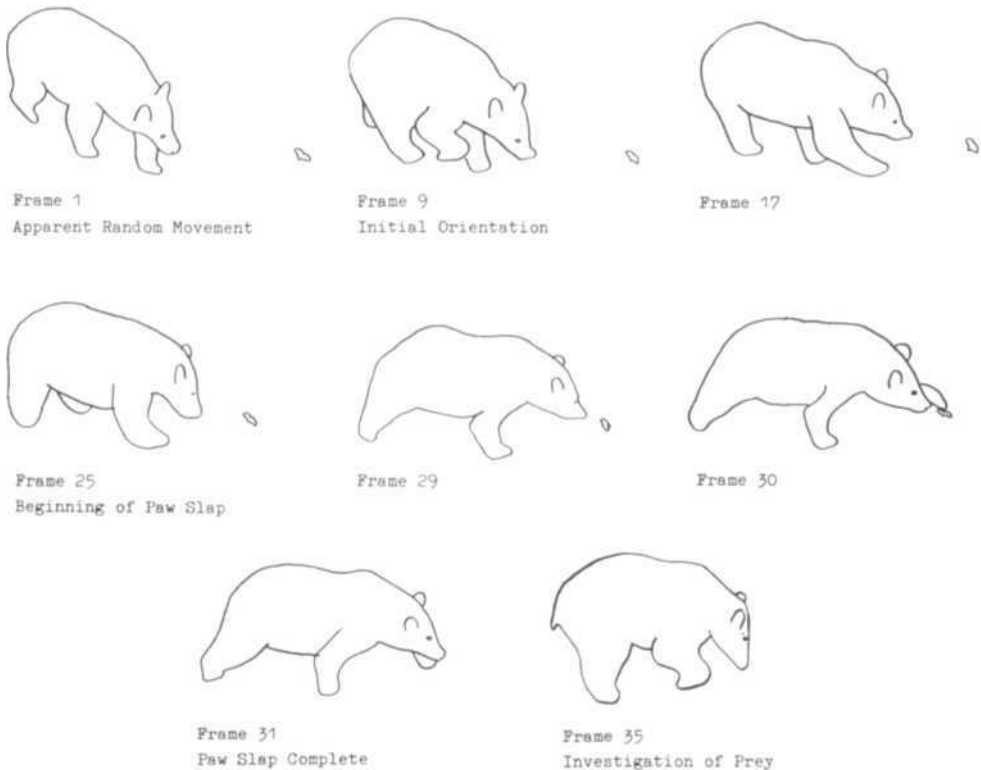


Fig. 7 Sequence of butterfly catching (18 frames per second).

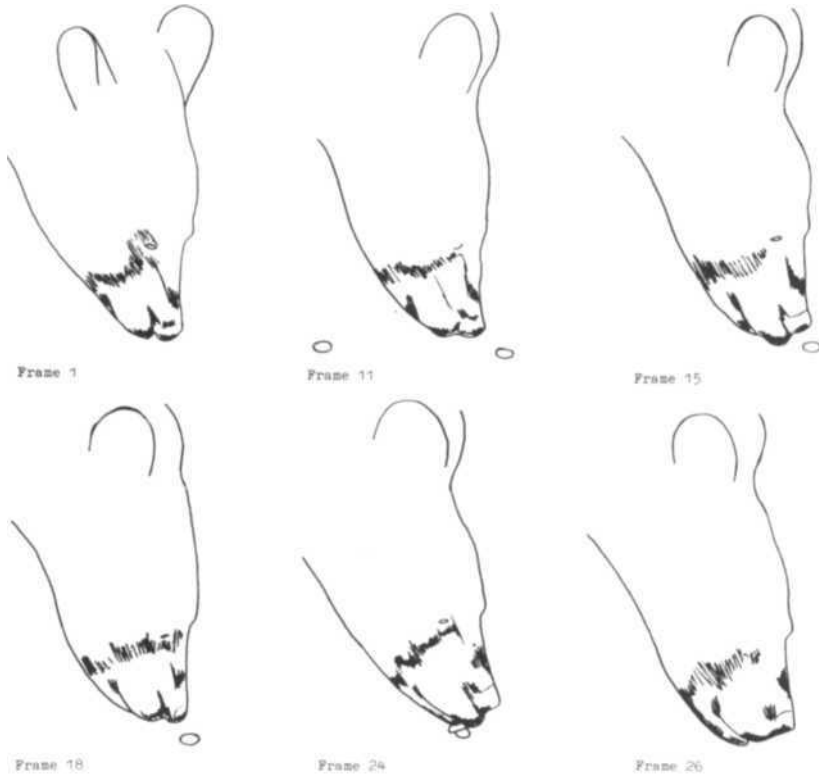


Fig. 8 Orientation and procurement of acorn (18 frames per second).



Fig. 9 Extension of upper lip in picking up acorn.

be visual and the ears remain in the lateral 45° position throughout the sequence.

Eisenberg and Leyhausen (1972) believe the use of the forepaws to grasp prey is a recent advance in prey capture that has evolved several times within various orders of mammals. Insectivores, dasyurid marsupials and small carnivores may use the forepaws to pin small prey to the ground before administering a killing bite or series of bites. However, only the Felidae favor use of the forepaws to clasp prey prior to killing.

Another use of the forepaws is considered unique to the Felidae (Ewer 1968). The serval (*Felis serval*) crushes prey, particularly those exhibiting agonistic responses, with a downward, slapping blow of a forepaw. Ewer believes that the paw slap in these cats functions to keep their heads away from potentially hazardous prey. The bears' use of the forepaw with the snake appeared to serve this function but no paw slap was observed. However, when an injured mouse was introduced to one bear, she oriented to the mouse, smelled it, delivered a crushing slap with the right forepaw, smelled the mouse again, and delivered another rapid slap with the left paw prior to taking the mouse into her mouth. The bear appeared to use the forepaw to kill or disable the prey prior to eating it.



Fig. 10 Kit using forepaw upon which to rest uneaten pieces of acorn.

CONSUMPTION

The major classes of vegetative foods bears consume in the Great Smoky Mountains National Park are nuts, berries and grasses (Beeman and Pelton 1974). In this study we observed how bears ate acorns, blackberries and grass.

Consumption of Acorns

Orientation to acorns appears to occur by both sight and smell. A film analysis indicates that the initial orientation is visual. This, of course, assumes that the bear is already in the vicinity of available food and does not discount a general olfactory alerting or prior scanning. While details of the orientation and procurement of food vary with the specific situation, the visual and olfactory orientation, along with procurement via tongue and upper lip, is fairly consistent.

Figure 8 illustrates a sequence of orientation and procurement of an acorn by Kit. Frame 1 is the first obvious orientation toward and acorn. The distance is approximately 16 cm. Since other acorns are scattered nearby and no upper lip movement associated with sniffing occurred, this initial orientation is considered visual. In frame 11 the bear is approximately 6 cm from the acorn. At this point the upper lip extension of the Sniff Close (Sc) begins. In frame 15 the upper lip is maximally extended and withdrawn three frames later (frame 18). This Sc possibly serves as a reliability check for the object to which the bear is orienting.



Fig. 11 Procurement of blackberries. (18 frames per second).

Immediately after olfactory orientation the bear obtains the acorn. Contact with the food occurs in frame 24. The tongue is extended and the acorn is picked up between the tongue and extended upper lip (frame 26). The extension of the upper lip often masks the role of the tongue in picking up the acorns. This is illustrated in Figure 9. This sketch of Kate is one frame prior to ingestion of the food. The upper lip is extended partially over the acorn and the tongue is not visible.

After the bear has obtained the acorn it is transferred to the rear of the mouth and chewed. The bear separates most of the hull from the meat, pushes the pieces of the hull out of the front and side of the mouth so that little of the hull is eaten. Interestingly, during the initial chewing of an acorn, pieces are often allowed to drop on the top of the front foot or on the leg. Later the bear would pick up the fallen pieces. However, debris is never observed falling on the foot. Using the front feet on which to rest uneaten food was frequently observed in the two subjects (Fig. 10). This was also observed in another enclosed black bear (R. Jordan pers. comm.). After most of the hull was removed, the chewing rate is rapid, up to three times per second.

The body position during acorn eating appears to depend on the situation. In the films the two bears are usually standing on all four feet, although they also assumed lying on the stomach and sitting positions. The ears are always at lateral 45° while the bears are orienting to food or eating. Frequently while eating both bears would look away from the food to other stimuli in and around the enclosure. At these times the ears move forward toward the sound or object to which the subject is orienting.

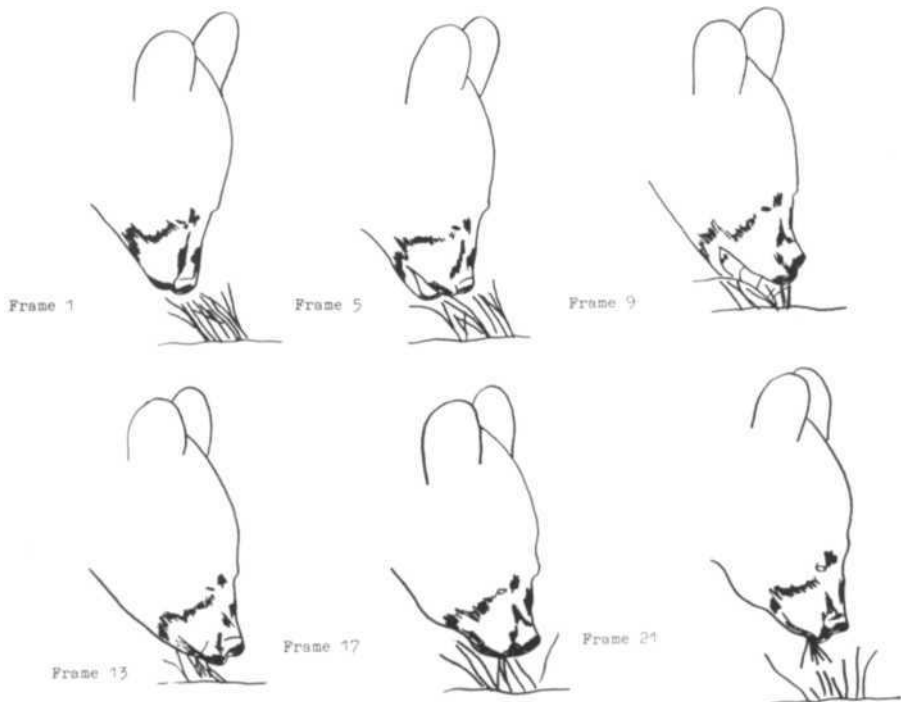


Fig. 12 Procurement of grass (18 frames per second).

Consumption of Blackberries

Orientation to blackberries is primarily visual. This may have been due to the lack of necessity to search for the food items. Unlike acorns scattered randomly on the ground, the blackberries were conveniently located on bushes placed in the enclosure. Very few overt Sc's are found in the film analysis. There is, however, obvious head nodding. This consists of lowering the nose slightly prior to movement toward a berry or group of berries. This lowering of the head could possibly bring the food into a clearer field of vision. The head nodding is illustrated in frames 1 and 5 of Figure 11 which contains tracings of a typical procurement sequence. The berry is approached and grasped behind the incisors in frame 9. Frames 17 and 29 are good examples of the incisor bite. The bear then pulls the head from the bush and the berry is removed from its stem (frame 35). In this manner very little of the stem is ingested. The bears use their tongues to guide the berries into the mouth, although berries were also obtained without the use of the tongue.

The rate of chewing is approximately the same as with acorns. The front paws are used only to hold or manipulate the bush. Holding consists of standing on the stems of the bush which appears to steady the plant. The lateral 45° ear position again occurs throughout ingestion.

Consumption of Grass

During procurement of grass (Figure 12), the mouth is opened wide and the bear bites into it with the incisors. The animal then lifts its head and pulls the grass from the ground. In eating grass the mouth is opened much wider than in eating either acorns or blackberries. The tongue is used to procure loose blades, but intact grass is initially grasped by the front teeth without the use of the tongue.

Chewing is more pronounced and slower than in the consumption of acorns and blackberries. The bear clearly manipulates the grass with the tongue during chewing. The front paws are used much more while eating grass than during consumption of the other two foods. Both bears used their paws to rake through the grass, hold it down, and lift the grass closer to their mouths. The body position varies from standing on all fours to lying on the stomach. The ears are again lateral 45° position during the ingestion.

DISCUSSION

Black bears are particularly clean and even delicate feeders. Although many foods are eaten in their entirety (e.g. apples, pears, whole fish), very little debris is ingested as they consume acorns, blackberries and grass. Most debris is either spat out or avoided. These results agree with observations on the black bear in Virginia (Cottam *et al.* 1939).

Orientation to food items appears to involve both sight and smell, both of which are well developed and efficiently integrated. The apparently frequent use of sight suggests the presence of a high degree of visual acuity and pattern discrimination. While the captive conditions undoubtedly affected the intensity and duration of the ingestive behaviors seen here, we feel that the topography and sequencing are probably quite normal. Since observations of wild black bears eating native food are scarce, it is hope that other investigators will take advantage of chance or unusual situations to film and record observations in order to evaluate further and to extend these results. Detailed comparison

of the topography of feeding behaviors with other bear species and mammals in general is also of importance.

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Paper 2

Learning and Color Discrimination in the American Black Bear

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INTRODUCTION

The black bear (*Ursus americanus*) has been thought to possess limited visual ability, especially compared to its good hearing and smell (Bray and Barnes 1967; Seton 1909; Skinner 1925; Wormser 1966). This view is not based on experimentation or controlled observation. In fact, the perceptual abilities of the black bear are virtually unknown aside from gross generalizations. Little more is known about the perceptual abilities of other species of Ursidae; however, Couturier (1954) states that brown bears are capable of discriminating bright colors (his source was unidentified) and Kuckuk (1937) demonstrates that young brown bears are capable of recognizing their keeper moving toward them at a distance of 110 m.

There is a general lack of information pertaining to the sensory abilities of bears and other carnivores. Hue perception in mammals, aside from primates, has been considered rudimentary or non-existent (Gregory 1966). Such conclusions too often have been based on poorly controlled experiments on relatively few species. For example, Walls (1942) in his compendium on the eye mentions research on color vision, much of which yielded questionable or conflicting results, for only ten non-primates. The primates are the only mammals in which both behavioral and physiological data convincingly establish widespread hue perception (Grether 1940; Walls 1942; Ducker 1965; Rosengren 1969; Hess 1973). However, behavioral research since 1950 indicates that several non-primates, including swine (Klopfer 1966) and horses, squirrels and prairie dogs (see review in Hess 1973), can readily discriminate between hues.

In carnivores color vision research has been limited to a relatively few species (Ducker 1965; Rosengren 1969): domestic dog and cat, raccoon (*Procyon*), red fox (*Vulpes*), civet (*Viverra*), mongoose (Herpestinae) and weasels (*Mustela*). This study was designed both to assess the ability of black bears to discriminate visually on the basis of hue and to develop a training method generally applicable to the study of discrimination in this species. Additional details of the methods described below, as well as comparable experiments on form discrimination, are found in Bacon (1973) and Burghardt (1975).

METHODS

Subjects

The two bears were named Kit and Kate; Kate was 19-31 months of age during testing and Kit 28-31 months. Both were hand-reared since 10 weeks of age

(Burghardt and Burghardt 1972) and were the same animals used in Bacon and Burghardt (Paper 1 this volume).

Apparatus

Stimulus Items. These consisted of 8 oz.(0.24 l) translucent polyethylene cups painted with a semi-gloss latex paint. Each cup was painted at least twice to insure a homogeneous appearance. Varying shades of each hue (or color) were produced by adding differing amounts of pigment to either a latex paint base or white latex paint. The shades, or saturations, ranged from dark to light for each hue. There were 5 hues with the following number of shades:blue—7, green—5, red—5, yellow—5, and gray—18.

Spectrographic Analysis. The intensity of transmission within the visible spectra was obtained for each hue and shade. Using a Bausch and Lomb 505 spectrometer, light transmission relative to a barium carbonate standard was obtained at every two nanometers between 400 and 700 nanometers. The shades of blue, green, red and yellow hues remained remarkably stable. The transmission spectra for the shades of each hue varied primarily in saturation (expressed as relative transmission) and did not show significant shifts up or down the visible spectrum. The shades of gray also exhibited an excellent homogeneity in that the relative transmission was almost constant along the visible spectrum.

Olfactory Control Boards. Olfactory cues were controlled by olfactory control boards upon which stimulus items were placed (Figure 3). Each board consisted of two 30 x 30 x 63 cm plywood squares bolted together. A hole the size of the stimulus item was cut in the top board, and a shallow well was hollowed out in the bottom board. Two squares of copper window screen were placed between the boards. During testing raisins were placed in the small hollow

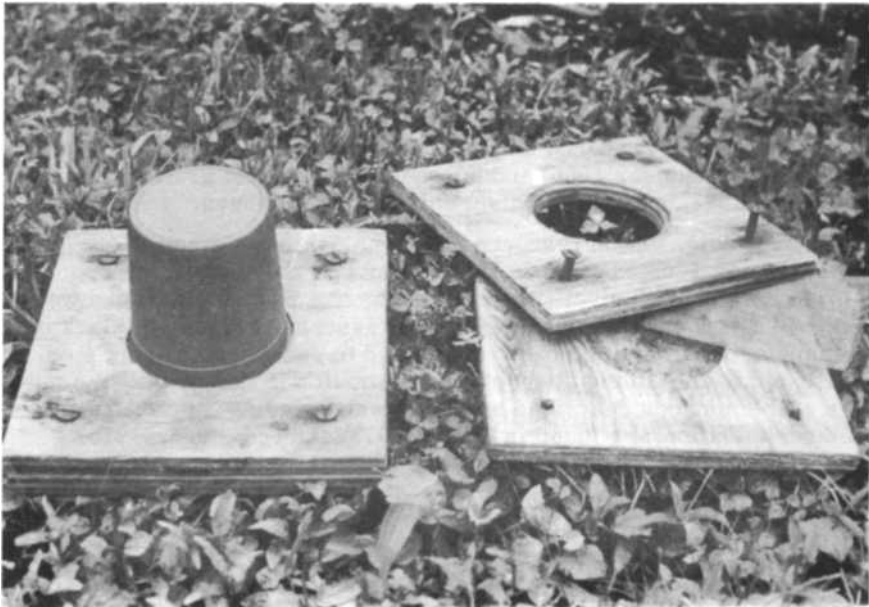


Fig. 1 Olfactory Control Board.

under the copper screen where the bear could not reach them. Stimulus items were placed on the control boards covering the copper screen, and two additional raisins were placed under the positive stimulus. In this way raisins were directly beneath each stimulus item but available only under the positive stimulus.

Procedure

Stimulus Arrays. Seven combinations of the five hues described previously were presented as two-choice discriminations during the testing. The two

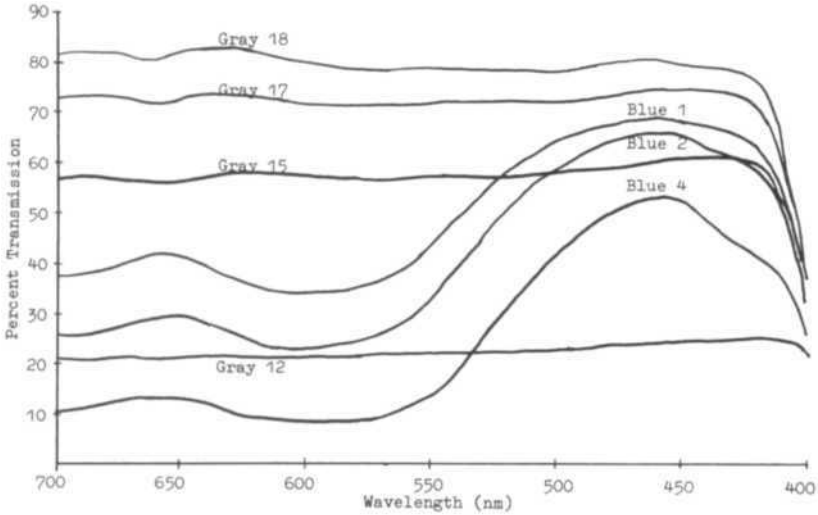


Fig. 2 Transmission spectra for selected blue and gray.

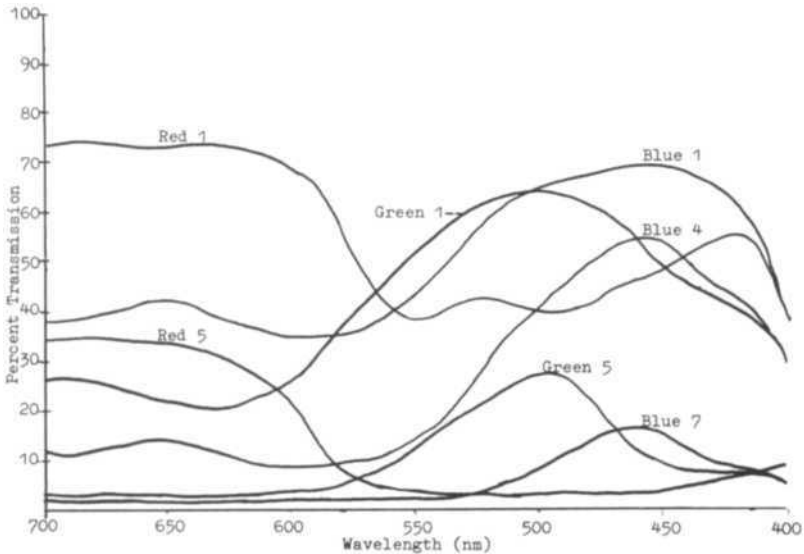


Fig. 3 Selected transmission spectra for blue, green and red.

stimuli were placed one to four m apart, and when possible, equidistant on either side of the line of approach of the subject.

Kate was trained positively to blue and was tested with four color pairs: blue-gray, blue-green, blue-red and blue-yellow. Kit was trained positively to green and was tested with three color combinations: green-gray, green-blue and green-red. The four remaining possible color pairs (red-gray, yellow-gray, green-yellow and yellow-red) were not tested.

Side preferences and hypothesis testing, such as perseverance and alternation, were corrected by the use of chance stimulus sequences (Fellows 1967).

Testing Routine. Testing was done in the animals' home enclosure. This enclosure was 18.3 m square divided by a center fence having a gate at each end. Before each trial the subject was manoeuvred to the end of the enclosure away from the apparatus. Two control boards and stimulus items were placed on the ground near the center of the testing side of the enclosure. The experimenter would leave the enclosure, obtain two stimulus items, and on return place each stimulus on the proper control board. The stimulus item to the left of the bear's path of approach was always positioned first. Attempts were made to equate the motions during placement of the two stimuli on the control boards. A clipboard oriented between the control board and bear prevented the latter from seeing the stimuli being placed. After this one of the center gates was opened allowing the subject to enter. The experimenter walked along the center fence while the bear approached the stimuli. Care was taken to remain behind the subject and not to present extraneous cues as to correct choice. After the bear obtained the reinforcement, she was given another raisin for a correct discrimination and was again placed on the side opposite the stimulus items. The entire trial formed a circular pattern of movement to which both bears became accustomed. As each subject was tested in a different half of the enclosure, both bears became well adjusted as to which side of the cage they would be allowed to enter during any particular test.

The average testing time for the 16-19 trials in a session was 37 minutes. This represents the time from the start of trial one to the end of the session. Approximately one-third of the time was devoted to preparing the stimulus arrays.

Criteria. A discrimination was considered correct when the subject turned over the positive stimulus item before touching or turning over the other (incorrect) stimulus. The bear was allowed to correct her response to obtain the reward (i.e. after the initial incorrect response, the animal could turn over the correct stimulus item for the reward). The bear was considered to be discriminating at a significant level when she responded correctly in nine of ten consecutive trials.

Control of Brightness Cues—Stimulus Bracketing. Since the testing occurred outdoors, precise control of brightness was impossible. Such precision, however, was rendered less critical by bracketing the positive stimulus. From the transmission spectra of the paints one could predict which colors would appear lighter or darker, under constant lighting, to a monochromatic animal. Figure 2 illustrates the spectral transmissions of several of the blues and grays used in the testing. Regardless of the spectral sensitivity of the retina of a monochromatic animal, under constant lighting blue 1 and blue 2 would always appear brighter than gray 12. For points within the visible spectrum the two blues reflect more light than the gray. Conversely, gray 15 and 17 will always appear lighter than blue 4. The shades with intersecting curves could appear

lighter or darker depending on the spectral sensitivity of the visual system of the monochromatic animal.

Selected spectral transmission curves for blue, red and green appear in Figure 3. The principle of bracketing the positive stimulus is again illustrated. Since certain colors will always appear lighter or darker to a monochromatic animal, it cannot consistently discriminate correctly using brightness cues when the colors are presented randomly.

Control of Brightness Cues—Variable Illumination. Stimulus bracketing of the positive stimulus depends on constant illumination of both stimuli. Because of the shifting light patterns in the partially shaded outdoor enclosure, an attempt was made to vary systematically the illumination of the stimulus items. Three lighting conditions were used: both stimuli in the sun, both stimuli in the shade, and one stimulus in the sun and the other in the shade. Two controls were introduced by varying the illumination. First, the relative brightness of the positive stimuli was further compounded, making it more difficult for the subject to respond to brightness cues. Secondly, with one stimulus item in the sun and the other in the shade, the relative brightness according to the spectral curves may be reversed. A slightly darker cup resting in the sun will transmit more light than the lighter cup resting in the shade. Varying the illumination made consistent discrimination using brightness cues still less likely.

Training the Subjects. The above procedures evolved during the 12 months prior to the final testing presented in this report. Kate was used for all of the preliminary testing, a total of 31 sessions. Kit was trained over 12 sessions with no procedural modifications made during her training. Kit had previously been trained in a form discrimination task using similar procedures which facilitated her acquisition of the new task.

RESULTS

The results of the seven discriminations are illustrated in Tables 1 through 3. The blue-gray, blue-green, blue-red, blue-yellow, green-gray and green-blue discriminations were all consistently positive. Only in the green-red discrimination by Kit did a subject fail to reach criterion consistently. With this color combination Kit reached criterion in only eight out of 17 sessions. However, her cumulative correct response was 225 of 312 total presentations. The cumulative probability of this response is less than .0001. This indicates the bear was making a correct, but not consistent, choice.

DISCUSSION

The results indicate that the bears could discriminate between hues. The blue-gray and green-gray discriminations by themselves illustrate the presence of more than a monochromatic system. Unfortunately, the exact type of chromatic mechanisms cannot be postulated from the available data. Muntz and Cronly-Dillon (1966) trained goldfish (*Carrasius auratus*) to discriminate successfully red-green, green-red, blue-green, green-blue, blue-red and red-blue color pairs. They concluded the fish were trichromatic since at least three types of photoreceptors with different spectral sensitivities were required to successfully discriminate the six color pairs. Yager and Jameson (1968), however, argue that with Muntz's data, a deuteranope could make similar discrimination. The success of the discriminations did not necessarily require a trichromatic

TABLE 1 RESULTS OF THE BLUE-GRAY, TWO-CHOICE DISCRIMINATION FOR KATE MADE IN 1972

Date	Shades of Stimulus Items		Illumination ^a		Number of Correct Responses	Criterion Reached
	Blue	Gray	Left	Right		
5May	1,2	10-18	Shade	Shade	12 of 18	no
11May	1-5	12-15, 17	Shade	Shade	24 of 25	yes
12May	1,3-6	11, 12, 14-16	Sun	Sun	25 of 27	yes
15May	3-5,7	11, 13, 14, 16	Shade	Shade	16 of 17	yes
24 May	2-5	9, 13, 15, 18	Shade	Shade	10 of 16	yes
25 May	2-5	9, 13, 15, 18	Sun	Shade	16 of 18	yes
26 May	1, 3, 4, 5	12, 14, 15, 17	Sun	Sun	16 of 19	yes
27 May	1, 3, 5, 6	10, 13, 15, 18	Shade	Sun	17 of 18	yes
30May	2,4, 6, 7	5, 11, 13, 17	Sun	Shade	17 of 18	yes

^a Illumination of the stimuli is relative to the path of approach of the subject.

TABLE 2 RESULTS OF THE BLUE-GREEN, TWO-CHOICE DISCRIMINATION FOR KATE MADE IN 1972

Date	<u>Shades of Stimulus Items</u>		<u>Illumination^a</u>		Number of Correct Responses	Criterion Reached
	Blue	Green	Left	Right		
14 May	1, 3, 4-6	1-5	Shade	Shade	25 of 27	yes
16 May	1, 3, 4-6	1-5	Shade	Shade	25 of 25	yes
17 May	1, 3, 5, 7	2-5	Sun	Sun	16 of 18	yes
26 May	1, 2, 5, 7	1-4	Sun	Sun	16 of 16	yes
1 June	1, 3, 5, 6	2-5	Sun	Shade	17 of 18	yes
1 June	2, 4, 5, 6	2-5	Shade	Sun	16 of 16	yes
2 June	1, 2, 5, 7	1-4	Sun	Sun	17 of 18	yes

^a Illumination of the stimuli is relative to the path of approach of the subject.

TABLE 3 RESULTS OF THE GREEN-RED, TWO-CHOICE DISCRIMINATION FOR KIT MADE IN 1972

Date	Shades of Stimulus Items		Illumination ^a		Number of Correct Responses	Criterion Reached
	Green	Red	Left	Right		
5 August	1-4	1-4	Shade	Shade	10 of 16	no
5 August	1-4	1-4	Shade	Shade	12 of 22	no
16 August	1-4	1-4	Sun	Sun	9 of 16	no
21 August	2-5	1, 2, 4, 5	Shade	Shade	15 of 20	yes
22 August	1, 2, 4, 5	1-4	Shade	Shade	15 of 24	no
23 August	1, 2, 4, 5	1-4	Shade	Shade	14 of 16	yes
24 August	1-3, 5	1, 2, 4, 5	Shade	Shade	10 of 16	no
25 August	1-3, 5	1, 2, 4, 5	Sun	Shade	15 of 20	yes
26 August	1-3, 5	1-4	Sun	Sun	10 of 16	no
26 August	1-3, 5	1-4	Shade	Shade	16 of 20	yes
27 August	1-3, 5	1-4	Shade	Shade	15 of 20	yes
29 August	2-5	1, 3-5	Sun	Shade	10 of 16	no
30 August	1-3, 5	1-4	Varied	Varied	18 of 21	yes
1 September	1-3, 5	2-5	Varied	Varied	7 of 12	no
2 September	1-3, 5	2-5	Shade	Shade	15 of 18	yes
2 September	1-4	1-4	Varied	Varied	17 of 19	yes
3 September	2-5	1-4	Varied	Varied	15 of 20	no

^a Illumination of the stimuli is relative to the path of approach of the subject.

system. This critique appears to apply to our study; therefore, no assumptions are made concerning trichromaticity in the black bear.

Nevertheless, hue discrimination was clear and, contrary to Courtier (1954), did not depend on 'bright' colors. The task acquisition was very rapid and the discriminations were consistently correct. The bears learned more rapidly than Grether's (1940) chimpanzees, and as fast as the dogs used by Rosengren (1969). This positive performance by the bears indicates that hue discrimination is most likely a strong and widely used component of the bear's visual perception.

The existence of color vision in the black bear belies some generalizations in recent literature concerning mammalian visual capacities, as does our work on form discrimination in black bears (Bacon 1973; see also Burghardt 1975). The foraging behavior of black bears supports our findings on their color vision. Black bears appear to use their eyesight during ingestive behaviors much more than previously supposed. The food items consumed indicate that the bear simply does not just smell these objects out. Consumption of small insects, berries, and scattered ground foods such as acorns, may require good visual acuity. A highly developed color sense would also aid in such discriminations.

The black bear has been assumed to be primarily nocturnal. Anatomical evidence for this lies in the well developed tapetum lucidum of the eye. However, the observed feeding behaviors indicate that the bear, in natural situations, may feed during the light or crepuscular hours of the day, and relies greatly on sight to locate and obtain food. A monochromatic retina would appear insufficient to cope with the needs of an animal that feeds by day on often small and scattered objects. In summary, the results show that black bears can be easily and quickly trained to perform learned hue discriminations.

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Paper 3

Behavioral Aspects of the Polar Bear, *Ursus maritimus*

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The following aspects of the behavior of polar bears, *Ursus maritimus*, are examined in this paper: (1) relationship of parturient and lactating females to man and a few animals having contact with them; (2) interrelation between females during the gestation and lactation periods; and (3) relationship of lactating females to their young. The author obtained information during expeditionary work on Wrangel Island in the fall of 1970-1971 and each spring from 1971 to 1974.

Polar bears generally experience fear during contact with people, and more often than not even a brief encounter with man leads to disruption of the normal breeding rhythm or rearing of young. The consequences are still unclear, but undoubtedly they have a negative influence upon the life cycle of the polar bear.

In late November and early December of 1970, and again in mid-October of 1971, we noted that several female polar bears abandoned dens a day or two after disturbance (Belikov 1973), even though we had no direct contact with the denned animals. Since they were easily frightened away, they could obviously detect our presence by smell and possibly by sound. The haste with which one female left the den gave a good indication of her panic. Apprehensive females abandoned dens by breaking the ceiling, which at this time of year is not so structurally firm as in the spring. According to our observations, snow density at the den site averages 1.5 times less during the fall than spring.

Pregnant females in the initial denning period and lactating females with cubs during the opening of the dens behave especially dangerously when meeting with people. The closer a man approaches a den, the more restless the female bear becomes, especially if the den is near the surface. A female can break through the thinnest section of such a den to rush a man standing close by. We once underwent an attack by a female who rushed from her den and forced us to use our weapon. However, such instances are rare, and not characteristic of the behavior of lactating and especially of gestating females. After a threatening display, the female, as a rule, returns to the den or her cubs. In some instances, females attempt to conceal their presence despite the proximity of people, the more 'patient' among them behaving as though still hidden even after the den is open.

The females disturbed by man do not necessarily abandon their dens immediately, but may do so 1 to 3 days later. Occasionally after disturbance, they remain in the den up to 8 days and, in exceptional cases, for a longer period.

Observations of one female were made when she denned in the fall, and continued after she opened the den in the spring. Despite disturbance caused by observers, she did not abandon her refuge. She sometimes came out in the snow to exercise and to clean her hair of grease and dirt, but she quickly re-entered the den when disturbed. The denning period of this bear was 183 days—from 14 October 1971 to 14 April 1972.

One den, located by its ventilating opening, was used in 1974 to obtain temperature measurements by telemetry. During 13-16 March, observations were taken

round-the-clock. Between 18 March, when the bear enlarged the ventilation opening into an exit, until 2 April, when the occupants were marked, temperature readings were obtained several times a day. Our visits disturbed the bear, since sounds of steps carried a hundred meters through the compacted snow crust, and the temperature recorder stood only 40 meters from the den. The female still did not abandon the den. After immobilizing her, we discovered that the den was new, nearly equal in size to the maternal den. The den was abandoned 2-3 days later. This particular female and cub had spent 16-17 days (mid-March to early April) in the partially opened den, from which the cub peered out several times daily. We did not once see the female at the exit during the time the den was under observation.

A few bears abandoned their shelters after disturbance and dug temporary dens several hundred meters, or more rarely several kilometers, from the maternal den. Digging a new den takes a short time, usually 15-40 minutes. One female dug a temporary den 400 meters from her maternal den while only 3 meters away was an abandoned den still not covered with snow. On the other hand, another bear with three cubs occupied an abandoned den just 500-600 meters from her old one. It is interesting to note that the female did not enter through the passage leading to the maternal chamber, but through an opening she dug over the entrance to the chamber. The polar bear apparently can readily sense an old excavation under the snow, and locate it quickly.

We also found temporary dens in places where females had not been disturbed. In two cases, we encountered solitary female bears. Their reactions to immobilization did not differ from the normal behavior of lactating females, but afterwards, neither female left her den, but dug a new chamber whose entrance began from one wall of the former den. One of these females, immobilized 22 March, had poorly developed teats, although milk could be extracted from them. She had probably had young, but had lost them. The second female, immobilized 12 April, appeared to be pregnant. Milk was exuded from teats and the abdomen was significantly more elastic than those of the lactating females examined earlier.

We observed varied behavior of cubs while working at dens. When captured, some conducted themselves rather peaceably; others furiously defended themselves, but only when a man tried to handle them. If released, they sometimes ran, not to the den nor even to the nearby mother, but away from the intruders. Once we released a cub 5 meters from an immobilized female; the youngster did not notice the mother until she raised her head.

The female is unafraid of dogs as a rule. If a dog becomes especially disturbing, the female can rush from the den to catch it, but instinct of motherhood forces her to return to the den quickly. Cubs, however, are very much afraid of a dog and will even run to a man to save themselves.

In the period of den construction, the female's basic diet is plants which she digs from under the snow. On very rare occasions, she may succeed in catching some kind of animal. In 1974, a herd of 9 and a herd of 15 deer, *Rangifer tarandus*, continuously grazed a short distance from the dens in the small mountain pass of the Drem-Head Mountains. The sows did not attempt to catch them, apparently understanding the futility of such endeavors. If a deer does become food for a sow, then it is accidental and most often is a sick individual incapable of running from a predator.

Arctic fox, *Alopex lagopus*, are less cautious than deer, since they are accustomed to bears and have become fellow-eaters on the ice. But the bravery of the small animal does not always pass with impunity. In 1973, we witnessed

one such careless fox who entered a den where he was swiftly killed. The sow appeared with the fox in her teeth. She passed above us on a slope and stopped. Letting go of the crushed animal, she pushed it with her nose to a cub, who only smelled it. Evidently at this age, cubs are still unprepared to ingest meat. Only part of the cranium remained of the fox when we immobilized the sow the next day and uncovered the den.

A high concentration of dens occurs on Wrangel Island, particularly in the Drem-Head Mountains. On a few slopes the dens are situated a few meters from each other (Uspensky & Chernyavsky 1965), which indicates females passively or tolerantly relate to each other during the denning period.

The following incident is an example of this relationship. On 7 March 1974, we discovered two sows with four cubs in one den. The second family arrived from a den 3 kilometers distant where a telemeter had been set up. The arriving female conducted herself so secretively that we became aware of her presence only when we had almost dug out the roof of the den. The den consisted of a huge chamber about 2.5 meters in diameter and 4 to 5 meters long. The sows differed insignificantly from each other in size, weighing 182 kilograms each; the four cubs were also of similar size and weight.

Within 1.5 hours after immobilization, the newly-arrived female began to lift herself by the front legs (she was given a lesser dosage). We had pulled the 'rightful owner' from the den for morphometrical measurements and weighing. Soon she began to regain consciousness and tried to return to the den. At this point, the female inside the den grabbed her by the nose. Peace was restored only after we released the cubs which had been taken from the den for marking. We again visited the den in a week to find a single family—the one that had arrived most recently.

The lactating female is a very solicitous mother, often sacrificing herself to defend her young. But how she relates to orphaned young under natural conditions is largely unknown. The following incident sheds light on this question to a certain degree.

We marked a female and two cubs from one den on 23 March 1974. The female was immobilized for about 5 hours and had several convulsions similar to those observed in a few other females. During the following week we repeatedly saw this bear looking from the den. On 31 March, 8 days later, the female abandoned the den and cubs and headed toward the sea. On 4 April, we took the abandoned cubs from the den to a sow with two cubs of her own. After she was immobilized for this procedure and had recovered partial motor activity, we introduced the cubs one at a time. The sow accepted them as if they were her own. She smelled and licked her foster children and soon the four cubs were suckling the sow as she laid on her side. We did not observe any differences in the female's relationship with her own offspring and the foster young. She fed them either lying on the ground or standing, and hardly paid any attention to us. On the next day we brought her some deer, fox and walrus, *Odobenus rosmarus*, meat. She ate a little fox meat and the bear family left for the ice 2 days later.

To summarize the above:

Behavior of pregnant and lactating polar bears can markedly change under influence of a 'disturbance factor.' Disturbance is especially critical in the fall period when pregnant females begin to den, for, as a rule, females will abandon their dens prematurely if disturbed.

Protective measures for polar bear denning areas must first provide for the

creation of a 'zone of peace' where visits of people are limited as much as possible.

The interrelations of pregnant or lactating females and relationships of the latter with foster cubs evolved primarily from the laws of survival and success of the species as a whole. In this connection, it is fully understandable that lactating females will accept orphan cubs who for some reason have lost their mother. However, whether a single female can rear four cubs at one time is not yet known.

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Paper 4

The Social Behaviour of Brown Bears on an Alaskan Salmon Stream

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INTRODUCTION

Adult brown bears *Ursus arctos* are typically solitary. Subject to few, if any, of the evolutionary pressures (e.g. interspecific predation, food procurement) that favour formation of social groups (Eisenberg 1966; Kummer 1971; Estes 1974), brown bears retain a simple social system that is probably little advanced over that of primitive carnivores (Eisenberg 1966). Social affiliations between brown bears are restricted to family groups of a female and offspring and sibling litter mates that remain together for 1 to 3 years after separation from the female (Stonorov & Stokes 1972). Brief male-female consort relationships occur during the breeding season (Murie 1944; Hornocker 1962; Stonorov 1972).

Like other solitary carnivores, however, brown bears form loose aggregations to feed on carrion (Craighead & Craighead 1967; Cole 1972; Glenn 1973), in garbage dumps (Hornocker 1962; Craighead & Craighead 1967), and on salmon streams (Stonorov & Stokes 1972). Though feeding aggregations are transient and clearly distinct from social groups formed by truly gregarious species, many of the associated behavioural contingencies are similar.

A gathering of brown bears on a small portion of a salmon stream provided the chance to study the social behaviour of this little-known, elusive carnivore. The objectives of the study were to learn the behavioural characteristics of various brown bear sex and age classes, to quantitatively describe the dynamics of their social behaviour over a 40-day summer fishing season, and to determine social and environmental factors correlated with the frequency of different types of behaviour. We further hoped to make inferences about the overall social system of brown bears and to determine the way in which brown bear behaviour parallels or differs from the behaviour of gregarious carnivores. Some of our preliminary results are presented here.

STUDY AREA AND METHODS

Stonorov & Stokes (1972) have previously described McNeil River State Game Sanctuary. The sanctuary is situated near the base of the Alaska Peninsula immediately north of Katmai National Monument. A series of rock slabs jut from the water about 0.8 km from the McNeil's mouth to form McNeil Falls. The width of the river is about 30 m at this point, and the rapids forming McNeil Falls extend for about 130 m. The falls impede the upstream movements of migrating salmon, mostly *Oncorhynchus keta*, and the bears gather during July and August to feed on the vulnerable fish. During the peak of the salmon migration, thirty or more bears may be present at one time; as many as 85 different bears have visited McNeil Falls in a single summer (Rausch 1958).

Data presented here were collected during the summers of 1972 and 1973.

Bears were observed daily from an observation post 8 m from the edge of the river near the upper terminus of McNeil Falls. Observation schedules were apportioned according to bear diurnal activity patterns. Most bears seemed unaffected by our presence, although large adult males avoided the falls when more than three or four people were present; a limited number of other bears would not cross to the near side of the river.

We defined an interaction (=encounter) as occurring when one or more bears responded overtly to the presence of another. We recorded all interactions observed. Records on each bear were kept on its time of arrival and departure from the falls, amount of time spent actively fishing, location of fishing effort, the time each salmon was caught, its behaviour during encounters, and the identity and responses of bears it encountered.

Individual bears were identified by ear tags, distinctive scars, claw color and other distinguishing features. Thirty-seven percent of the bears observed had been captured by biologists of the Alaska Department of Fish and Game and were of known age. Bears of unknown age were classified by their size relative to known-age animals. The sex of untagged bears was determined by the direct observation of sexual organs, urination patterns or by the presence of young.

POPULATION COMPOSITION

The composition of the bear population at McNeil Falls for 1971 to 1973 is listed in Table 1. Fully-mature adult males were characterized by massive bone structure and conspicuously large size (350 kg or more) in relation to adult females. Bears classed as adult females were of known age or had, with four exceptions, been observed with cubs or yearlings; the size and behaviour of the other four indicated they also were fully mature. Subadults were 2½ or 3½ years of age, ranging in estimated size from 75 to 120 kg. Males and females are technically sexually mature by 4½ years of age (Erickson *et al.* 1968; Glenn 1973), but females continue to grow for 2 to 3 additional years and males may not attain full size before age 10 or 11 (Glenn 1973). For this reason, males from 4½ to 8½ years of age and females 4½ to 5½ were classified separately as adolescents.

SEASONAL AND DIURNAL BROWN BEAR ACTIVITY PATTERNS

The seasonal abundance of brown bears at McNeil Falls for the 1972 and 1973 seasons is shown in Fig. 1. Salmon were observed at McNeil Falls during the first week of July each year, but the arrival of bears was variable, ranging from 8 July 1973 to 25 July 1971 (Stonorov 1972, unpublished report).

The reasons for the disparate arrival times for bears are not clear. It may be related to water levels at the falls, with high water making the salmon less accessible and delaying the onset of fishing. Bears also graze sedge extensively during June and into July, but only until the plants mature and presumably become less palatable. Phenologically 'late' years, as 1971, delay sedge growth. In 'early' years the sedge matures at a faster rate (early July in 1972 and 1973), perhaps forcing bears to turn elsewhere earlier for alternative sources of food.

Bears that were present in previous years were generally the first to arrive at McNeil Falls each fishing season. Sixty-one percent arrived during the

TABLE 1. POPULATION COMPOSITION OF McNEIL RIVER BROWN BEARS, 1971 to 1973

	Males	Females	Females with young	Number of cubs	Number of yearlings	Subadults ^e (2.5 to 3.5 yrs)	Unclassified (125 kg)	Total
1971	7 ^a	9 ^c	12	14	6	13	6	
	7 ^b	2 ^d						
	$\overline{14}$	$\overline{11}$	$\overline{12}$	$\overline{14}$	$\overline{6}$	$\overline{13}$	$\overline{6}$	76
1972	11 ^a	11 ^c	9	9	9	3	4	
	7 ^b	3 ^d						
	$\overline{18}$	$\overline{14}$	$\overline{9}$	$\overline{9}$	$\overline{9}$	$\overline{3}$	$\overline{4}$	66
1973	7 ^a	11 ^c	5	6	3	10	5	
	14 ^b	5 ^d						
	$\overline{21}$	$\overline{16}$	$\overline{5}$	$\overline{6}$	$\overline{3}$	$\overline{10}$	$\overline{5}$	66
Mean percent	17.7 26	13.7 20	8.7 12	9.7 14	6.0 9	8.7 12	5.0 7	69.5 100

^a Adult males, 350 kg or more.

^b Adolescent males 4.5 to 8.5 years old, less than 275 kg.

^c Adult females, 175 kg or more.

^d Adolescent females 4.5 to 5.5 years old, less than 140 kg.

^e Both sexes, 2.5 to 3.5 years old, 75 to 125 kg.

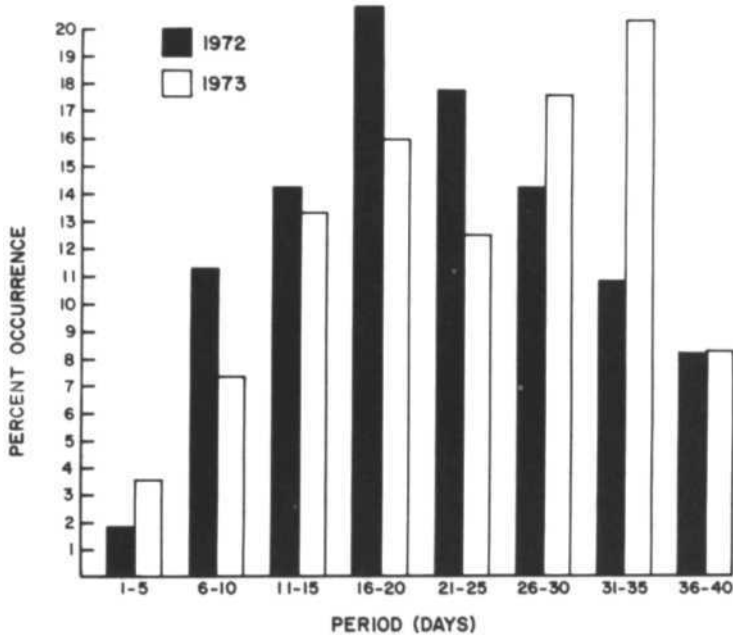


Fig. 1 Seasonal abundance of brown bears at McNeil Falls, 1972 and 1973. Days are numbered consecutively from the first day (Day 1) bears were fishing each year.

first 15 days following the onset of fishing. Twenty-seven percent were present for 30 days or more, 47 percent were present for at least half the season, and about 9 percent stayed for 5 days or less. In general, adult females and adolescent males and females persisted the longest.

Bears were active at McNeil Falls at all hours of the day. The level of activity was lowest during the early and mid-morning hours, steadily increased to a peak at 1800 to 1900 hours, and then declined again. Activity dropped sharply between 2200 and 2300 hours. No more than three bears were present at once from midnight to 0600 hours during our two overnight observations in 1972 (Days 11 and 28). These data were corroborated by time-lapse photographic records obtained during the first 13 days bears were fishing in 1972.

FREQUENCY AND FORM OF BROWN BEAR ENCOUNTERS

Brown bear interactions consisted of behavioural components variably and unpredictably sequenced. For purposes of analysis, we have simplified interactions into seven generalized forms: (1) head-low threat (low intensity); (2) head-high threat (high intensity); (3) charges; (4) contact or fighting; (5) approach-avoid; and (6 & 7) two forms of non-agonistic interactions (see below). Charges, threat, and fighting often occurred in combinations during a single encounter. Fighting, for example, was usually associated with threat, but since threat and charges did not always culminate in fighting, we arbitrarily treated each separately here. The characterizations omit for the most part the subtle aspects of brown bear social behaviour concerning head and body positions, facial expressions, and sequencing of behavioural components.

Head-low Threat involved variable body orientations toward the opponent. The head was held below the horizontal line of the body, ears were laid back flat against the head, and low monotone roaring accompanied a slowly opening and closing mouth. Distances separating interacting bears were generally less than 4 m.

Head-high Threat occurred at close range. One or, most often, both bears extended their heads diagonally upward toward the opponent. Their mouths were continuously open giving the impression they were about to interlock jaws. Body orientations were frontal. Body weight was shifted to the hind-quarters, presumably to free the forelimbs for striking or fending off the opponent. Loud roaring was continuous, changing in volume and amplitude with sudden head movements. Bears were typically less than 0.2 m apart.

Charges occurred in a variety of forms. 'Direct' charges were hard, fast rushes at an opponent. The charging animal's gaze was fixed on the receiving bear, and its head was held slightly below normal. The ears were erect initially and oriented toward the other bear but were laid back flat as it closed or when the receiving bear began to flee. Low growls at the start of the rush gradually increased in volume to a loud roar. 'Short' charges appeared identical to the initial phases of direct charges except that the rushes were terminated after three or four strides. A third form, seeming to involve a combination of threat and avoidance (ambivalence), was characterized by a series of exaggerated rocking and hopping movements toward an opponent.

Contact consisted of striking an opponent with one or both forepaws occasionally coupled with biting. Striking was oriented to the opponent's chest and shoulder region, and most biting was directed to the head and neck.

The most common agonistic interaction consisted of a simple avoidance of an in situ bear or the withdrawal of one animal at another's approach. Head and ear positions were variable. Direct gazes at an opponent were generally associated with lowered heads and erect ears, but as avoiding bears moved away or circled, heads were raised slightly, and the ears were alternately erect, compressed, or at various intermediate positions.

Non-agonistic encounters were classified into two broad categories. Brief interactions in which two or more bears pawed, mouthed, rubbed, or otherwise lightly contacted each other in the head and neck regions and which involved no elements of agonistic behaviour, were termed 'amicable' after Ewer (1968). Prolonged interactions involving mock fighting and, more rarely, sexual mounting, were labelled 'play'. Exaggerated head movements, restrained striking and biting, and a lack of loud growling distinguished play from serious fighting.

The balance of bear encounters consisted of little more than glances toward each other accompanied usually by slight shifts in body orientation, alternately erect or lowered ears, and an occasional lowering of the head. In some instances bears moved past each other at close range (2 m or less) without either making an observable response.

The occurrence of the above forms of social behaviour varied with the sex, age and size, and reproductive status of bears (Table 2). In general, combat and both forms of threat were most likely to occur in interactions between bears of roughly similar social status and within the same sex and age class. Overt fighting was usually momentary, and we never directly observed the infliction of serious wounds.

The low frequency of aggressive behaviour recorded for interactions that involved large adult males is misleading. They were widely avoided by bears

TABLE 2. PERCENT OCCURRENCE OF SIX BEHAVIOUR CATEGORIES IN BROWN BEAR SOCIAL INTERACTIONS AT MCNEIL FALLS, 1972-73.

	Head-low threat		Head-high threat		Charge		Contact		Play		'Amicable'	
	1972	1973	1972	1973	1972	1973	1972	1973	1972	1973	1972	1973
Adult males	11.5	4.2	5.6	1.1	6.3	2.9	2.2	1.1	0.0	0.0	0.0	0.0
Adult females	22.8	16.4	8.0	3.8	7.0	4.0	3.0	1.3	0.0	0.0	0.0	1.5
Females with young	36.1	27.0	13.6	6.5	17.2	13.5	6.2	5.7	0.0	0.0	0.0	0.0
Adolescent males	20.8	12.6	6.7	3.4	2.7	1.3	4.6	0.9	0.0	7.3	0.0	9.0
Adolescent females	29.2	13.8	7.8	2.5	4.0	2.5	4.6	1.0	0.0	5.4	0.0	6.9
Subadults	0.0	0.9	4.2	0.5	0.0	0.0	0.0	0.5	0.0	0.9	0.0	2.8
Mean	23.4	13.2	8.0	3.3	6.6	2.8	4.0	1.3	0.0	4.0	0.0	5.4

of other sex and age classes, and four or more present at once caused most other bears to leave the area of the falls. Males were most active at McNeil Falls in late evening, and the abrupt drop in activity of bears between 2200 and 2300 hours seemed to correspond with their arrival. Though overt aggression between males was rarely observed, most of them bore scars and battered ears. Males were much more irascible toward other bears, and especially other males, when they were consorting with or trailing females in oestrus. The alpha male, Number 22, attacked and dislodged a subordinate male copulating with a female in 1973. Fresh and partially-eaten remains of a 2½-year-old subadult were found on 22 July 1973, and autopsy showed it had been killed by another bear (James Faro pers. comm.); this occurred at a time when at least four large males were variously consorting with five oestrous females.

Females with young (cubs or yearlings or, in one instance, a 2½-year-old) were highly intolerant of other bears and were the only individuals to consistently challenge adult males. Forty-two percent (10 of 24) of the head-high threat and 50 percent (5 of 10) of the overt fighting interactions that large males engaged in were with females accompanied by young. Unless the males pressed them, the females usually retreated, but often they seemed ambivalent, repeatedly rushing toward the males and then running away. Females with young were most tolerant of single adult females, but they were particularly irascible toward adolescent males and, to a lesser extent, adolescent females. On three occasions their yearlings independently rushed an adolescent male and two subadults.

As Hornocker (1962) reported, single adult females were more tolerant of other bears than were females with young. Yet tolerance varied greatly between different individuals; females that were highly aggressive when single were especially so when they had cubs or yearlings. Older females, in excess of 10 to 12 years of age, seemed more aggressive than younger females, but the differences could have been due merely to individual variation. Excluding those in oestrus, single females were generally wary of adult males, but their responses to them varied. Two aggressive females regularly fished side-by-side with a few of the large males. In 1972, a 22-year-old female regularly approached and occasionally supplanted two of the lower-ranking males.

Adolescent males, ranging in age from 4½ to 8½ years, were the least aggressive of all sex and age groups. Two males (4½ and 5½ years old, respectively) were never seen initiating an aggressive encounter. These animals would slide in beside other bears without attempting to displace them by threats. An indication of the overall tolerance of adolescent males for one another occurred in 1973, when two males walking side by side approached an oestrous female and 'tested' her simultaneously. Seventeen percent (70 of 411) of the intra-class interactions between adolescent males and 11 percent (17 of 154) of the interactions between adolescent males and adolescent females were non-agonistic in 1973. Adolescent males initiated fewer charges than any sex and age group other than subadults. The two oldest adolescent males, each 8½ in 1973, were the most aggressive of the class.

The behaviour of adolescent females was not appreciably different from single adult females. They were less tolerant of other bears than were adolescent males. As with the other sex and age classes, there were wide differences in aggressiveness between individuals. Two 4½-year-olds seemed extremely timid and were little different behaviourally from subadults. Two sibling females, still associating closely and travelling as a unit at 5½ years of age, were moderately aggressive, particularly toward adolescent males. Adolescent females were distinguished, however, by participating in a relatively high

frequency of non-agonistic encounters in 1973, though not to the same extent as adolescent males. None of the adolescent females to our knowledge had ever been in breeding condition.

Subadults were in few encounters involving overt aggression mainly because they usually gave other bears wide berth. Subadults were occasionally chased by some adolescents and other subadults, but it is doubtful that these posed a serious threat. Their wariness for other bears in general, however, coupled with the mortality record described above, indicate that other bears on occasion do pose a serious threat to subadults. In general, subadults patrolled the periphery of McNeil Falls scavenging for salmon scraps; occasionally during morning and midday they occupied fishing sites when few other bears were present. One 3½-year-old female was unusually large, and behaviourally she resembled an adolescent female rather than a typical subadult.

Overall levels of aggression were considerably lower in 1973 compared to 1972 (Table 2). There were fewer females with young during the 1973 season, with only two staying at the falls for a significant period. More important, however, was the much larger salmon run of 1973. Index figures and the average number of salmon bears caught per hour (1.04 in 1972, 2.06 in 1973) indicated roughly twice as many fish entered McNeil River in 1973. Consequently, there was less competition for lucrative fishing sites since almost any spot in the falls would yield salmon. Moreover, the bears were simply less aggressive, at times to the point of appearing lethargic. Whereas in 1972 it was extremely rare to see an animal not react agonistically to the close approach of another, it was commonplace in 1973. Altogether there was an approximate twofold decrease in the proportion of interactions that involved elements of aggression from one year to the next.

Also associated with the abundance of salmon in 1973 was a higher incidence of non-agonistic encounters, especially among and within the adolescent and subadult classes (Table 2 and Fig. 2). Fully-mature adult males and females



Fig. 2 Adolescent brown bear males (4.5 and 5.5 years old) playing, McNeil Falls, 1973.

that had produced cubs at least once were not observed playing; single adult females engaged in a limited number of 'amicable' encounters, usually with adolescent males.

BEHAVIOURAL CHANGES WITHIN EACH FISHING SEASON

The social behaviour of brown bears during the first days of each fishing season appeared no different qualitatively from encounters observed in other contexts (e.g. as bears grazed in tidal sedge meadows). Interactions usually were limited to long-range avoidance, and bears generally seemed extremely wary, even to the extent that two interacting animals might flee each other simultaneously. Indiscriminate avoidance and flight were most characteristic of subadults and adolescents. Adult females initially ran from adolescent males, however, and on one occasion a fully-mature adult male fled from a much smaller adolescent male. Overt fighting, never common, was seldom observed during this period since bears did not often approach one another to short range.

The tendency of young bears to flee indiscriminately often seemed to invite pursuit. Many so-called 'charges' developed only after one of the animals had begun running. Other chases were initiated when animals made brief, tentative rushes (characterized by a few exaggerated hops, elevated heads and erect ears, and a slightly gaping mouth) toward potential rivals; the receiving animals usually fled and chases ensued. If chases were prolonged, fleeing bears eventually turned to face the pursuers. Pursued animals tended to stop on a crest or promontory to confront the pursuers. The latter stopped 1 to 2 metres short, and most soon backed away. Striking and biting in these circumstances were initiated by bears that had been chased.

The rate of agonistic encounters did not vary from period to period. Bears moving to and from fishing locations invariably precipitated encounters with others already occupying sites. Many encounters were the result of direct competition for specific fishing locations. Thus, the number of agonistic interactions was strongly correlated with the number of bears present in successive 5-day periods ($R^2=0.92$ for 1972, 0.92 for 1973). Encounter rates during the first 5 days, however, were the lowest recorded for each year (0.44 per hour in 1972, 0.80 in 1973). The few bears present at the start of the fishing season avoided one another by dispersing widely over the falls. Encounter rates in subsequent periods varied from 1.49 to 2.37 per hour.

The frequency of different forms of brown bear interactions changed with successive 5-day periods, corroborating the results of Stonorov and Stokes (1972). Fleeing and chasing declined rapidly during the first 10 days. All bears, including some of the small subadults, began gradually reciprocating threats. Subordinate animals continued to defer to larger bears but did so to an increasing extent by walking away rather than running. Bears also progressively approached one another to closer range (Table 3), culminating with some individuals standing 2 m or less apart mid-way through the 40-day season. These animals were generally similar in size and, by definition (see below), roughly equal in social status. Bears in the youngest sex and age classes showed the most dramatic changes in behaviour. More subtle behavioural changes, mainly in the form of tolerance to the proximity of others, occurred in older sex and age classes. Females with young remained highly intolerant at all times, however, and most bears continued to give the large adult males wide berth.

TABLE 3. SEASONAL CHANGES IN MINIMUM DISTANCES (M) BETWEEN BEARS DURING SOCIAL INTERACTIONS AT McNEIL FALLS, 1972-73. DATA ARE EXPRESSED AS THE MEAN PLUS OR MINUS STANDARD ERROR. THE NUMBER OF OBSERVATIONS FOR EACH 5-DAY PERIOD ARE IN PARENTHESES.

Period (days)	1972	1973
1-5	13.8 ± 2.7 (14)	9.7 ± 0.6 (49)
6-10	8.0 ± 0.3 (267)	7.4 ± 0.3 (209)
11-15	5.8 ± 0.2 (264)	7.2 ± 0.2 (384)
16-20	5.3 ± 0.2 (296)	6.1 ± 0.2 (304)
21-25	5.8 ± 0.2 (424)	5.0 ± 0.2 (235)
26-30	5.1 ± 0.2 (388)	5.1 ± 0.2 (333)
31-35	5.0 ± 0.3 (207)	3.8 ± 0.1 (384)
36-40	6.0 ± 0.5 (64)	5.7 ± 0.3 (127)

While the frequency of head-low threat ('jawing', Stonorov and Stokes 1972) increased as the season progressed, the occurrence of head-high threat and fighting did not vary significantly from period to period (Figs. 3 & 4). The rise in mild threats was correlated directly with the tendency of bears to approach one another to shorter range; by so doing, the opportunities for head-low threats, and presumably for other forms of aggression as well, were enhanced.

That the more intense forms of aggression did not increase correspondingly suggested that (1) bears had habituated to the proximity of one another and (2) individuals learned to avoid approaching too closely bears likely to respond to them aggressively. 'Dominant' bears were much more likely to initiate encounters with subordinates than vice versa.

Tolerance among bears also varied within seasons in relation to fishing success much as it did between years. This relationship was most apparent during the last 15 days of the 1973 season. The number of salmon bears caught per hour decreased from an average of 2.1 during days 26 to 30 to 1.0 during days 31 to 35. Threat and striking and biting concomitantly increased during days 31 to 35 (Figs. 3 & 4), and the rate of non-agonistic interactions (amicable and play) between bears declined 74 percent. In the following period (days 36 to 40), salmon abundance again increased, and fishing success averaged 1.6 caught per hour. Threat and fighting declined sharply and non-agonistic encounters rose 70 percent.

SOCIAL DOMINANCE RELATIONSHIPS

Not all agonistic interactions between bears gave clear indications of relative social status. For consistency, a bear was considered dominant when (1) the bear it encountered moved off by backing up, walking away or running away,

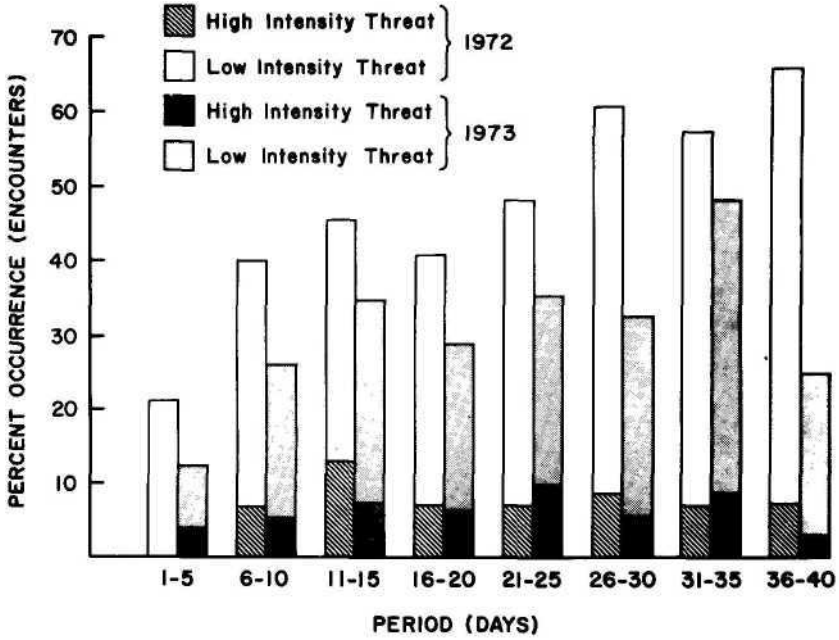


Fig.3 Changes in the occurrence of two forms of threat in brown bear interactions over the 40-day fishing season at McNeil Falls, 1972 and 1973.

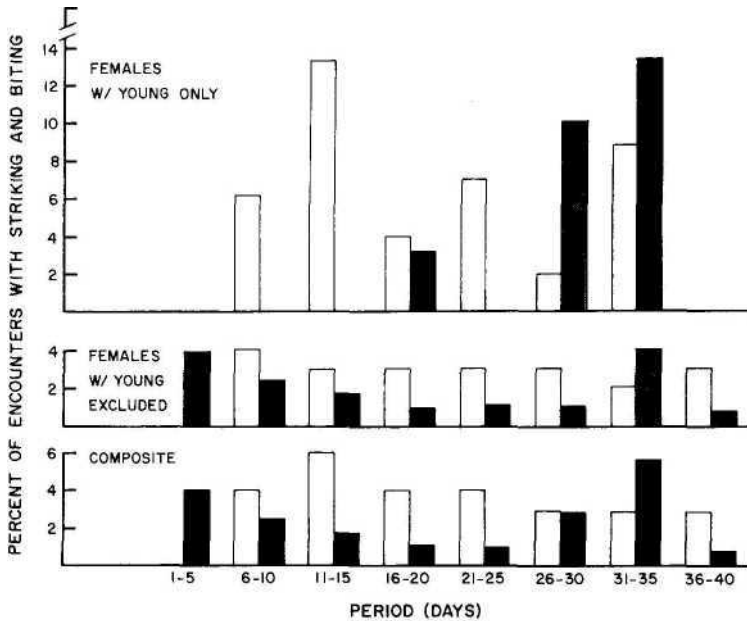


Fig. 4 Changes in the occurrence of contact (striking and biting) in brown bear interactions over the 40-day fishing season at McNeil Falls, 1972 and 1973.

TABLE 4. PERCENT OF DECISIVE ENCOUNTERS WON BY INDIVIDUAL BEARS OF DIFFERENT SEX AND AGE CLASSES AT McNEIL FALLS, 1972-73. DATA PRESENTED HERE ARE FOR INTRA-CLASS INTERACTIONS.

Sex and age class	Percent of encounters won	
	1972	1973
Adult males	91	97
Adult females	63	55
Females with young	82	84
Adolescent males	15	42
Adolescent females	30	27
Subadults	0	2

or (2) its presence caused an approaching animal to alter its direction of movement. Encounters that involved comparatively high levels of aggression, such as charges or striking and biting, were occasionally indecisive by these criteria but probably served to establish status relations between the two in subsequent encounters. A bear charged by another might defend itself in that instance but would later defer. The outcomes of decisive encounters between bears of different classes are shown in Table 4. Large adult males were unequivocally the most dominant animals. Most of their losses (19 of 35) were to females with young. Females with offspring deferred consistently only to large males, losing 34 of 53 encounters to them during the two years. Females with young were occasionally supplanted by single females (31 of 152). Adolescents of both sexes were generally subordinate to single females, but some of the older adolescent males and the two sibling females, acting in concert, occasionally were dominant over low-ranking single females.

Status relationships within classes were equally variable. Only the top-ranked male (Number 22) never 'lost' an encounter. A 22-year-old single female won 46 of 53 encounters with other single females in 1972. Reversals and triangular relationships within classes were common, and dominance between individuals in many cases could be assigned only in a relative fashion. Patterns of relative dominance have generally been attributed to an inability by interacting animals to recognize one another as individuals (Etkin 1964). Though likely true in cases where two bears interacted infrequently, there is no doubt that bears can learn to recognize individuals.

Hornocker (1962) reported that male grizzlies 'vied' for dominance, suggesting dominance in itself was a goal among adult males. The alpha male (Number 22) at McNeil River, however, seemed firmly entrenched and was never challenged by another adult male. Moreover, he was consistently intolerant of the general presence of other males. In one case, Number 22 left a fishing location to approach another large male that had just arrived at McNeil Falls and was standing about 40 m distant. Number 22 approached slowly, his lowered head held vertical to the ground, with his eyes and erect ears oriented in the other's direction. After closing to about 10 m, he charged and attacked, striking and biting the other male on the head and neck until it withdrew

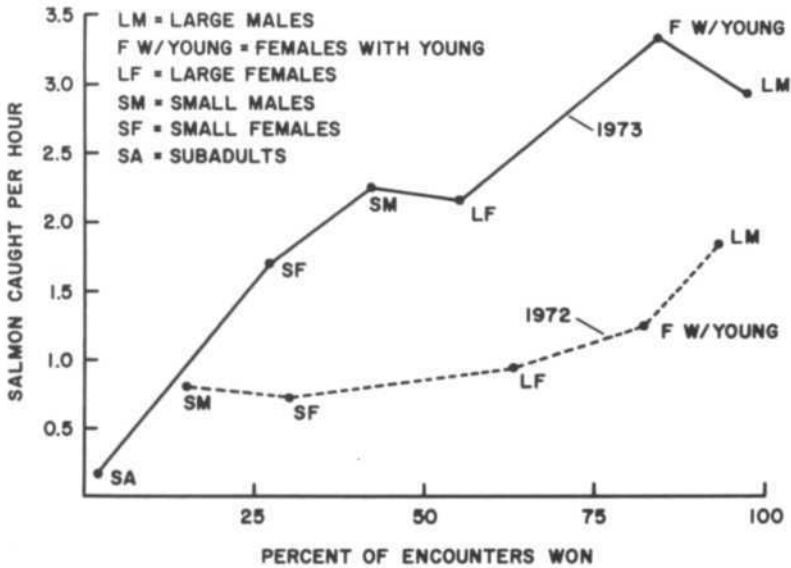


Fig. 5 Relationship between brown bear social dominance (percentage of decisive encounters won) and the rate of fishing success, McNeil Falls, 1972 and 1973.

running. On a separate occasion, the alpha male walked up to another adult male from behind and first knocked it to the ground and then into the river.

Lower-ranking males were considerably less aggressive toward one another, except that all were highly aggressive when associating with females in oestrus. Status relationships among five adult males, excluding Number 22, were triangular in 1972 but were linear in 1973. Male social rank in the latter year was, however, based on a total of only 19 encounters.

Status relationships among bears of different classes varied between years. Adolescent males 'won' 15 percent of their decisive encounters in 1972 but 42 percent in 1973. Whereas other animals (mainly single adult females and adolescent females) that engaged young males in 1972, generally reacted to them aggressively, the same animals a year later were more likely to defer. Consequently, adolescent males won a greater proportion of their encounters the latter year because other bears were simply less aggressive.

The main consequence of social status was that it determined when and where an individual bear could fish, and, in large measure, its rate of fishing success (Fig. 5). The impact of high social status on fishing success rates was most evident in 1972, when only a limited number of locations consistently yielded salmon. Socially-subordinate animals were largely excluded from these sites. Status was less a factor in 1973, because the abundant salmon could be taken at fishing sites that had, at best, been marginally productive the previous year.

For reasons presently unknown, all bears, regardless of age or status, captured salmon at a faster rate during mid-afternoon and evening. Whereas adolescent bears and subadults were present in roughly equal numbers throughout the day (0600 to 2200), bears in the adult sex and age classes, the most dominant animals, were most active during the most lucrative afternoon and evening period (1500-2200). Consequently, while subordinate bears occasionally

occupied profitable fishing locations during morning and mid-day, they were generally excluded from these sites by mid-afternoon.

THE SOCIAL BEHAVIOUR OF A SOLITARY CARNIVORE

Recent comparative studies on the social behaviour of some species of Canidae indicate solitary forms have a smaller, less complex array of close-contact visual social signals than the gregarious species (Kleiman 1967; Fox 1970). These results suggested social species have evolved communication repertoires to minimize aggression among group members by the substitution of ritualized behaviour for actual fighting. Brown bears seem to fit this pattern in that being solitary they do not have a wide assortment of visual signals in comparison to other carnivores. 'Submission' postures, for example, are lacking; the nearest analogous behaviour in brown bears is similar (perhaps homologous) to the 'defensive threat' Leyhausen (1956) described for felids. Bears further lack the dramatic forms of 'weapons threat' (Geist 1971) typical of many other carnivore species (e.g. retraction of the lips to expose the canines). The small tail of bears precludes its value as a signaling device (Stonorov & Stokes 1972).

Yet despite retaining conservative patterns of social behaviour, most bears accommodated easily to conspecific proximity at McNeil Falls. The greatest changes in behaviour occurred among adolescents and sub-adults. Adults of both sexes were neither as wary at the onset of the fishing season nor did they habituate to the same extent as younger animals. Whereas non-agonistic relationships actually developed and persisted between some adolescent males, the behaviour of adults changed only by degree in that they tolerated closer proximity, with neither a concomitant increase in high-intensity threats nor actual fighting. Low-intensity aggression (head-low threats) by all bears gradually increased as distances declined and reflected an increasing unwillingness on the part of interacting bears to give way. Bears became progressively less likely to initiate encounters with animals that were appreciably higher in social status; in 1973, adolescent males initiated only 23 percent (24 of 103) of their encounters with the highly aggressive and more dominant females with young. While there was no group integration and coordination typical of social carnivores, and while individual relationships were flexible, the sum of these factors resulted in formation of a social organization that was relatively stable. The presumed relationship between the social organization of a species and complexity and quantity of close-contact social signals has been questioned by Kleiman & Eisenberg (1973). They suggest that information value of signals may be as important or more so than complexity or number, and that the context of an interaction may carry considerable information as well.

Intensity of brown bear aggression was strongly related to salmon abundance. Formation of a stable brown bear social system did not result in a more efficient exploitation of salmon, but rather salmon abundance determined in large part the degree of social stability. A decline in salmon numbers was reflected by an immediate increase in intolerance among the bears. There is evidence that lions (*Panthera leo*), a gregarious species, also show significant increases in aggression when food becomes scarce (Schaller 1972; Kleiman & Eisenberg 1973).

There is growing evidence that killing and cannibalism may be common among bears (Larsen *et al.* 1972). Bears responsible in eye-witness accounts

are generally described as large or are known to be adult males. The wariness most bears retain for large males at McNeil River indicates they are perceived as a serious threat. Bears in the young age classes and sows with young are most wary of males, but even oestrous females reflect this pattern, seeming more receptive to sexually-mature, but relatively small, adolescent males than to the big adults. Regulation of black bear populations is related to mortality in young age classes that is induced by adult males (Kemp, this volume, Paper 17). Circumstantial evidence suggests the same may be true for brown bears.

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Paper 5

Threat behavior of the Black Bear (*Ursus americanus*)

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INTRODUCTION

The elements of threat occur in black bears in a stereotyped manner in reliable sequences. In this paper I will present representative descriptions in different contexts. Then the most common elements of offensive and defensive threat will be described in more detail.

European ethologists have contributed to the understanding of bear behavior in general and European brown bears (*Ursus arctos*) in particular. Direct observational studies of captive and wild North American black bears which equal the methodological sophistication and depth of the European ethologists are only beginning to appear in the United States and Canada. Pruitt, Bacon & Burghardt, and Ludlow (Papers 8, 1 and 2, and 6 in this volume), Henry & Herrero (1974), Burghardt & Burghardt (1972), and Burghardt (1975), have made detailed observations of behavior of wild and captive black bears and performed some well-controlled experiments. In the case of the first three authors, agonistic behavior, including threat, has been studied. Some recent detailed observations of Alaskan brown bears competing for salmon on the McNeil River (Stonorov, Stonorov & Stokes 1972b, and Egbert & Stokes, this volume Paper 4) will aid in putting black bear agonistic behavior in comparative perspective.

Ewer (1968, p. 154) has characterized threat as follows:

'A threat may be defined as a signal denoting that, contingent upon some act or failure to act on the part of the recipient of the signal, hostile action will be taken. One may distinguish an offensive from a defensive threat: the former carries a message whose equivalent is "If you do not retreat, I will attack you"; the latter means "I am not about to launch an attack, but if you take the offensive, I will retaliate." The function of the threat is to deter the opponent; to drive him away in the first case, to prevent him from making an attack in the second.'

Ewer's definition also can be stated in terms of probabilities of the withdrawal of the opponent and the non-occurrence of attack following threat.

SUBJECTS AND METHODS

Over a two-year period many black bears in a variety of contexts were observed. These include two pairs of captive adults (a male-female pair and a female-female pair, all of whom were yearling cubs at the beginning of the study); three captive cubs; and many free-roaming bears in the Great Smoky Mountains National Park (hereafter referred to as GSMNP). Videotapes, films and taped recordings, in addition to systematic and adventitious written accounts, were used to record behavior. The descriptions in this paper were

drawn primarily from single-frame analysis of super-8 mm ciné films and field notes.

The male-female pair was enclosed in a 15 x 87 m grassy space. The female-female pair was kept in an enclosure 18.3 x 18.3 m² erected in a wooded setting in the GSMNP. Most of the trees were preserved intact (see also Burghardt 1975, and Bacon & Burghardt, Paper 1 above). Observations of free-roaming bears in the GSMNP were conducted primarily on the grassy bald and in the woods of a saddle-back ridge called Spence Field.

THREATENING BEHAVIOR BY ADULTS AND CUBS

Throughout this paper reference will be made to the following vocalizations:

- (1) **Huffing**—a single rapid, highly audible, exhalation of a breath of air through the open lips, produced both by cubs and adults.
- (2) **In-out huffing**—a rapid, highly audible, inhalation and exhalation produced in a manner similar to simple huffing and repeated in rapid succession. It is nearly always produced by a cub threatening defensively.
- (3) **Bellowing**—a hoarse, pulsing sound, resembling the sound of the starter of a balky automobile that won't start.
- (4) **Grunting**—a short 'un' or 'kuh' sound produced deep in the throat with the mouth closed.
- (5) **Jaw-popping**—rapid, hollow-sounding, snapping of the jaws and popping of the lips.

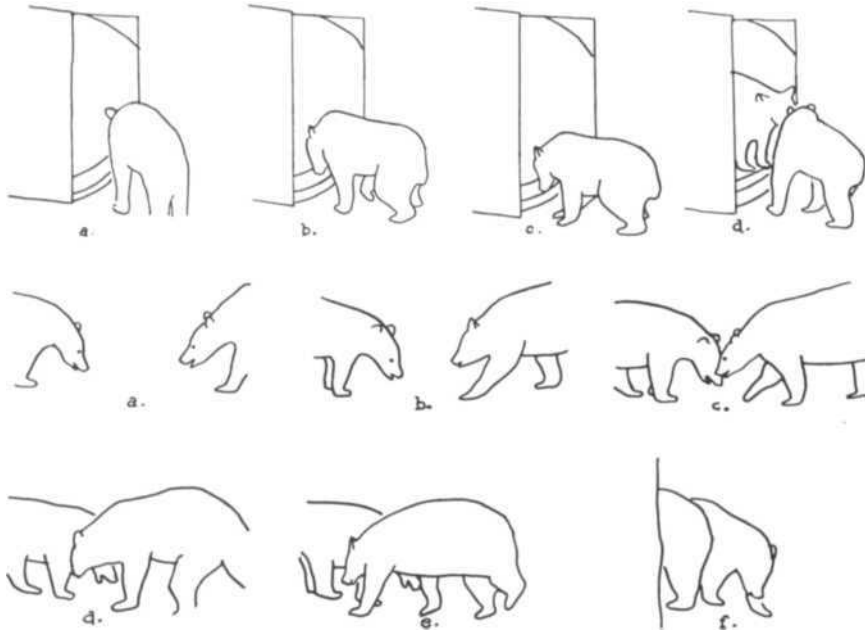
Threat by a free-roaming wild bear directed towards a conspecific.

A sow with her cub at a distance of 30 m was eating from a discarded can. A second, slightly smaller bear of unknown sex approached. The sow looked up, walked to the edge of the woods, stood up grunting towards her cubs, then returned to sniffing the ground. The second bear approached slowly through the woods to within six meters of the sow, slapped the vegetation sharply with its front paw and huffed. The sow rose quickly and huffed back. The second bear turned and ran off bellowing. The sow walked, then ran, after it.

Threat by captive bears directed toward conspecifics.

Example 1 (Fig. 1). A newly introduced wild adult male was standing inside a cement culvert cage which opened out on a large enclosure. Another adult, 2-year-old male was standing in front of the culvert. His muzzle was pointed down at a 45 degree angle, but his gaze was directed to the other bear (Frame a). He crouched slightly, shifted his weight, raised his right front paw (Frame b), then brought it down hard on the ground in the front of the cage, huffing loudly as he slapped (Frame c). Finally he raised his head and turned it to the side (Frame d). During all this his ears were laid partially back. The male inside the culvert bellowed loudly and the jaw-popped.

Example 2 (Fig. 2). Female A (3 years) with head and neck lowered and mouth open, ears slightly back, approached and passed female B (also 3 years) who stood in place, head and neck lowered more than A's, mouth opened widely bellowing (Frames a, b, and c). A turned her head towards B as she passed but B stood without turning (Frames d, e, and f).



Figs. 1 and 2 Threat by captive black bears directed towards a conspecific.

Threat by a free-roaming wild bear directed towards a human (offensive threat).

A sow with cubs nearby was eating berries in an open field as we approached and disturbed her. She lifted her muzzle high, sniffed the air, and looked in the direction of her cubs who were standing almost hidden in high grass. She turned her head, then body towards us, charged, stopped suddenly, slapped and huffed. She turned away and walked back to her cubs sniffing the air and grunting to them.

There were variations in this threat. Sometimes bears simply pant loudly as they charge without slapping and huffing, sometimes slapping the limbs with an even louder effect than slapping the ground.

Threat by a captive bear directed towards a human.

A female bear (Kate) had been raised from age 2 months to adulthood in our care. We were able to enter the enclosure although she threatened most humans. (Kate's littermate, Kit, was also present in the cage at the time these observations were made).

Example 1 (Fig.3). Kate occasionally threatened humans who were inside the cage. In a typical instance, she eyed her target steadily, but without her head directly towards him as she circled slowly behind. Then she charged (Frame a and b), slapped and huffed at him (Frame c). Finally, she turned her head away and walked off (Frame d). More common was a lower intensity threat which consisted of running or walking quickly while panting heavily, stopping, then panting or jaw-popping.

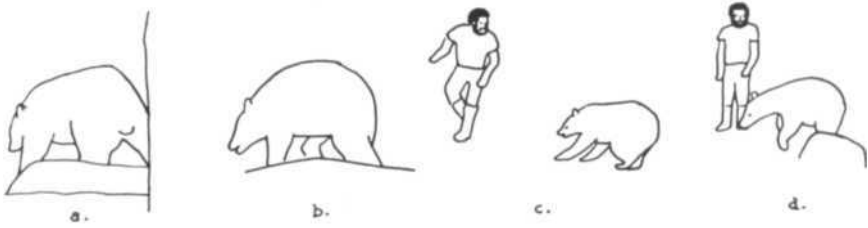


Fig. 3 Threat by a captive black bear directed towards a human also inside the enclosure.



Fig. 4 Threat by a captive black bear directed towards a human outside the enclosure.

Example 2 (Fig. 4). The above female was much more likely to threaten humans who were standing outside her cage than inside. In a typical instance she would sit with her head down, sniffing the fence of the ground close to the observer. Then, with her head still pointed down, she looked directly at the observer for one to several seconds (Frame a) before standing to her full height (Frame b), raising her paws as she stood, and slapping them hard against the fence, huffing as she slapped (Frame c). Sometimes in a threat of high intensity the huff/slap was followed by jaw-popping. Then she sat or stood down on all four feet, turning away as she did so, and resumed sniffing or walked away (Frame d and e).

Stiff-legged walking

Stiff-legged walking behavior was observed in wild and captive black bears. It has also been reported in the Alaskan brown bear (Stonorov 1972a). One instance by the captive 4-year-old, Kate, will be described, since my urinating on the fence of her enclosure evoked the behavior; this was done prior to the following events. Kate approached, sniffed and licked the urine, then walked away in normal fashion for a few steps until reaching a point near the center of the enclosure, whereupon she walked with her front legs locked stiffly and extended out in front of her farther than normal. The paws of her extended front legs slipped forward with each step. Her rear legs seemed stiffer than normal as well, though perhaps not locked. Urine dribbled down her hind legs as she walked. Her body shook noticeably each time she took a step. She stopped and looked around before resuming a normal walk. Often she performed this behavior at a considerable distance from someone or something that might be disturbing. Also she was as likely to be facing away from as towards the source of possibly disturbing stimuli. Because of this seemingly random orientation, the behavior might not properly be called a threat display. However, it may well serve to mark the environment visually and chemically, thus serving indirectly as a threat.

Threatening behavior by cubs.

Threat in both captive and free-roaming cubs seems identical whether directed towards humans or other bears. While in the GSMNP I approached a yearling cub standing on the ground. The cub walked, then ran to the nearest tree and hopped swiftly up the tree huffing in and out as it climbed. It reached a perch, looked at the person standing below, and slapped the side of the tree, huffing simultaneously. Then it jaw-popped, and after a short pause, huffed in and out and jaw-popped again. Finally, after several repetitions of in-out huffing and jaw-popping, it looked away and moaned.

DISCUSSION AND CONCLUSIONS

Simple threats, both offensive and defensive, towards humans and other bears were remarkably similar. Threats by captive bears (including hand-reared animals) were identical to those of wild bears at least in terms of the elements present, if not in rate. Females and males threatened in the same way, although my sample of male threat behavior was too small to be certain of this.

An offensive threat by an adult might occur in the following sequence:

- (1) Sniffing the air or objects with unfamiliar odors.
- (2) Looking directly at the individual to be threatened (heavy panting may occur before or during looking directly),
- (3) Charging at the individual or veering slightly into bushes or trees (sometimes panting while charging) and stopping suddenly.
- (4) At the moment of stopping, slapping one or both feet down on the ground or to the side against any object such as a tree or bush which would produce a sudden surprising sound. Concurrent with the slap, air is expelled from the mouth with a startling rush (i.e. huffing). (The charging bear may stand on its hind feet as it stops and slaps; or the bear may not charge at all but simply slap or stand up in place and slap).
- (5) Opening and closing the mouth rapidly to produce a series of loud pops (i.e. jaw-popping).
- (6) Turning the head away and averting the eyes, often accompanied by licking the lips and panting.
- (7) Standing, walking, or running away.

Depending on the intensity of the threat, the types of elements that occur, the repetition of elements within the sequence and, to a limited extent, the order of the elements vary. A high intensity threat generally contains more elements and repetitions of elements than one of low intensity. None of the elements always occurs. However, given the occurrence of one element, the likelihood of the occurrence of the one that follows it may be very high. For example, charging and stopping suddenly is very likely to be followed by slapping or huffing. Detailed film analysis will be needed to characterize these behavioral sequences more clearly.

What I call defensive threat usually occurs after, or in response to, offensive threat. That is not to say that it is a response elicited only by the offensive threat of another bear, since, I have been able to elicit defensive threat by running towards bears while shouting and brandishing a stick. A defensive threat might include lowering the head and neck, sidelong glances, sitting,

bellowing, and jaw-popping. Because the elements and sequence of defensive threat seem more variable than those of offensive threat they are not represented in sequential tabular form. This variability derives in part from the necessity of constantly readjusting one's behavior to the other.

Elements 5, 6, and 7 of offensive threat are similar to those just described for defensive threat. The threat behavior of many species consists of elements that would be conflicting in another context (e. g. flight and fight behaviors occurring simultaneously or consecutively). Perhaps elements 5, 6, and 7 occurring at the end of offensive threat actually represent a shift from offensive to defensive threat.

The primary difference between threat behavior of the cubs and adults was that cubs usually threatened from the safety of trees and that in-out huffing usually preceded or followed huffing/slapping and jaw-popping. The moan probably doesn't occur in the context of agonistic behavior but only after threats have failed.

Yearling cubs are known to bellow and jaw-pop in a manner similar to adults threatening defensively. I would classify both types of threat by cubs as defensive since they occur in response to threat by others.

Stiff-legged walking in black bears may or may not be threat behavior; it has been designated as such by Stonorov (1972a) in brown bears. In any case it may serve as a way of marking ground visually or chemically since sliding marks are produced by the front paws on the ground and urine trickles down the rear legs when this behavior is occurring.

Bears often sniffed odors on surfaces within the cage and airborne from the outside before threatening. Often they sniffed places where our hands or feet had been within the cage. When they sniffed human urine they were especially likely to threaten. Wild free-roaming bears frequently sniff the air before threatening.

Results of this study support the contention of many ethologists that the behavior of captive animals can tell us much about that species' behavior in a natural context as well. The threat behavior of the captive bears I observed was remarkably similar to the behavior of bears in the wild. It is likely that the environment, especially the social environment, exerts great pressure on the species to evolve highly specific signals. These signals, which are pre-disposed genetically, maintain their integrity even under the unusual circumstances of captivity.

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Paper 6

Observations on the Breeding of Captive Black Bears, *Ursus americanus*

by JEANNE C. LUDLOW

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INTRODUCTION

Although breeding of black bears is rarely seen in the wild, black bears have bred successfully in captivity (Lucas 1970-1971; Duplax-Hall 1972-1973). Surprisingly, there have been no descriptions of these matings. This paper reports on the breeding of a pair of captive black bears observed in 1973.

METHODS

The bears were kept in the Goldrush Junction Amusement Park, Pigeon Forge, Tennessee, just outside the Great Smoky Mountain National Park. They were acquired from the Gallop Animal Farm, Vermont, as unrelated cubs, in 1970, and had been kept together since. The enclosure for the bears was approximately 25 m x 80 m. A shelter in the south end of the enclosure had two separate sheds on each side with a roof attaching the two. The male and female were individually housed during the night. The bears had no access to these sheds during the day, but could lie between them under the center roof for shade or shelter. There were no trees in the enclosure, but the west and north sides were bordered with forest. A stream about one meter wide traversed the north end of the enclosure.

The bears were fed Purina Calf chow, given individually into each side of their shelter. Water was available from the stream, but only during the day when the bears were free to leave the shelter.

A super-8 mm ciné camera (Nizo S-80) and a 35 mm still camera (Minolta SRT-100) were used to film the bears' activity. In analyzing the data, the three movie films were viewed in blocks of 10 frames, to determine frequency of behaviors.

RESULTS

The following is a composite description of the mating behaviors observed July 2 and 4. Once the female was receptive, the male and female showed little courtship behavior prior to copulation. The male approached the female, sniffing the ground near her, and then sniffing or licking her head, trunk and external genitalia. The male mounted her from behind at an angle with one paw placed mid-way up her back. The male then grasped her stomach with both forepaws and lifted himself up on two legs. While mounting he often bit her neck (Fig. 1), behind the ears, and to one side. The neck bite was intermittently renewed throughout copulation. Occasionally, the male would bite

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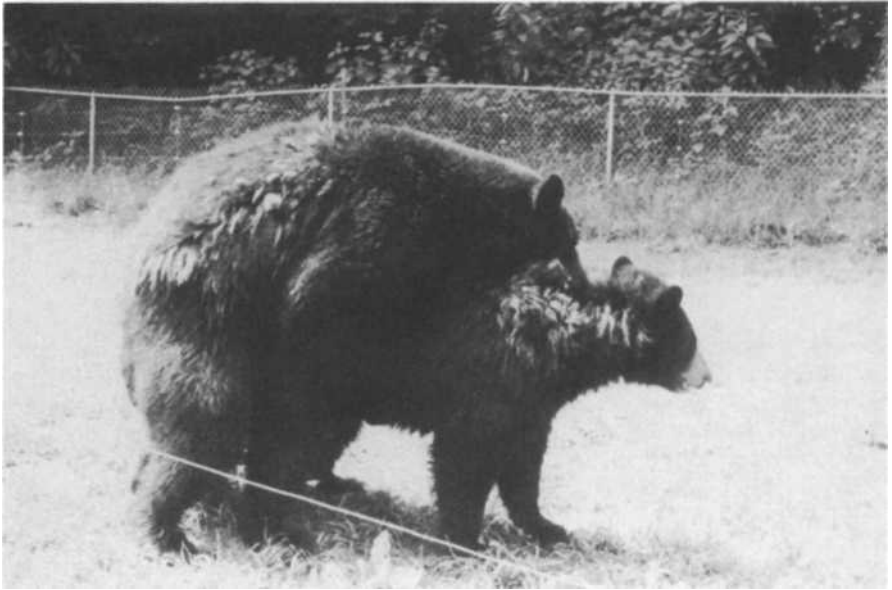


Fig. 1. Neckbite.



Fig. 2. Male's head held above female's back.

Table 1. Analysis of films of mating behaviors on 2 July 1973, 10:15 A.M.

Mounted	Male					Female				
	Bite Female	One Paw-Down	Head Down	Paw on Female's Back	Quiver	Walk	Stand	Bite Male	Head Low-	
361*	66	6	43	20	--	124	237	1	43	
<u>FILM 1</u>										
359*	25	16	20	54	25	147	212	1	56	
<u>FILM 2</u>										

*Activity at every tenth frame is recorded as totals for each film, thus total frames in film 1 = 3610; total frames in film 2 = 3590.

Table 2. Analysis of film of mating behaviors on 4 July 1973, 10:30 A.M.

Total No. of 10th frames viewed	Male					Female									
	Mount	Follow	Bite	Lay	Mo. W	Mo. St	W	St	Lie	Sit	Bite	SC	Tail Lift	Quiver	Str
37	16	1	18	2	14	3	9	5	3	1	6	8	2	--	--
33	--	--	--	33	--	--	12	4	3	15	--	13	--	--	--
22	--	--	--	22	--	--	--	--	22	--	--	--	--	22	--
40	--	--	--	40	--	--	--	--	40	--	--	--	--	11	5
27	--	--	--	27	--	--	10	4	12	--	--	1	2	--	--
120	--	--	--	120	--	--	6	74	--	42	--	29	--	4	51

Activity at every tenth frame is recorded as totals for the film. There were six noncontinuous sequences. Total frames in film = 3120.

Key to abbreviations used: W Walk
 St Stand
 SC Sniff Close (nose close to object)
 Str Stretch (back or front legs out, stiff)
 Mo Mounted

the female's face. During the earlier stages of copulation, behavior patterns most often seen in the male were biting the female and holding his head down by her side. The female stood still while mounted (Table 1). During the later parts of copulation, more frequent behaviors were the following: the male rested one paw on the ground or by the female's side, and he placed one or both paws up on the female's back; the female walked and sniffed or scratched the ground while mounted (Table 2).

When the male was not biting the female's neck, his head was either resting on her back, pressed against her side, hung down near her side or held above her back (Fig. 2). The female did not remain stationary for the entire copulation, but walked several meters every few minutes. The female both initiated and returned bites towards the male, biting his ears, head or forepaws. While mounted, the female might walk, look around, sniff the ground, eat grass, drink water, or stand still with her head up.

After mounting, the male assumed an arched position with both forepaws pressed in against the female's pelvic area. His hind legs were usually bent somewhat, although on occasion he would stretch them back and out or go up 'on his toes.' Once mounted and positioned on the center of the female's back, he began pelvic thrusts, occasionally varied by circular movements. These continued whether the female was stationary or moving. After several minutes of copulation, the male might remove one forepaw and either hang it down by the female's side, rest it on the ground, or place it on her back. While standing, the female's legs were in a braced position, her back slightly arched. Both bears panted heavily during mating and at times stood with mouths open. Once, the male stood on his left hind foot while resting on the female. Of the seven mounts observed, three were timed. They lasted 3'10", 30" and 29'0". It was impossible to determine accurately when intromission and ejaculation occurred. However, during one copulatory sequence, the male was mounted on the female and quivered every 25-30 seconds. He 'hung' on to the female until the quivering began, then grasped her in the pelvic area and arched his back. The mean interval between quiverings was 30 seconds. This particular behavior was observed only once, and no further mating occurred on this day. Meyer-Holzapfel (1957) reports that in brown bears it is during quivering that ejaculation occurs.

Copulation was usually terminated by the female walking and the male 'standing down.' The male then sat or lay flat on his side. Several times he walked to the stream and lay in the water for up to ten minutes. The female was more active than the male after mating and appeared restless: lying down, then walking around the enclosure, sniffing the ground or the male. It was after copulation that the female exhibited quiverings or muscle spasms of her hindquarters. She did this while walking around the enclosure, standing, or lying down. When this occurred while walking, she would stand, with apparent muscle spasms twitching her body from the pelvic area back. If the quivering occurred while she was lying down, she would rise and walk a meter or two. At times her back legs were extended stiffly out and back. During one post-copulatory sequence, her hind legs gave way five times. The quiverings appeared to be due to exhaustion, but may be related to the success of breeding by aiding the sperms' course up the vagina.

DISCUSSION

In general the mating behavior of bears is similar in some ways to the canids (the mount and the pelvic thrusts) and in other ways to the felids (the neck bite)

(Ewer 1973). The duration of successful mounts and intromissions was about 20 to 30 minutes. Copulation occurs while both animals are standing, and there does not appear to be a copulatory tie (as in canids, where the male and female stand for over 10 minutes in a locked position). However, several reports state that the bear has a penis bone which maintains the joining of the pair for a relatively long time (Meyer-Holzapfel 1957). The mating of black bears appears to be very similar to that of the brown bears (as described by Meyer-Holzapfel 1957): mating foreplay involves licking the female's face and sex organs; actual mating lasts more than 15 minutes; copulation occurs on several successive days; and, when the female is no longer receptive, she moves away from the male.

The breeding of the two black bears filmed was successful, and two cubs were born in early February, 1974. The gestation period was about 30 weeks.

ADDITIONAL NOTE

Several participants in the Binghamton Conference mentioned that they had observed breeding of bears in the wild: Lyn Rogers, Univ. of Minn.: *americanus*; Frederick C. Dean, Univ. of Alaska: *U. arctos horribilis*, Mike Luque, Utah State Univ.: *U. arctos*. Rogers observed mating from a plane and from the ground; Luque noted brown bears quiver two to three times.

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Paper 7

Fishing Behaviour of Alaska Brown Bear

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INTRODUCTION

Each summer 60 to 80 brown bears (*Ursus arctos*) congregate at McNeil River Falls, located 320 km southwest of Anchorage on the Alaska Peninsula, to fish for migrating chum salmon *Oncorhynchus keta*. The falls impede upstream movement making salmon vulnerable to bears. As many as 25 bears may fish simultaneously, many only a few metres apart. Many bears stay at the falls over 30 days each summer and return yearly. Because we can observe so many bears throughout a fishing season and during subsequent seasons, McNeil Falls provides an excellent opportunity to study prey-catching behaviour and its development in a natural situation.

The purpose of our study was to describe brown bear fishing behaviour, its development, and its relation to environmental and social factors. This paper describes fishing behaviour and its relation to salmon abundance. Elsewhere in this volume (Paper 4) Egbert and Stokes report on other factors influencing fishing success, notably time of day and status of the bears.

METHODS

During 1972 and 1973, we spent 25 consecutive days each summer watching the bears fishing. Observations were for five hours daily between 1400 and 2200 hours (Alaska Standard Time) from a cave 10 m from the river.

We observed 16 bears regularly in 1972 and 14 of the same 16 in 1973. They ranged in age from 3.5 to 22 years. Individuals were recognized by ear tags, scars, facial and body characteristics, and behaviour.

To measure salmon abundance we counted the number of times a fish broke the surface of a large, deep pool near the cave in a two-minute period each half hour. The average of the half-hour counts for each day provided an index of relative salmon abundance. This index compared closely with the rate of catching fish by bears and the number of fish observed in the pool.

We used a super-8mm ciné camera and a 35 mm still camera to record behaviour for later analysis.

RESULTS

Fishing for salmon at McNeil River is a cultural tradition among bears. Many of the same bears return year after year, and females bring their young to maintain the tradition. Some bears appeared only for brief visits but most fishing was by bears that returned regularly each summer. Bears had a wide choice of specific fishing locations. A suitable location had to be where salmon could be caught profitably. The omnivorous bears could always return to eating plants should fishing not be sufficiently profitable.

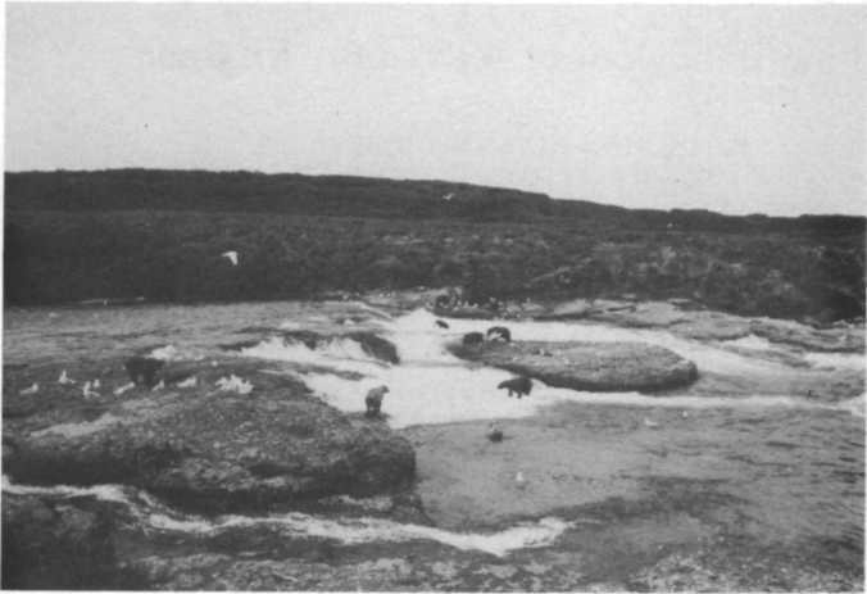


Fig. 1 Bears fishing at McNeil Falls.

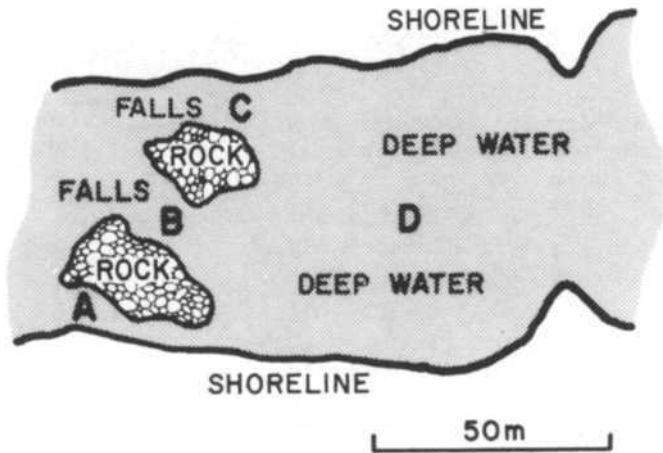


Fig. 2 Map of McNeil Falls showing points of salmon movement.

Choice of Fishing Location

The topography of the falls greatly affected salmon availability and, in turn, preference for fishing area. The falls consist of large rock slabs flanked by bare rock shorelines, creating rapids and pools of varying depth (Fig. 1). In one deep pool (D in Fig. 2), salmon congregated before ascending the falls. At high water level, they could ascend at points A, B, and C. At low water most salmon moved upriver through the deep rapids at C. Bears preferred to fish

at point C because the shore provided good fishing locations at all water levels. Fish were especially vulnerable wherever they momentarily halted in their upstream movement: at the head of eddies along shore; in shallow pools half-way up the falls; and wherever their upward struggle was halted by the force of the current. They were virtually secure as they milled about by the hundreds in the deep pools below the falls.

A bear's size influenced its selection of fishing location. Some fished regularly by standing waist-deep in rushing water that would have swept humans and smaller bears off their feet. Bears usually left a fishing location to eat the fish, the more subordinate ones going up the banks into the adjacent alders where they were free from disturbance.

Social status also influenced the fishing area selected. Large adult males, who topped the social hierarchy, used the preferred locations near point C, as did a few large adult females, but usually only when large males were absent. Lower status bears used the remaining areas of the falls.

We recorded 50 fishing locations, of which 14 were used frequently. Individual bears often used from one to three locations. Although social status divided fishing areas, individuals preferred certain locations within an area. For example, one large subadult male generally had free access to several locations within a small area of the falls without being threatened by other bears. But he continually used only one of those locations.

The combination of social status and salmon availability effectively controlled where bears fished. The higher a bear's status the more easily could it explore different fishing areas. Once it had found a productive location, it could remain there until displaced by a higher ranking bear. This system was beneficial at McNeil Falls because it allowed division of the food resource and younger bears to gain proficiency at fishing.

Technique Use

Fishing involves three steps: orientation, approach, and capture, each with several forms (Table 1). Orientation components are self-explanatory. One of the several forms of approach, the lope, was a slow run; plunging was a quick movement into the water from an orientation position. In 'head under water' a bear appeared to be searching for fish, often moving its head back and forth. Since loping and 'head under water', when they occurred, preceded plunging, these components were subdivided making possible four-part techniques. For actual capture, a bear could use forepaws alone in which its forepaws pinned a fish to the bottom, then lowered the head to grasp the fish with the mouth (Fig. 3). In 'forepaws and mouth' capture bears used both paws and mouth simultaneously to capture fish. Bears used only their mouth in the

TABLE 1. BASIC COMPONENTS OF FISHING TECHNIQUE

Orientation	Approach	Capture
Sitting	Loping	Forepaws
Standing	Head under water	Forepaws and mouth
Walking	Plunging	Mouth
		1 forepaw
		1 forepaw and mouth

'mouth' capture. The last two capture components listed in Table 1 are similar to the first two except only one forepaw is used.

Any combination of the components in these three parts to fishing we call a technique. For example, the combination of standing-plunging-forepaws and mouth is one technique (Fig. 4, a and b).

Of 90 possible techniques, bears used 37 in 1972 and 43 in 1973. Individuals used from 9 to 28 techniques with old bears using fewer than young bears. We thought bears would use fewer techniques over the weeks as they learned the most efficient techniques. This was not so. Three techniques were used in about half of all attempts both years (Table 2). Bears changed technique very frequently, after a mean of 1.4 attempts both summers.

To some extent the technique used depended upon salmon abundance. Many infrequently used techniques were more efficient (fish caught per attempt) and were used more when salmon were abundant. For example, the 'walking-plunging-forepaws and mouth' technique increased in use from 3 percent in 1972, a poor salmon year, to 7 percent in 1973, a good salmon year. There was a corresponding increase in efficiency from .12 to .40 fish caught per attempt. This was a significant increase considering that the most preferred technique was used in only 20 percent of all attempts.

The varied topography of the falls and changes in salmon abundance and water level coupled with a bear's frequent change in location seemed mainly responsible for the steady use of many techniques and the high frequency of change in technique.



Fig. 3 A bear exhibiting the forepaws only component of capture. Note that the head is up during the plunge.

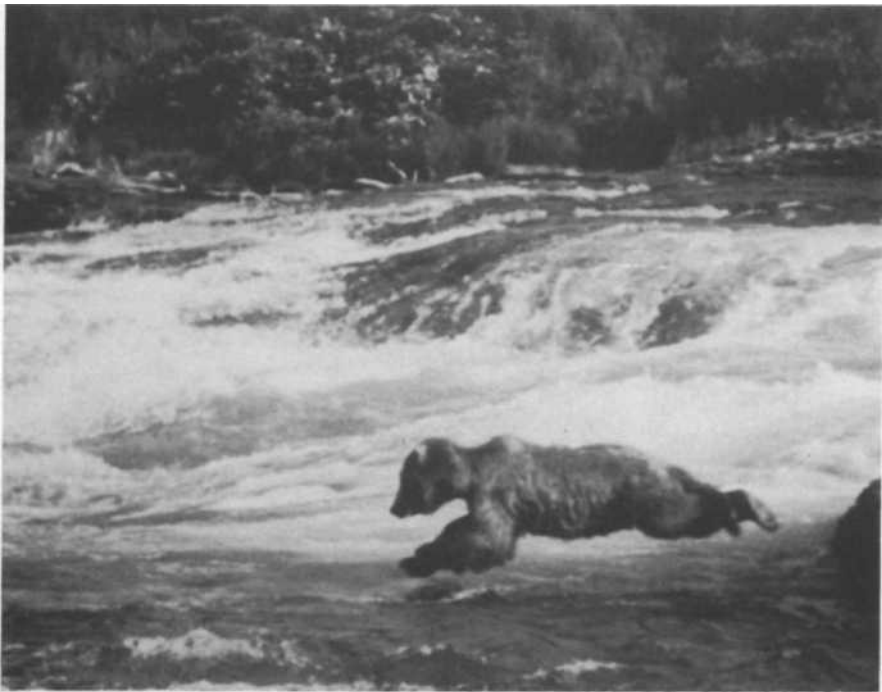


Fig. 4 a and b. A bear exhibiting the standing-plunging-forepaws and mouth fishing technique.

TABLE 2. EFFICIENCY AND RELATIVE USE OF THREE MOST FREQUENT FISHING TECHNIQUES

	<u>Use*</u>		<u>Efficiency**</u>	
	1972	1973	1972	1973
Standing-plunging-forepaws/mouth	23	20	35	55
Standing-plunging-forepaws	19	§	9	11
Standing-mouth	10	18	25	44
Number of attempts	781	1178		
Salmon index			21	99

* Percent of all attempts.

** Fish caught per 100 attempts.

Fishing Efficiency and Fishing Success

The three most frequent techniques were also the most efficient (Table 2). Bears in general used those techniques which worked best for them. An exception was the 'standing-plunging-forepaws' technique in 1972. This high use of an inefficient technique was due to low salmon abundance. Bears were making many half-hearted attempts, using this technique on fish which were not close enough to be caught. Bears did not waste much energy at these low-return attempts, for there was little time or motion involved.

Technique efficiency improved with salmon abundance from 23 percent in 1972 to 42 percent in 1973 (Table 2). In fact, 56 percent of the variation in efficiency was related to salmon abundance (analysis by linear regression, $r^2 = .56$). Much of the remaining variation was due to high fishing efficiency the first week of each fishing season. Despite the scarcity of salmon at that time, the few bears present had little competition, so could select the most favourable fishing locations.

Fishing success (fish caught per hour of effort) also increased with salmon abundance. In 1972 bears caught 1.5 fish per hour, while in 1973 they caught 2.8. Seventy-three percent of the variation in success was attributed to salmon abundance (analysis by linear regression, $r^2 = .73$).

Changes in Fishing Locations

When fishing was poor a bear changed its location or its method of fishing. In 1972, bears changed to a new location after a mean of 3.4 attempts at one place, with a range of 1 to 33 attempts. In 1973, they changed location after a mean of 2.5 attempts, ranging from 1 to 25 attempts. This more frequent change in 1973 was related to high salmon abundance. With more salmon there were more attempts and at more locations. For example, if a bear were unsuccessful at one location its chase of the fish might carry it into another adjacent location. With so many salmon in 1973, the bear might immediately spot another fish and attempt to catch it from the new location. In 1972, bears were unlikely to see a second fish, so tended to return to their original location, where presumably they had worked out a suitable fishing strategy. Good

fishing was a second factor contributing to more frequent change of location. When a bear left a preferred location to eat its fish away from the falls, this let bears of lower status temporarily use these locations in addition to their regular more inefficient ones.

The second way to improve fishing success, changing the method of fishing, was also common. In both years bears changed technique after an average of 1.4 attempts. Undoubtedly many of these changes were matching of a technique to the particular situation in which successive salmon were seen. But other changes probably stemmed from the low rate of reinforcement from a particular technique.

DISCUSSION

A characteristic of bears at McNeil Falls was the constancy of their return throughout a season and from one season to the next. We rarely saw a newcomer establish itself permanently in the two years of intensive study. Those bears that did appear sporadically stayed so briefly we generally didn't learn them well enough to identify in later years. The high intolerance between bears probably discourages newcomers. Cubs brought to the river during the two or three years they stayed with their mother could work their way gradually into the hierarchy and into competitive fishing situations. In general, after weaning at 2.5 years of age, cubs moved about below the falls looking for scraps of discarded fish. Gradually they worked farther and farther into the central fishing locations, stealing fish from satiated larger bears and even doing a little fishing. Few bears entered the fishing circle at McNeil Falls until fully mature at six or more years of age.

This behaviour is in contrast to that at smaller streams. On the small tributaries leading into Becharov Lake farther south on the Alaska Peninsula, Derek Stonorov (pers. comm.) regularly observed younger bears fishing. On such streams bears could spread out over much greater distances to avoid competition, the lower-status bears going farther upstream where fishing was less good.

We observed fishing for red salmon *Oncorhynchus nerka* along nearby Mikfik Creek. Fish were available over most of the stream albeit in less abundance. On Mikfik Creek bears rarely staked out a fishing location; instead they fished for a few minutes only, then moved along the stream. Such streams with low fish abundance are not likely to generate the strong homing tradition seen in McNeil River bears. This sort of fishing situation would seem much easier for bears unable to withstand the heavy competition at McNeil River Falls.

Observations in other areas on how bears fish differ in part from ours. George Frame (pers. comm.) observed black bears *Ursus americanus* fishing in south-eastern Alaska. Black bears fished by plunging into the creek, running through the water, and leaping upon a fish and capturing it with their mouth. Since he does not give any orientation components, we cannot be sure how many techniques his bears actually used based on our classification system. Using our orientation components there would be at least four techniques. This is much less than our 37. Clark (1959) also describes only one technique for brown bears fishing at Karluk Lake, Alaska. These bears used the forepaws to pin the salmon to the bottom before grasping it with the mouth. Frame never observed this technique. Similarly, W. B. Sisson (pers. comm.) observed that brown bears fishing at Kodiak National Wildlife Refuge use only two techniques. In one creek where fish were emaciated, bears would capture

them with just the mouth. In other streams where fish were more lively, bears would herd fish toward shallow water and use their paws and body to capture fish. Sisson also noted that bears would slap the water to aid in herding fish, but he never saw a fish slapped out of the water. Bacon and Burghardt (this volume Paper 1) also noted that penned black bears would slap at prey. We never observed this behaviour at McNeil.

In all the above reports bears were fishing in shallow flat streams. This lack of varied topography, in contrast to McNeil Falls, could be the reason bears used far fewer and somewhat different techniques. Bears can chase fish in these shallow streams while at McNeil Falls they can seldom do this because of the deep water and the ease with which salmon can evade bears.

In all these studies bears have used the forepaws, although generally at one time or another in combination with the mouth. Eisenberg and Leyhausen (1972) consider capture with the forepaws more evolutionarily advanced than use of the mouth. This suggests that bears are not as advanced as the Felidae in which selection has favoured the use of forepaws to grasp prey. But cats rarely fish. If bears were to lose the ability to catch fish in the mouth, then they would not be able to capture salmon in the deep, fast-flowing water of McNeil Falls. Bears remain generalists, not only as omnivores, but as carnivores. The wide range of techniques they have available permits them to fish in a great variety of waters.

The rise in efficiency of capture from 23 percent to 42 percent between 1972 and 1973, was probably because bears made fewer wild attempts. In addition, the higher turnover of good fishing locations allowed more bears to use those places where salmon were most vulnerable. A third factor stemmed from the tendency of salmon to mill around for varying lengths of time in the deep water below the falls. At these times bears caught virtually no fish. When the fish did start upstream five or more bears might suddenly catch fish. When salmon were moving upstream in high numbers, more were forced close to shore or into other vulnerable locations, thus raising the efficiency of fishing.

ACKNOWLEDGEMENTS

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Paper 8

Play and Agonistic Behavior in Young Captive Black Bears

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With few exceptions (Leyhausen 1948; Meyer-Holzapfel 1957; Krott and Krott 1963; Stonorov and Stokes 1972) we have known little about social behavior in bears. Until recently, the often solitary black bear has been treated as a relatively non-social carnivore. Lorenz (1953), Krott (1961) and Ewer (1968) have maintained that the bear does not possess a consistent repertoire of social signals, and based their opinions on the solitary habits of bears in general. However, they neglected to consider the two major social episodes within a bear's lifetime: the breeding season (Rausch 1961; Jonkel 1967), and the sow's year and a half or longer association with her cubs (Jonkel 1967). Additionally, bears may meet at prime fishing spots or other concentrated food areas (Egbert and Stokes, this volume Paper 4). At these times not only are bears social, but communication should be frequent and necessary. This paper reviews two aspects of social behavior in the black bear, play and agonistic behavior, both of which may occur during breeding, rearing of the young and chance meetings. A more extensive discussion of these behaviors may be found elsewhere (Pruitt 1974; Pruitt and Burghardt, in press).

SUBJECTS AND PROCEDURES

Two seven month old captive female black bears, *Ursus americanus*, were observed in a semi-natural environment within the Great Smoky Mountains National Park. The bears were maintained together in an 18 x 18 meter enclosure over a three-year period. Burghardt and Burghardt (1972) have analyzed the cubs' behavior during the first eight months. The social behavior of these sibling cubs was observed intensively from August 1970 through November 1971. Instances of intraspecific social play, solitary play (with inanimate objects), naturally occurring aggression, and experimental manipulated aggression were singled out for particular emphasis during the research.

The bears' behavior was observed from the second floor of a storage shed located adjacent to the enclosure. Full view of the bears and the area was available from that site and allowed observations to be made without interacting with the animals. Data were collected in three ways: (1) written or taped descriptions of continuous, uninterrupted observations at one-half and one-minute intervals; (2) checklist notation during one-minute intervals; and (3) super-8 movie filming of play and agonistic encounters. The first two methods provided descriptive data for behavior patterns and a molar sequence of events, while the third method allowed a more detailed analysis of specific, fine body movements which occurred during the encounters.

During the study, 341 social play encounters were recorded. Additional interactions were filmed. 'Naturally occurring' aggression occurred only 55 times during the same observation period. In 'naturally occurring' aggression no experimental procedures were used to elicit the aggression. These episodes

occurred primarily during feeding sessions and in reaction to ear sucking attempts by the littermate.

Agonistic encounters were difficult to capture on film and analyze precisely in terms of latency to encounter, duration and defensive reactions. To observe and film aggressive behavior more reliably an artificial situation was created to elicit aggression. A hog feeder was altered so that only one bear could feed at a given time. After 20 hours of food deprivation, one bear was allowed to enter the feeding area. As soon as the first bear had begun to eat, the second was released into the area and timing begun. Records were kept of: the time which elapsed until onset of the attack (latency to attack), the length of any physical contact (duration of aggression), the methods by which the aggressor was challenged (confrontation) and the type of termination of the encounter (resolution). In 18 staged encounters, 15 agonistic sequences were recorded. In the remaining three, the second bear did not challenge the first, physically or vocally.

RESULTS

Social Initiation

The types of behavior shown during initiation of play or aggression were placed in five categories: biting; paw movements (swatting, pushing, pawing out); locomotion (run, walk, circle, jump); head movements (mouth open, jaw wrestle, sniff close, ear movements); and vocalization. As shown in Table 1, use of the several types of play initiation was fairly equally distributed, with biting only slightly preferred. The bears never vocalized during play, neither at the initiation nor in later phases. On the other hand, they often vocalized at the onset of aggression, using mostly long, low moans, jaw pops and gurgles. The concept of these vocalizations as threats or threat intentions has been further supported by recent studies (Jordan, this volume Paper 5). In another study, Henry and Herrero (1974) reported no vocalizing during bear play. In contrast, the closely related canids vocalize routinely in both play and agonistic encounters (Fentress 1967; Fox 1970, 1971; Bekoff 1973, 1974).

In aggression the bears did not use any locomotor movements to initiate an encounter. Instead visual threats in the form of head movements were important. The most common (and possibly most important) component of visual threat was the lip extension shown in conjunction with neck stretching, ear flattening and frontal orientation. Lip extensions and ear flattening were

TABLE 1. Types of behavior used by black bears in initiating social play and agonistic encounters.

	Play (N = 341)	Aggression (N = 55)
Biting	29.0%	38.2%
Paw Movements	23.6	5.4
Locomotion	22.4	0.0
Head Movements	20.8	27.3
Vocalizations	0.0	29.1
Unknown	4.2	0.0

rarely observed in initial phases of play; instead, the animal seemed gradually to work up to the higher intensity level characterized by those postures and subsequent play-biting. Bears used paw movements less often to initiate aggression than play. If seen at all during agonistic behavior, paw movements took the form of hard slaps to the face and rump of the partner, or to the ground. In play, paw movements were slower and directed to the limbs and shoulders of the partner.

Common to both play and agonistic behavior was redirection (Burghardt 1973). If a partner terminated play, the other animal frequently began solitary play (especially with trees) or initiated play with a human. Similarly, in the manipulated agonistic setting, the non-feeding animal was observed to threaten vocally and visually. Upon receiving no response it in turn attacked a nearby object. Over the course of the staged encounters the bears totally demolished through redirected activities an originally 2 meter high, 5 centimeter diameter tree located next to the feeder.

Duration of Play and Aggression

Play sessions recorded on film lasted an average of 14 seconds. In addition, play occurred in bouts at 30 second to 5.0 minute intervals. This short latency between play acts gave an impression of longer play periods. Naturally occurring aggression lasted 39 seconds. While agonistic encounters lasted longer than play, they occurred as single, non-repetitive episodes and presumably resolved a conflict situation. The latency to a second agonistic interaction was at least 10 to 24 hours.

In contrast to play, agonistic behavior had three clear major stages: preparation to attack, physical contact or threat, and resolution (Figures 1, 2, 3). In a typical aggressive encounter, the threatening animal approached, looked toward the opponent, might at times vocalize, partially flattened the ears, and extended the lip with neck out-stretched during the first stage of experimentally induced aggression. In stage two the aggressor made physical contact (usually biting or swatting) in response to which the opponent would charge or leave. In the final stage both bears looked toward each other, with heads lowered. This position was held for several seconds, after which one animal claimed the objects or area over which the conflict was begun. Mean duration of each of the stages of experimentally induced aggression was as follows: 4 minutes and 5 seconds for the preparation to attack; 29 seconds for the actual physical contact, and 7 seconds for resolution of the conflict. The average duration of contact and resolution lasted 36 seconds, about the same as the 39 second duration of naturally occurring aggression. Photographs of the various stages are published elsewhere (Burghardt, 1975).

CAUSAL FACTORS IN PLAY AND AGGRESSION

Specific factors causing social play were not determined. However, play periods reliably could be predicted after feeding periods or with the approach of persons involved in the study. This supports the theory that play is more likely to occur after the satisfaction of more basic physiological needs (Meyer-Holzapfel 1956; Bekoff 1972). In contrast with play, several precipitating factors were recognized for naturally occurring agonistic behavior. Potential conflict situations, involving food objects, ear sucking, human presence or attention and object possession, were likely to elicit agonistic behavior in one



Fig. 1 Display of visual threat during preparation to attack in experimentally induced aggression.

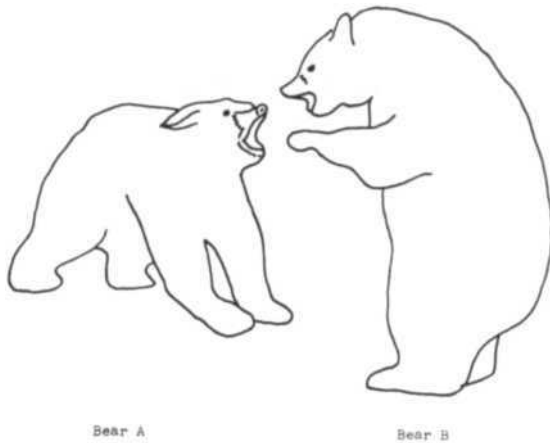


Fig. 2 Postures immediately following physical contact in experimentally induced aggression. Bear A is in a charge position and bear B is in a bipedal stand posture.

or both bears. Given a thorough knowledge of the bears' daily habits, it was possible to predict onset of aggression far more reliably than for play.

Film Analysis

To further explore the predictability and possible signal value of bodily expressions in social interactions, 8 mm movie films of play and aggression were analyzed frame by frame. From the analysis of 10 filmed play sessions, certain postural relationships emerged. For example, laterally oriented ears and mouth droop occurred simultaneously, with durations averaging less than one second. The most pervasive aspect of the analysis was the relatively short duration of discrete body movements. Durations of ear position within a one-minute film segment, for example, ranged from .06 seconds to 2.4 seconds.

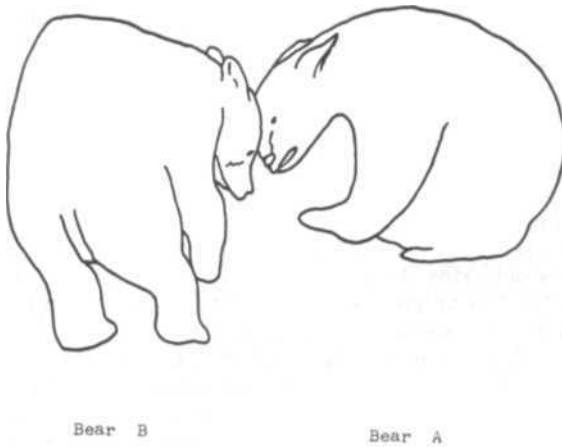


Fig. 3 Postures assumed by black bears during the resolution of conflict in experimentally induced aggression. Bear B is coming down from a bipedal stand and is turning away from bear A and toward the feeder.

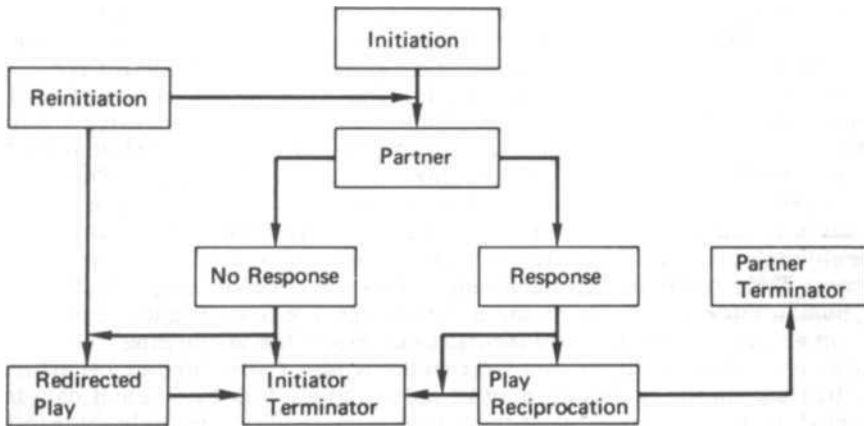


Fig.4 Model of intraspecific interaction in young captive black bears.

Given the rapid change and short duration of specific body positions, it is no wonder that mammalian play patterns have been considered so unpredictable. It is possible, however, to devise a model of social interaction in the black bear in which one can predict the *course* of a play session or agonistic encounter given certain decision points (Figure 4).

From the data obtained in these observations, particular postures can be used as guidelines for the model's decision points. For example, if the bear is displaying a lip extension during play, that bear is not likely to terminate the play, inasmuch as a lip extension did not occur simultaneously with walking or running away from the partner. A specific example of the use of the model can be drawn from the staged agonistic encounters. The initiator's lip extension and vocalization to the partner (Fig. 1, Bear 2) indicates that aggression,

or the threat of it, is about to occur, rather than play. If the partner responds with a charge or vocalizations we would predict reciprocation or termination by the initiator (see the right side of Fig. 4). If a bear visually threatens the partner and receives no response, termination, redirection or reinitiation by the initiator will occur (left side of Fig. 4).

Several relatively stereotyped behaviors are common to both play and aggression (e.g., ear flattening, lip extension) but occur at different points in each type of interaction. It has been suggested that the selection of body expressions is more limited in aggression, leading to a notion of aggression as a more highly stereotyped, predictable behavior than play. In fact, play has been theorized as a means of practice for the more 'serious' adult behaviors such as aggression (Meyer-Holzappel 1956). As such a practice behaviour one would expect the immature animal to draw upon a wider repertoire of skills and expressions, gradually eliminating those with lesser signal value (Ewer 1968). Further analysis of the data is currently in progress to determine precise signal values of the expressions observed in play and aggression. The hypothesis behind that analysis holds that a specific body position (e.g., muzzle wrinkle, lip extension, flattened ears) may not possess highly specific signal value in itself, but may contribute to a pattern or Gestalt, which conveys specific information to the partner during the social interaction. Additionally, the contextual aspect of a situation may aid in determining 'correct' responses to the body posturing.

With the advent of ethological studies such as this one, we are beginning to assemble a more complete picture of the black bear and its habits. Not only will we understand its reproductive and dietary habits, but we will have gathered further knowledge of its behavioral and perceptual capabilities. The anecdotal and historical views of the black bear as a non-expressive species quickly are refuted by behavioral data from this and other recent studies (Stonorov and Stokes 1972; Henry and Herrero 1974; Bacon 1974). The precision and extensive patterning of social interactions in young bear cubs provides very vivid evidence for the expressive aspect of their behavior. Unfortunately, the ursids too often are compared to their more social canid relatives and on that basis their behavior has been judged less expressive and predictable. Also, human interactions or contacts with bears are less frequent than with many other carnivores, thereby limiting our expertise at 'judging' the social signals given when we do meet a bear in the wilds. Given further behavioral investigations on the bears, we may be able to apply this ethological data to the conservation and management of the species, particularly in their interactions with humans in public access areas such as the national parks.

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PART II BEARS IN NATIONAL PARKS

Paper 9

Homing of Black Bears in the Great Smoky Mountains National Park

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INTRODUCTION

The interactions between nuisance black bears (*Ursus americanus*) and people create many problems in the Great Smoky Mountains National Park (GSMNP or Park) as well as in other areas of North America. These interactions necessitate management guidelines determined from biological data about the bears. Personnel of the National Park Service (NPS) have handled nuisance bears by moving them to various areas within the Park, transporting them to state wildlife management areas or in some instances destroying habitually nuisance animals. Generally, bears have been destroyed only when other management procedures failed and the animal was judged to present a potential danger to Park visitors.

Eliminating the causal factors that create nuisance bears is the most effective and economical method of reducing the number of bear-people interactions. Park personnel have attempted to do this by transporting roadside and campground garbage to landfills outside the Park. Feeding of bears is prohibited in the Park. 'Regular' garbage cans are being replaced by 'bearproof' ones. Back-packers must pack all trash and garbage out of the backcountry. Although these precautionary measures have alleviated some of the problem, they have not been completely effective and some unnatural sources of food are still available thus creating nuisance bears.

Once a bear has 'established' itself as a nuisance animal, removing it from the area of nuisance is the most humane method of handling it; this procedure presents problems. The limited size of the GSMNP (approximately 32 by 70 kilometers) introduces the question of whether the Park is large enough for this management practice. The limited road system within the Park hinders the transplant of bears into more remote areas (Fig. 1). Capturing nuisance animals and moving them into remote areas is time consuming and limited by the availability of manpower. Most of the areas surrounding the Park have a high human population density with no buffer zone between the Park and areas inhabited by people.

This research investigated one aspect of the problem of handling nuisance bears, that of homing. The ability of an animal to return to its homesite has been reported in birds (Bellrose 1958; Sauer and Sauer 1960), dogs (*Canis domesticus*) (Carthy 1956:183), gray squirrels (*Sciurus carolinensis*) (Hunger-

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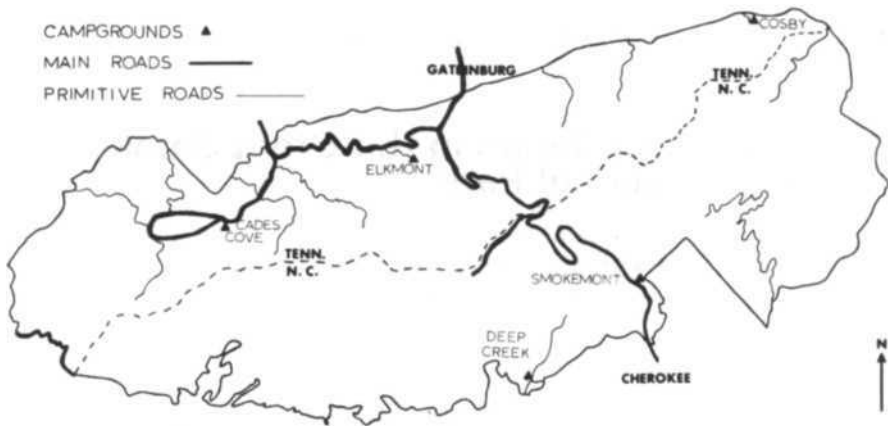


Fig. 1. A map of the Great Smoky Mountains National Park showing areas of black bear nuisance (campgrounds and main roads) and the limited number of primitive roads allowing access into more remote sections of the Park.

ford and Wilder 1941) and mice (*Peromyscus* spp.) (Griffo 1961; Bovet 1968; Furrer 1974).

Wasem (1968) reported that 8 of 13 (62 percent) habitual nuisance bears in Glacier National Park homed. In Michigan, Erickson (1964) transplanted 17 black bears an average of 63 kilometers and considered only two of these to have homed. One of these was an adult male that was killed within 9.7 kilometers of the capture point after being moved 151.6 kilometers. The other was an adult female captured 30.6 kilometers from the original capture point after being moved 103.2 kilometers. Of the transplanted bears, Erickson concluded that males moved greater distances than females and adults farther than juveniles. Harger (1967) found a definite tendency for transplanted black bears to move toward the original point of capture. Of the 18 bears furnishing movement records, Harger considered that 12 individuals had homed, with cubs exhibiting poorer homing ability than older bears. Sauer *et al.* (1969) transplanted 52 nuisance black bears 13.9 to 106.6 kilometers and found 43 percent were able to home. They concluded that homing fell off sharply when bears were transplanted more than 64 kilometers from their capture point. Other than these studies (many of which present limited sample sizes), there is little available literature that statistically quantifies the homing ability of black bears.

Since the study area was in the GSMNP where over 8,000,000 people visit annually, the researchers were required to trap and relocate bears as deemed necessary by NPS personnel. The NPS supervised the relocation of nuisance animals; this altered the experimental design and limited the interpretation of some of the results.

METHODS

Bears that habitually entered campgrounds or roadsides and were judged bold enough to cause damage or injury to Park visitors and their equipment were considered nuisance animals. These animals were captured with culvert traps and Aldrich snares or immobilized while free-roaming with Etorphine (M99)

or Sernylan injected with a syringe rifle. Bears were then transported to the release site in a culvert trap. Individuals were ear tagged with cattle Roto-tags (Nasco Co., Fort Atkinson, Nebraska) using various color combinations so individuals could be identified without recapturing. A bear was considered to have homed if it returned to within 8 kilometers of the original capture point. In every case but two, bears that homed in this study returned to within 2 kilometers of the original capture point. Individual bears were identified by members of the research team. At times, employees of the GSMNP and repeated reports of individually-marked bears by Park visitors were helpful in identification.

Age of most bears was determined by the cementum-annuli (Willey 1974). When a tooth was not extracted, age was estimated by comparative body size and dental wear. For this study bears 4.5 years old were considered 'adults' and bears less than 4.5 years old were considered 'juveniles.' No cubs and only one yearling were moved as a nuisance animal. Thus, with one exception, the juvenile group in this study is subadults 2.5 and 3.5 years old.

Inexperienced bears are defined as individuals trapped and transplanted for the first time. Experienced individuals are bears trapped two or more times and transplanted. The time of homing was calculated from the date of release

Table 1. Transplant of nuisance female bears (adults) in the GSMNP, 1967-1974.

Date	Bear Number	Displacement (km)	Comments
6/15/67	1	46.4	Never reobserved
7/16/67	2	16	Never reobserved
7/27/67	3	Not recorded	Given to North Carolina
8/11/67	4	Not recorded	Given to North Carolina
6/1/68	5	9.6	Homed in 15 days: recaptured 6/16/68
6/16/68	5	Not recorded	Given to North Carolina
7/2/68	6	7.2	Homed in 31 days: recaptured 8/2/68
8/2/68	6	7.2	Never reobserved
9/9/70	7	19	Homed the following spring; recaptured 5/23/71
5/23/71	7	19	Reobserved and captured 8/30/71 at original capture point
8/30/71	7	19	Never reobserved
7/28/72	8	24.8	Never reobserved
8/11/72	9	58	Never reobserved
11/14/72	10	28	Never reobserved

to the date of first observation or recapture within 8 kilometers of the original capture point. The recorded time period is the minimum time of homing since bears could have returned without being trapped or seen until a later date.

Distance between two locations within the Park is given in air-kilometers and, therefore, due to the mountainous terrain is less than the actual minimum distance.

Chi-square contingency tables, Fisher Exact Probability Test and Student's t-test were used to test for statistical significance. Levels of significance were set at $P < .10$ since tendencies rather than absolute differences between bears were being measured.

RESULTS AND DISCUSSION

Males versus females

From 1967 to 1974, 76 nuisance bears were captured and displaced a total of 155 times. Individual bears were captured one to 13 times and were displaced an average of 21.7 air-kilometers (range 5.8 to 64.8 kilometers). Males comprised 87 percent of the nuisance bears and juveniles (all males) 20 percent. All females were adults and only one (10 percent) was recorded as having cubs (Table 1).

The predominance of males classified as nuisance bears is in general agreement with Erickson (1964), Harger (1967), Wasem (1968), and Sauer *et al.* (1969), who reported between 71 and 80 percent males. Although the sample size of females is small ($n = 10$), the results suggest that females having young may be more wary of people and less likely to enter campgrounds and roadsides. Since females have the potential to give birth to young in alternate years and yearlings remain with the sow for a period of time into the summer, this may have a 'dampening' effect on females establishing a garbage-seeking behavior.

The greatest homing distance in the GSMNP was an adult male returning 64 kilometers. The greatest homing distance of the three females that homed was 19 kilometers (Table 1).

There was no significant difference ($P = .22$) between the homing ability of inexperienced females (30 percent) and inexperienced males (50 percent) (Table 2). Differences between experienced males and females was not tested statistically due to the limited sample size of females (Table 1).

Approximately 33 percent of the inexperienced juvenile males ($n = 15$) and 55 percent of the inexperienced adult males ($n = 51$) homed. However, these differences were not significant ($.20 < P < .10$). As previously mentioned, none of the juveniles were cubs and only one bear was judged to be a yearling. Therefore, it would be more precise to state that no statistical difference was found between subadults (2.5 and 3.5 years old) and adult bears.

Distance transplanted and homing

There was a tendency for bears transplanted farther from their capture point to have a lower probability of homing. The females that homed ($n = 3$) were displaced an average of 11.9 kilometers (range 7.2 to 19 kilometers) and the females not known to home ($n = 7$) were transplanted an average of 35.6 kilometers (range 16 to 58 kilometers) (Table 1). Approximately 54 percent ($n = 56$) of the male bears displaced less than 30 kilometers homed (Table 2).

Table 2, A summary of transplanting nuisance male bears in the Great Smoky Mountains National Park from 1967 to 1974.

	Before July 1 ^a		July 1 - August 15		After August 15									
	<u><4.5 years old</u>	<u>i 4.5 years old</u>	<u><4.5 years old</u>	<u>i 4.5 years old</u>	<u><4.5 years old</u>	<u>i 4.5 years old</u>								
	Displacement ^b <30km i 30km	Displacement <30km i 30km	Displacement >30 km	Displacement <30km i 30km	Displacement >30km	Displacement <30km i 30km								
Homing														
Inexperienced	4	0	12	0	1	0	11	1	0	0	0	2	2	
Experienced	0	0	16	1	0	0	0	10	3	0	0	24	3	
Not Homing														
Inexperienced	3	1	13	2	3	1	2	1	2	1	2	0	3	2
Experienced	0	1	2	3	0	0	0	6	1	1	0	3	1	

^a Date bears were displaced.

^b Displacement of bears from the capture point to the release area in aerial kilometers.

The probability of distance causing a difference in homing ability ($P = .08$) was significant.

The total area in the GSMNP (2072 km²) is relatively small for animals as mobile and wide-ranging as black bears (Erickson 1964; Harger 1967; Sauer *et al.* 1969). However, the Park has rugged topography typified by narrow valleys and steep slopes creating rapid elevation changes ranging from 275 to 2,200 m. This rough topography combined with thick vegetation may hinder long movements of bears within the Park.

Experienced versus inexperienced bears

There was a significant difference ($0.1 < P < .05$) between the homing capabilities of experienced (includes second capture only) and inexperienced male bears ($X^2 = 3.2, 1 \text{ d.f.}$). Fifty percent of the inexperienced males ($n = 66$) homed and 70 percent of the bears transplanted for the second time homed. Bears transplanted after August 15 were excluded from these analyses since there may have been inadequate time for reobservation before the denning period. Data on female bears were inadequate for statistical analysis.

The average homing rate for experienced male bears transplanted the second time was 0.51 kilometers/day. Inexperienced male bears that homed averaged 179.5 days to return for an average rate of 0.17 kilometers/day. Nine of these bears were not reobserved at their capture point until the following summer. Bears homing the second time did so in statistically significant less time ($.10 < P < .05$) than bears homing the first time.

Comparison of release areas

Poaching is an important factor influencing the homing of displaced bears in the Park. Records of the NPS and the Tennessee Wildlife Resources Agency indicate heavy hunting along the periphery of the Park. To test the hypothesis that bears released along the periphery are less likely to return than animals released at more centrally located release sites, a comparison was made between two release points. One release point, Tremont, is centrally located within the Park and is not easily accessible to anyone except Park personnel (Fig. 1). The other area, Parson's Branch Road, is near the border of the Park and also near a major U.S. Highway (US 129). Tremont is 19 air-kilometers from Cades Cove. While Parson's Road is 4 kilometers farther away from the capture point than Tremont, the difference is assumed to be negligible.

It was found that bears released at Tremont homed 86 percent of the time ($n = 18$) while only 56 percent of the animals released at Parson's Branch homed ($n = 16$). These differences were significant ($P = .09$).

Habitat and terrain differences were not evaluated but could have affected homing incidence along with poaching. In addition to poaching, the lack of a buffer zone between the Park and outlying areas should be considered when relocating bears.

Orientation

Besides indicating that experienced bears are more likely to home and home in less time, our data suggest that bears are either capable of learning and memory of terrain outside their home range, and/or previous homing experience increases their efficiency of homing. Motivation is another aspect of homing. Griffo (1961) stated home range may not only satisfy the physical

needs which might often be provided equally well or better in other areas, but may also provide a psychic function. This psychic function may allow bears to move about areas with which they are familiar with assurance and to efficiently utilize the resources with which they are intimately attached. Also, whatever intraspecific social relationship was present may be altered when bears are moved to unfamiliar areas. Territoriality, if existent, would also be affected. These factors may motivate bears that have been artificially transplanted to seek their original homesite. Many of the animals transplanted were released in areas near sources of garbage (campgrounds, shelters, etc.). Of those bears transplanted only one (1.3 percent) became a nuisance animal in an area other than near the original capture point. This presents additional evidence that bears were not inclined to remain in unfamiliar areas outside their home range and were motivated to return home. Since bears are highly mobile, evidently motivated to return to their homesite, and capable of learning and memory, they are thus quite successful in returning to their original homesite.

If we accept that bears possess a homing ability and for one reason or another are motivated to return to their established home range, the question arises as to how bears are capable of relocating this area after being transplanted. Griffo (1961), Furrer (1973) and others have postulated that small rodents homed by randomly wandering in unfamiliar terrain until familiar terrain is encountered and nonrandom movements in terrain with which the animal has some previous familiarity.

It is reasonable to assume that bears are familiar with their home range. However, it is known that animals occasionally make excursions out of their home range. In Burt's (1943) classical definition of home range, he includes the idea of an animal's occasional excursion outside its normal home range. Also, it is a well accepted observation that many young animals disperse from their birthplace to unfamiliar areas to establish a homesite. In the GSMNP there is evidence of extensive wanderings by yearling and subadult bears (Beeman, unpublished data). The movements of animals beyond their established home range allows an opportunity for bears to familiarize themselves with terrain beyond their home range. Furrer (1973) and others have employed the term life range for including the total area an animal has traversed during its lifetime. A life range may have little biological significance for normal day to day activities, but could be important in a bear's ability to orient itself after being artificially displaced.

The above discussion introduces the question of how well bears can learn features of the terrain and their ability to retain a memory of such features for long periods of time. In testing for color and form discrimination by black bears, Bacon (1973) concluded that bears can make rapid visual discrimination and can remember a task for long periods of time. He also stated that their retention ability may be related to their high degree of persistence.

While much of the evidence presented in this study is circumstantial, experienced bears were more likely to home and homed in less time than inexperienced bears. It, therefore, appears that learning and memory of the terrain encountered do play a role in homing ability.

Orientation other than by previous association with the terrain is also possible. For example, polar bears (*U. maritimus*) would be unable to return to areas previously visited while living on drifting ice which changes form and carries them elsewhere, if they were not somehow able to navigate (Lentfer, personal comment). However, other means of orientation were not tested in this study.

Management implications

Creating conditions to reduce unnatural food available to bears is probably the most important management tool for reducing the number of nuisance animals. Eliminating all sources of unnatural food is not realistic in the GSMNP (or any other park) so the problem of nuisance bears will not be totally eliminated. Another precautionary step is to move a bear as soon as possible after it enters a campground or roadside and thus reduce the amount (frequency) of reinforcement (food) that a particular animal receives.

Since 50 percent of the male and 70 percent of the female bears transplanted for the first time did not home, the first transplant may be important in eliminating future encounters with a particular animal. Although this study only provided limited data to evaluate how well inexperienced bears will home from transplants over 50 kilometers ($n = 3$), distance appears to be an important parameter of homing. While it may require much time to move a bear the first time to an appropriate area, it likely reduces the chances of having to handle that particular bear again.

The relatively small area of the Park may prove to be inadequate to successfully transplant bears captured in some areas. There are a limited number of places within the Park that are less than 10 kilometers from a source of unnatural food (campgrounds, roadsides, or backcountry shelters). Yet, only one out of 76 bears transplanted was reported to have caused a nuisance other than at the original capture point. Our data indicate that the probability of a bear becoming a nuisance other than in its established home range is quite low; this should be considered when determining possible locations for transplanting bears. Thus, an area for relocating a bear does not necessarily need to be eliminated as a choice because of its proximity to another campground, roadside, etc.

Poaching may be an important factor when selecting a release site in the GSMNP. While moving bears to a peripheral area of the Park may eliminate a nuisance problem, it may do so at the cost of the bear. This difficulty is magnified by the lack of any buffer zone around most of the Park's periphery and the proximity of areas of relatively dense populations of people.

SUMMARY

From 1967 to 1974, 76 nuisance black bears were moved to other parts of the Park. Most nuisance bears were males (87 percent). Bears less than 4.5 years old comprised 20 percent of the nuisance animals. There was no significant difference between the ability of inexperienced adults and inexperienced juveniles to home. Within the range of distances that bears were moved (5.8 to 64.8 km), there was a significant difference between homing and distance transplanted, i.e. fewer homing with greater distances moved.

Experienced male bears were significantly more likely to home and homed in less time than inexperienced males. Bears released on the periphery of the Park were significantly less likely to home than bears released in the central part of the Park.

Bears seem to be strongly motivated to home. A bear's home range probably provides psychic needs as well as physical ones. They likely find their way by random wanderings combined with learning and memory of areas previously traversed. Other means of navigation were not tested in this study.

Creating conditions that reduce the amount of unnatural food available to bears is probably the most basic management tool for eliminating the transformation

of 'wild' bears to nuisance animals. Selection of release sites is also an important consideration in handling nuisance bears.

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Paper 10

Grizzly Bear Ranges and Movement as determined by Radiotracking

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INTRODUCTION

Yellowstone National Park consists of 8,800 km². Additional National Forest and Wilderness areas surrounding the Park constitute an ecosystem approximately 50,000 ha in size (Craighead *et al.* 1974). Within this extensive coniferous forest habitat, movements of grizzly bears, *Ursus arctos horribilis*, were determined by observing 264 marked animals and monitoring 23 radio-tagged bears (Craighead & Craighead 1972; Craighead *et al.* 1974).

The closure of the open pit dumps and the control measure initiated in Yellowstone National Park to cope with the increased incidence of grizzlies visiting campgrounds affected movements and home ranges of grizzlies within the ecosystem (Craighead & Craighead 1971). This paper deals with the general patterns of movement and characteristics of home and seasonal ranges prior to the closure of dumps.

Many grizzlies in this vast area were seen at one or more of the earth-filled garbage dumps at some time during their life spans. In a 12-year period, 39 percent of bears censused at dumps were marked, and 76 percent of the ecosystem population was observed and counted at the dumps during this time (Craighead *et al.* 1974). Thus 76 per cent of the average population of approximately 229 animals moved to and from garbage dumps. This massive movement within and beyond Yellowstone Park affected the character of home ranges. Since this movement pattern became established over 60 to 80 years, it represented a well-established pattern, similar to movements observed in Kodiak brown bears, *Ursus arctos middendorffi*, attracted to salmon streams (Berns & Hensel 1972). Data analyses are within the context of these habitual movements to available food sources.

We extend thanks to J. Varney, who designed and constructed radiotracking equipment and to M. Hornocker, R. Ruff, H. McCutchen, C. Ridenour, H. Reynolds, III, H. Reynolds, Jr., J. Sumner and J. Seidensticker for assistance in tracking grizzly bears. Thanks are also due L. Garrison, former superintendent, and other personnel of Yellowstone National Park; M. Payne, President, National Geographic Society; V. Schaefer, Director Atmospheric Sciences Research Center, State University of New York at Albany, L. Gould, Past-President AAAS; D. Ozmun; and C. Pihl, F. Goodyear, S. Scrivener, Jr. and G. Stout, Directors, Environmental Research Institute. All, in different ways, encouraged us in our research efforts. This study was supported by the National Geographic Society, Research Grant GB-2672 from the National Science Foundation, Grant AT-(45-1)-1929 from the Atomic Energy Commission, and funds from the U.S. Fish and Wildlife Service, the Environmental Research Institute, and the Philco-Ford Corporation. We received co-operation from the National Park Service, University of Montana, Montana and Wyoming Fish and Game Departments, State University of New York at Albany, (Atmospheric Sciences Research Center), and the Yellowstone Park Company.

METHODS

From 1961 through 1968, 48 radio instrumentations were made involving 23 different grizzlies. Twenty different ranges of grizzly bears were delineated: five in 1963, five in 1964, three in 1965, two in 1966, three in 1967, and two in 1968. Of these, seven were home ranges and one a lifetime range. Entire families were involved when one member was instrumented, thus the home ranges of family groups as well as the ranges of the radio-tagged individuals were plotted.

Grizzlies were radiomonitored up to 3 months with standard model transmitters and for as long as 9 months with extended life transmitters featuring a timer circuit that turned the transmitter on and off at 30-second intervals (Craighead & Craighead 1972; Varney 1971). Radio signals were used to accurately fix the position of instrumented bears and to determine the approximate location of bears within home or seasonal ranges. Lines connecting peripheral fixes were used to construct ranges on topographic maps (Craighead 1968). Unless there was extensive movement, usually only one daily fix was recorded. A single radio bearing often indicated whether a bear was within a tentatively established range or possibly moving beyond it. A change in signal strength with regulated volume often provided the approximate distance from signal source (bear) to the receiver.

The percentages of successful days in locating by radio were high. Failure to obtain a fix or locate an instrumented animal was due to limited receiver range or shielding effect of terrain. Ranges were delineated from fixes, bearings, and sightings while tracking.

Two hundred and sixty-four grizzlies were immobilized and color marked. Some sightings of marked grizzlies were used in determining bear movements and others supplemented radiotracking data on ranges.

RESULTS**Home Range Characteristics**

Seasonal and home ranges varied in size (Tables 1 and 2) as influenced by availability and distribution of food, proximity of mates, den site requirements, habitat preference, foraging habits, age, sex and condition of the animals, and other factors. Home range with some modification is defined as 'that area traversed by the individual in its normal activities of food gathering, mating and caring for young.' (Burt 1943). An area occupied in one or more seasons or years is designated a home range if it included a den site. A seasonal range is an area utilized during spring, summer or fall but excludes the den site. The periods coincide generally with those derived from the spring and autumn equinoxes and summer and winter solstices. (Craighead *et al.* 1973). A lifetime range is the range determined for a bear throughout all or most of its life. Although a home range tends to be a stable unit, it may vary from year to year. In general a lifetime range is larger than a home or seasonal range but some seasonal ranges closely approximated home ranges, as for example the 70 km² area of grizzly No. 150. The den, which was not located, was either within the seasonal range or very close by (Tables 2 and 3). Home ranges varied from a maximum of 324 to the smallest of 18 km². Seasonal ranges varied from 435 to 20 km².

The ranges were affected by a prevalence of food at the Trout Creek refuse area but natural food sources such as animal carcasses, berries and pine nuts

TABLE 1. GRIZZLY BEAR HOME RANGES DETERMINED BY RADIOTRACKING

Bear No.	Sex	Tracking Years	Tracking Days	Range Area in km ²
7	F	1963	44	275
40	F	1963-68	400	78
101	F	1966-67	125	111
150	F	1963	33	70
158	M	1964	51	57
39	F	1964	51	57
187	F	1967-68	98	104
202	M	1965-66	174	324

TABLE 2. GRIZZLY BEAR RANGES DETERMINED BY RADIOTRACKING 1963-1964.

Bear No.	No. of Bearings Used	Tracking Days	No. of Fixes	Range Area in km ²	Remarks
7	256	44	32	275	Female with yearlings
40	140	29	32	202	5-year old female
75	145	44	21	93	Female with yearlings
76	129	28	21	435	5-year old male
150	227	29	35	70	Female with cubs
6	49	19	11	31	5-year old female
14	58	41	5	31	Large adult male
34	151	34	26	34	Female with yearlings
40	106	67	27	39	Female with cubs
158	98	51	14	57	Yearling (Family of female and 3 yearlings)

influenced movements and thus the sizes of individual ranges. Some grizzlies had relatively small seasonal ranges because they foraged and denned nearer the dump in Hayden Valley and fulfilled other requirements including mating and the need to have daytime retreats and a combination of timber and open meadow in this rather localized area.

Grizzly bear No. 76 had a seasonal range of 435 km². His center of activity was Hayden Valley, but foraging trips from Hayden Valley to outlying areas expanded his range. In a 1-week period he was tracked for 80 airline km. His signal was lost during fall migration to the north-eastern portion of Yellow-

TABLE 3. FEMALE GRIZZLY BEAR RANGES.

Bear No.	Age	Year	Tracking Days	Range Area in km ²	Type of Range
6	5	1964	19	31	Summer & fall
7	Adult	1963	44	275	Summer
34	Adult	1964	34	31	Summer
40	5	1963	29	20	Summer & fall
	6	1964	67	39	Home
	7	1965	106	52	Home
	8	1966	76	18	Home
	9	1967	16	28	Home
	10	1968	106	58	Home
75	Adult	1963	44	93	Summer
150	Adult	1963	29	70	Summer & fall
101	Adult	1967	49	111	Home
187	Adult	1967	65	106	Home
187	5	1968	33	87	Home

stone Park, an indication that his home range was many times the size of the measured summer range and consisted of two seasonal ranges connected by a corridor. Grizzly No. 14 also had a summer range of unknown size in Hayden Valley. During fall dispersal this bear moved directly to forage in upper Pelican Valley. This seasonal range apparently included his den site and measured 31 km². Although the home range of No. 14 was extensive, only the approximate size was determined. A year after we plotted his fall range, he was observed at Flat Mountain Arm of Yellowstone Lake, 39 airline km away on the opposite side of the lake. This was an estimated ground distance of at least 97 kilometers from the location last observed. The home range of No. 14, though not entirely disclosed by radio fixes, was 2,600 or more km² in size. Other grizzlies also had similarly large home ranges. Long term movements of some bears indicated that a large portion of the ecosystem might be covered in a lifetime. However, seasonal ranges were localized and not excessively large. The availability of food during spring, summer and fall more than any other factor tended to limit seasonal range size.

Types of Ranges

Two types of home and seasonal ranges plotted by radio consisted of a discrete, well-defined one used throughout the year and a summer foraging area connected by a migratory corridor to a late fall-early spring range that contained a winter den site. This pattern of summer and fall ranges separated by considerable distance is typical of some male and female grizzlies. As examples, bears No. 76, 14 and 12 exhibited such ranges as did sows No. 96, 164 and 34. In the course of a week No. 96 and her cubs travelled 50 airline km from her spring range and den area to her summer range. The largest discrete range

of a female was that of No. 7 measuring 275 km² (Table 3). This bear over the years established a summer range in the Sour Creek drainage east of Yellowstone River. Her sibling, No. 6, developed a range partially within her mother's. This group regularly foraged east of the river but periodically swam the Yellowstone River to obtain food at the Trout Creek dump. In contrast, grizzly No. 150 and her cubs had a summer and fall range of 70 km² west of the dump, but during the period of tracking never visited it.

Ranges of mature and young males were larger than those of females (Table 4). The summer range of male No. 76 was 435 km², the home range of No. 202 was 324 km², and the fall range of No. 14 was 31 km². However, the home range of No. 14 was many hundreds of km² and his lifetime range was several thousand or more km². Yearling male No. 158 had a home range of 57 km², a range influenced by and identical to that of his mother No. 39. Before weaning, grizzly No. 188 had a range identical in size to his mother's, 52 km². His summer range was reduced following weaning, but in fall he travelled rapidly to an unknown but distant denning site, thus expanding his individual range over that of the family range before we lost his radio signal. He developed a pattern of a summer range separated by a migratory corridor from a late fall-early spring range. The range of grizzly No. 202 was taking on the pattern of a discrete range expanding in size from 70 km² in 1965 to 324 km² in 1966 (Table 4). The control-killing of this bear in August 1966 prevented further study of his life range. He denned on the steep slope of Yellowstone Canyon, within a home range which included Canyon Village campground where he associated food, in some cases handouts, with man. This foraging habit cost him his life. Had this grizzly followed the movement pattern of many sub-adult bears, he might eventually have left this early established range to forage or to wander and thus either establish a migratory corridor to a new summer or fall range or greatly expand his life range.

Range Overlap and Territoriality

Although grizzly bear ranges conformed to two patterns, they were discrete entities with only minor modifications. Within any one spatial entity, numerous grizzlies conducted daily and seasonal activities without major conflict or defense. Ranges overlapped and thus were not spatially separated as with territorial species (Craighead & Craighead 1956). Grizzlies congregated at

TABLE 4. MALE GRIZZLY RANGES DETERMINED BY RADIO-TRACKING.

Bear No.	Age	Year	Tracking Days	Range Area in km ²	Type of Range
14	Adult	1964	41	31	Fall
78	Young Adult	1963	28	435	Summer & fall
158	1	1964	30	57	Home
188	1	1965	19	52	Summer
	1	1965	56	70	Home
202	2	1966	118	324	Home

such food sources as refuse dumps, carrion, berry patches, pinenut stands, clover fields, and sedge seepages. Their daytime beds were made nearby in dense timber, and numerous grizzlies regularly used the same timbered retreats simultaneously. When 'closing in' on an instrumented grizzly, we on separate occasions jumped 7 and 13 bears within several hundred meters. Territorial defense of seasonal or home ranges has not been observed, and all behaviour indicates that defense activities are largely non-existent. Range peripheries are definitely not defended, feeding areas are sometimes temporarily defended, and den sites are not defended against mature members of the same sex. Grizzlies No. 40 and 101 with their families visited one another's dens regularly (Craighead & Craighead 1972). Occasionally at refuse dumps or around carcasses a show of dominance is used to temporarily delay communal feeding.

Observations in April and May 1965, revealed a slight indication of territorial defense related to status in the bear social hierarchy. This hierarchy is based on aggressive-submissive behaviour (Hornocker 1960). We had been watching a large unmarked boar feeding on a buffalo, *Bison bison*, carcass on an island in the Yellowstone River. The radiotagged sow No. 40 and her yearling No. 188 also approached this food source. The sow and her yearling usually waited on a nearby river terrace and fed only toward morning after the boar had left. On one occasion the boar, sow and yearling approached the carcass at the same time. The boar upon detecting the sow turned and slowly circled in a manoeuvre to get between the sow and a wooded retreat. This caused the sow and yearling to retire keeping 250 to 450 m from the boar. As the boar circled, the sow also moved back. This could be interpreted as an exhibition of territorial defense of an extensive area surrounding a temporary food source, but was more akin to submissive behaviour in the presence of an aggressive male.

Range Activity Centers

Within their seasonal or home ranges grizzlies spent much of their time in localized areas or activity centers. For example, grizzly No. 150 and her three cubs foraged within approximately a 25 km² area, obtaining prehibernation food requirements within this restricted locale. Their efficiency as omnivorous foragers was revealed. Two heavily utilized foods were meadow mice, *Microtus* spp., at peak population densities, and grass showy melic, *Melica spectabilis*, whose starchy, onion-like bulbs form a staple fall food for Yellowstone grizzlies. Pocket gophers, *Thomomys talpoides*, were also preyed upon. The size of this activity center which was determined by available food and nearby timbered retreats indicated the potential carrying capacity of an open meadow, grass-sagebrush sub-climax for grizzlies (Craighead 1968).

Lifetime Range

A lifetime range was plotted for female grizzly No. 40 from age 3.5 years to death. She was instrumented for 8 consecutive years from 1961 through 1968 (Table 5). She was tracked by radio for 32 days in 1961 and 10 days in 1962. Radio fixes plus sightings revealed that her seasonal range as a subadult was about 21 km² but this did not include her den site. In 1963 as a mature sow her range was 21 km², but again this did not include the den site. In 1964 No. 40 and her cub was tracked 67 days and her den located. The cub was one of her initial litter of two. One disappeared and was presumed dead. The increasing amount of foraging with a cub and movement to a den site at higher elevation expanded the size of her home range to 39 km². In 1965, she was tracked for 106 days. In the early spring she extended her known range eastward by crossing the

TABLE 5. LIFETIME RANGE OF FEMALE GRIZZLY
NO. 40

Age	Year	Tracking Dates	Tracking Days	Range Area in km ²
5	1963	8/7-9/4	29	20
6	1964	9/4-11/9	67	39
7	1965	6/28-9/6 10/13-11/16	106	52
8	1966	9/1-10/29 10/30-11/15	76	19
9	1967	9/11-9/26	16	29
10	1968	7/25-9/4 9/5-11/17	106	57
Total Area Lifetime Range ...			78	

Yellowstone River with her yearling. They had moved here to feed on a bison carcass. She weaned her yearling, No. 188, in May and mated. We tracked this pregnant sow throughout the summer and to a new winter den. Her 1965 range was 52 km². Her range was smaller in 1966 but within the same area as in 1965. With two cubs she was tracked to a new den. In 1967, she roamed over 29 km² in approximately the same area but a den was not located. In 1968, when No. 40 again had cubs, she covered an area of 57 km². Some of this was new territory where she had not previously foraged. Some expansion was due to movements in search of pine nuts.

The basic size of this sow's range, including her den sites, was about 39 km². The attraction of various foods such as pine nuts, huckleberries, *Vaccinium* spp., and carcasses caused her to slightly alter or extend her range from one year to another so that the total area covered in a lifetime was approximately 78 km². In 1969, at age 11, No. 40 moved from this changing but well-established range when food at the Park Service Trout Creek dump was greatly reduced. Her range included this regular source of summer food that supplemented her natural diet. With her yearlings she travelled to the Yellowstone Lake utility area about 5 km beyond the boundaries of her established life range. This was an abrupt movement into new territory. Here two of her cubs were captured in culvert traps and she was shot by a park ranger while protecting her offspring.

The basic range of this animal remained substantially the same year after year. The first major movement away coincided with the drastic curtailment of a once dependable food supply. No. 40 developed a discrete range not the pattern of a separate fall and spring range connected by a migratory corridor. It was smaller than ranges of many females and definitely smaller than ranges of most mature males. Food abundance and availability altered grizzly bear ranges more than any other factor. An abundance and variety of food kept range size small and food scarcity increased range size. Apparently variations in food supply, whether natural or man-caused, will alter grizzly bear ranges, but will not change their fundamental nature.

Movement

During a 5-year period (1959-1963) 72 movements involving 43 different marked bears were determined by measuring distances between the positions where captured and where recaptured or re-observed. The average linear distance moved was 34 km. The maximum linear distance travelled was 96 km over extremely rugged terrain.

From observing marked and monitoring radio-instrumented grizzlies, eight types of typical movement are identified.

1. Regular and routine daily movement from a daytime retreat to a dependable food supply (dump or animal carcass): this was intra-range movement within an established seasonal range. This type of movement was typified by grizzlies No. 40 and No. 75. For example, No. 40 habitually made a 5-km trip to a refuse dump starting approximately 1800 hours and taking 1.5 hours. She was usually resting back in her daytime bed by 0600 or 0700 hours.
2. Daily foraging consisting of short linear distances covered but considerable and continuous amounts of travel performed: this again was intra-range movement well illustrated in the fall of 1963 by radio-instrumented grizzlies who were active day and night, resting only at short intervals. Their airline movements were measured between radio fixes made approximately 12 hours apart. In 13 movements, No. 150 travelled an average of 3.7 linear km and No. 7 averaged 5.1 km in 12 movements. The maximum linear distances travelled in one direction by No. 150 and No. 7 were 8 km and 9.6 km, respectively. Both females foraged within relatively small areas and fed extensively on meadow mice and bulbs of showy melic. Their daily activity and movement can be summarized as considerable roaming without moving very far.

The daily movement of males under similar conditions was greater than of females. No. 76 averaged 11.5 airline km for eight 12-hour movements. The longest airline distance covered by No. 76 in a 12-hour period was 16 km recorded on four different occasions. He travelled 14 km in a single afternoon.

3. Movement to new food sources: when bears detected food, usually animal carcasses, by their keen sense of smell, they moved directly to it. One grizzly travelled rapidly 29 km to feed on a carcass. It was not determined just when and how the carcass was detected. In 36 hours, No. 37 travelled an airline distance of 30 km from one food source to another. However, it took instrumented sow No. 150 approximately 60 hours to locate and move to a carcass only 2.8 km away when the wind was unfavorable.
4. Fall dispersal to den sites or foraging areas: such movements were often rapid as when instrumented grizzly No. 34 and family, and boar No. 14, travelled 24 linear km overnight and 24 km in 24 hours, respectively, from summer to fall ranges. No. 7 travelled 19 km in 2 days to a fall foraging area. Male No. 76 and female No. 96 left summer ranges and travelled rapidly for 32 and 64 airline km to fall ranges. Within a 12-hour period No. 164 moved 25.6 km from a fall foraging area to a winter den. All were mature radio-instrumented animals travelling to den sites and foraging areas previously used.
5. Fall dispersal of young bears into territory previously unvisited: this was exemplified by a movement of No. 202 from a summer range to a fall

site where he dened and by yearling No. 188 who left an established summer range and travelled rapidly 30 or more km to a den site. No. 194 with three other yearlings left its summer range and travelled rapidly an undetermined distance, but more than 24 km, to a winter den area.

6. Migration: the fall dispersal of grizzlies from summer feeding areas annually resembled a migration, that is a simultaneous movement of population members to distant areas, some beyond park boundaries. Conversely, there was an annual return movement, although more irregular, from winter dens and spring-fall ranges to more bounteous summer food supplies. One of the longer migratory movements was made by a large marked boar who travelled from Rabbit Creek to Hawk's Rest just outside the south-east corner of Yellowstone, an airline distance of 80 km.
7. Wandering: this seemed to consist of the wandering of young, insecure bears that were seeking food and establishing home ranges. Number 37 was shot by a hunter in spring south of Yellowstone Park, having travelled a minimum of 80 airline km since late the preceding fall. Yearling No. 52 travelled an airline distance of 88 km in 20 days and was shot in Grand Teton National Park 21 km south of the Yellowstone Park boundary.
8. Induced movement and homing: most grizzlies trapped and distantly transported returned to established ranges. Instrumented grizzly No. 170, when trapped, transported and released, travelled 54 airline km over rugged country in 62 hours to return to her point of capture. When again trapped and released, she returned a distance of 85 km. Released male grizzly cub No. 78 travelled an airline distance of 43 km in a week to return to his point of capture. Male grizzly No. 38 when released on Promontory Point of Yellowstone Lake travelled 50 airline km in 4 days to return to his established summer range.

A radiotagged sow and two yearlings, intercepted while being tracked, ran a measured distance of 1.6 km in 3 minutes, and average speed of 32 km/hr across rolling sagebrush country.

Rivers, canyons or rough country did not deter grizzlies. Sow No. 34 and her family made 11 known Yellowstone River crossings in a 23-day period in August.

Male No. 76 circled Mount Washburn and made five crossings of the Yellowstone River including traversing the steep-walled canyon. Instrumented sow No. 7 made six Yellowstone River crossings in 44 days, two down the canyon and up the other side to the high slopes of Mount Washburn.

The type of movements involving long distances revealed that Yellowstone Park grizzlies ranged far beyond park borders so their management is the responsibility of several resource management agencies.

Population Densities Influenced by Movement

Using the computed population average of 229 grizzlies in the Yellowstone ecosystem, approximately 20,000 km² (Craighead *et al.* 1974), we can determine that this supported an average of one grizzly per 88 km. Such densities occur in early spring and late fall when grizzlies disperse throughout this extensive area. In summer most grizzlies within this ecosystem were concentrated at five sites within the park. Trout Creek has attracted between 98 and 132 grizzlies annually (Craighead & Craighead 1971). These grizzlies covered an area no greater than 5 km², a density of one bear to approximately 0.05 km². During daylight hours, these same grizzlies were dispersed over an area of approximately 31 km² with a density at this time of one bear to 0.36 km².

Daily and seasonal movements of grizzlies is obviously in response to available food which alters their density over any given area. Extrapolation of bear numbers is questionable unless bear movements in time and space are well known and documented. Likewise grizzly bear densities computed for large areas from data based on local concentrations must take movement factors into consideration.

During our research we experimented with animal carcasses or baits to attract grizzlies. One objective was to see how effective this might be in moving grizzlies away from campgrounds at times of high park visitor use. A maximum of 23 grizzlies was attracted to a single carcass at one time. The greatest distance a marked grizzly moved to a carcass in a 3-day period was 47 airline km. Whether this movement was coincidental is unknown but grizzlies appear to locate carcasses and other food sources from considerable distances. Both movements and densities can be temporarily influenced by strategic placement of baits.

At the suggestion of the author, the U.S. Forest Service and the Wyoming Game and Fish Department censused the Clark's Fork and Wapiti Districts of the Shoshone National Forest bordering Yellowstone National Park. One purpose was to determine whether there were small, local population units unaffected by seasonal movements. Fifteen bait stations (animal carcasses) were placed out during the August peak of grizzly bear concentration in Yellowstone. During this census only three grizzlies were observed at bait stations, but 41 black bear were sighted (Mullen 1969; Winter 1969). In addition more grizzlies were observed throughout this extensive area in spring prior to migration to the Park and in the fall after bears dispersed throughout the Park and beyond the borders (Mullen, pers. comm.). The results suggested that few grizzlies resided in areas surrounding the Park at the height of grizzly bear concentration within Yellowstone. This was expected, based on grizzly habits and known movements. According to Mullen (pers. comm.) approximately 25-30 percent of the grizzlies seen during 1969 and 1970 in Shoshone National Forest were marked animals tagged in Yellowstone. The results tended to confirm our findings that because of annual movements to long established earth-filled dumps in Yellowstone, few grizzlies did not at some time feed at the garbage dumps (Craighead & Craighead 1971). Grizzly bear population figures determined for Yellowstone Park during periods of high local grizzly density represented a grizzly population inhabiting a far more extensive area, the Yellowstone ecosystem.

GRIZZLY BEAR MOVEMENTS AND RANGES AS RELATED TO MANAGEMENT

Information on grizzly bear ranges and movement reveals that the grizzly bear population shifted between Yellowstone Park, administered by the National Park Service, and four National Forests administered by the U.S. Forest Service. This situation, though now altered, still exists. There is no coordinated management program between federal agencies and state departments having jurisdiction over the wildlife inside and outside the Park. An urgent need exists for cooperative state and federal management within this ecosystem. Unilateral decisions by one agency resulting in excessive mortality could endanger the grizzly population over the entire area. In a 3-year period (1969-71) the Park Service's revised management policies, including abrupt closure of dumps, caused the known mortality of 120 grizzlies. In a 5-year period (1968-1972) the known and documented mortality was 160, with 42 percent females. Since identifying grizzly ranges and determining bear move-

ments, elimination of dumps has diverted bears into campgrounds (Craighead & Craighead 1971) and altered fall and spring dispersals and migrations. Some grizzlies formerly moving into Yellowstone during summer months are no longer doing so and are subject to legal hunting and predator control activities outside.

Problem grizzlies, resulting from dump closures, when transported to areas adjoining the Park have in most cases returned only to be eliminated (Craighead & Craighead 1971). of 17 such transplants by helicopter, only one was known to be alive a year later and 13 known to be dead (Greer 1972). When transplanting grizzlies from one area to another, managers should consider their strong homing instincts. It appears that grizzlies when moved no more than 80 km return quickly to the point of capture.

The currently changing movement pattern throughout the Yellowstone ecosystem needs to be studied in relation to population numbers and distribution, to make wise management decisions. Movement data could be obtained through instrumenting grizzlies and monitoring migratory movements by satellite (Craighead *et al.* 1972; Craighead *et al.* 1971). Likewise satellite (ERTS-1) multispectral scanner imagery can be used in habitat delineation and analysis (Varney 1973). To a degree the size of grizzly bear ranges can be altered through habitat manipulation, perhaps based on extensive satellite surveys. Any alteration of well established food sources, such as dump closures and elimination of bait annually placed out for hunting, will change grizzly bear ranges and movements. Knowledge of such movements can be incorporated in management plans as an aid toward developing techniques to estimate bear populations and decrease grizzly mortalities. Emphasis should be on decreasing mortalities, particularly among mature females. Such precautions seem mandatory when a small population is declining and the size of a viable population is unknown. The most probable figure for the grizzly bear population of the Yellowstone ecosystem was computed to be 136 in 1974, a decline from a peak of 245 in 1967 (Craighead *et al.* 1974).

Baiting with animal carcasses can be an effective management technique to census grizzlies throughout the Yellowstone ecosystem. The location and timing of baits are important as is the duration of observation periods. Placement of animal carcasses to entice grizzlies from campgrounds could be a more realistic and effective management policy than capturing, transplanting and eventually killing those that return.

Baiting bears for hunting has until recently been permitted in Wyoming. Its desirability is being debated. Grizzlies can only be hunted under special permit. Twelve permits were issued for 1974, none for 1975. Hunting over bait is certainly not a sporting way of shooting a grizzly, ostensibly a trophy animal. However, baiting has an advantage of permitting selectivity, that is, taking large or old bears rather than young ones. Baiting can also be used to lure grizzlies away from outfitter camps. Annual spring and fall baiting by hunters and outfitters provides a substantial food source for grizzlies. The sudden elimination of baits could further alter established grizzly bear movements as well as behaviour, especially during seasonal food shortages. The result could increase grizzly bear mortalities.

The State of Idaho does not permit grizzly hunting. Wyoming plans to close the grizzly season for at least 2 years starting January 1975. Montana amended big game regulations in 1974, to prohibit grizzly hunting adjacent to Yellowstone Park. If these measures are supplemented with a management policy in Yellowstone Park based on minimizing grizzly deaths due to control programs, it should reverse or at least halt the populations' downward trend.

Grizzly bear management outside the Park through trophy or special permit hunting appears to be a sensible approach to preserving yet regulating a definitely dangerous and at times destructive carnivore. Under some conditions, particularly when and if grizzly populations again expand, they can be detrimental to man's economic interest. Grizzly management, though aimed at preservation, should include means of control as necessary. Hunting by special permit can accomplish needed control. If it becomes necessary to classify the grizzly as an endangered species, steps to control troublesome individuals will be more difficult. Likewise, insufficient control when control is justified could arouse public antagonism detrimental to the grizzly.

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Paper 11

Aspects of Grizzly Bear Population Ecology in Mount McKinley National Park

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INTRODUCTION

Scientific knowledge of grizzly bears, *Ursus arctos*, in interior and northern Alaska and, more particularly, in Mount McKinley National Park, is based on work of Dixon (1938), Murie (1944, 1961) and Sheldon (1930).

The long-term objectives of this study include: (1) determination of population composition, density and mobility for given units of range, which will allow comparisons of protected and hunted populations; (2) development of an accurate census method; (3) determination of as many of the bear's range requirements as possible; (4) filling as many gaps in the factual knowledge of the grizzly's life history as possible.

DESCRIPTION OF STUDY AREA

The study area is roughly the north side of the Alaska Range in the eastern half of Mount McKinley National Park.

The physiographic setting of Mount McKinley National Park is well described in Wahrhaftig (1958). The Park lies astride the Alaska Range and the associated fault-valley and perimeter mountain chains, stretching from the Nenana River west approximately 150 km and varying in width from about 37 km to about 60 km. Most of the peaks in the eastern half of the Park are less than 2,000 m in height. Above 1,400 m there is a great deal of bare rock and ice. North of the main part of the Alaska Range and paralleling the high peaks, is a broad valley which is a functional part of a major fault system. The valley floor is approximately 1,000 m msl and is about 10 km in maximum north-south width. The low mountains north of the valley are rounded with slopes covered by rather open vegetation; the peaks in this range are from 1,200 m to 1,500 m msl. The east end of the Park is drained by rivers spaced at about 5- to 10-km intervals and flowing north or northwesterly (see Figure 1).

The climate of Mount McKinley National Park is variable; on the north side of the Alaska Range it is primarily continental but not as severe as that of the interior lowlands. Summer daily mean temperature is about 10° C to 15° C, but freezing and even snow may occur in any month. Persistent snow generally occurs by October and dissipates from the lowlands and unshaded portions of the foothills by mid- to late May. Snow may remain on north-facing slopes and in some deep beds almost the entire summer. There is much perennial snow along the crest of the Alaska Range. Annual precipitation is about 35 cm. During the summer, the time of greatest concern to this study, the weather tends to be extremely variable from day to day, year to year, and place to place. Wind frequently blows about 16 km per hour, and heavy rain squalls

MOUNT MCKINLEY NATIONAL PARK



Fig. 1 Grizzly bear study areas in Mr. McKinley National Park.

and sunshine frequently occur in neighboring valleys. It is seldom hot enough to preclude using spotting scope magnifications of 20X or 30X.

There is little forest cover in the Park. In the intermontane valley most tree cover occurs as isolated stands of white spruce, *Picea glauca*, on southern slopes of the lower range of mountains (the 'outside range') and more extensively along major rivers. The valley bottom itself and most mountain slopes are covered with shrubs, mostly willow, *Salix* spp. and tundra vegetation. Most of the tundra is relatively dry or very dry. North of the outside range there are extensive areas of wet sedge-tussock tundra. The broad, flat valley bottoms are covered by wide gravel bars of braided streams; these support patches of vegetation. Dixon (1938) and Murie (1944) have provided more extensive descriptions of the Park.

METHODS

Ground observations were made from early or mid-June through August in 1957-1959 and from late May through early September in 1973. Most aerial observations were made in late April and in September and October.

The major portion of the eastern half of the Park on the north side of the Alaska Range was divided into an intensive and an extensive study area, based on frequency and thoroughness of coverage. Open country, low vegetation, and approximately 128 km of road, mostly in the intermontane valley, permitted effective and efficient searching for bears.

Two basic approaches were used. The first was simply to drive along the road or hike through the back country searching for bears. Once bears were found, they were watched ideally from the closest possible distance that would permit observation while minimizing the possibility of detection of the observer. At times, observation distances were a few tens of meters, but many observations were made from a kilometer or more. An attempt was made to visually identify family groups or individuals in order to associate information with particular bears and to provide a basis for a population estimate.

The second basic approach was in connection with specific attempts to determine the density of bears within the study area. In such cases the road was driven slowly through the entire study area during the course of a single day. Stops were made frequently to search the landscape very thoroughly with spotting scopes. All bears seen were recorded and, when possible, identified as individuals.

In connection with a study of vehicular impact on animals along the road system during 1973, students recorded observations of all animal species from tour and shuttle buses as well as from our own vehicle. A minimum population estimate of grizzlies for that summer incorporated these data. A series of plots established for the traffic impact study provided additional density estimates.

Supercub aircraft, capable of relatively slow, low-level flight, were used frequently. Observations during calm weather were made from altitudes of 30 m to 150 m; the general strategy of flying varied but frequently involved very detailed and thorough coverage of each major drainage including small side valleys whenever feasible.

To ascertain the minimum number of families in the population, I conservatively applied a series of tests to each family unit, i.e. a sow with young. Five

principal criteria were used: number of young, their age, location, description, and timing. Only when potential duplicates were eliminated was a family treated with individual status. The tests for individual status of the families were applied on a within-year and between-year basis.

Single bears were tested for duplication in much the same way but with obviously less confidence when long time intervals occurred between sightings. The same procedure was followed for both families and singles, counting as distinct *only* those for which the probability of duplication was either zeroed or reduced to an extremely low level. The population estimates are therefore truly minimal.

RESULTS

Density

The estimate of minimum density varies between years from 0.026 to 0.041 bears/km² or 24 to 38 km² per bear (Table 1). Estimates are based on the entire study area with no attempt being made to eliminate unutilized habitat. In both 1959 and 1973, density levels appear to be relatively high; in 1973 several people knowledgeable about bears commented that there were a great many bears in the Park. Judging from the subjective impressions of individuals who have observed the Park closely for 20 years or more, I believe that the densities observed in 1959 and 1973 are near the upper end of the range that one can expect in this area. There is no basis for believing that the population maintained a constant density level between 1959 and 1973. The estimates relating to singles are considerably more conservative than those for families due to the greater potential for identification of different families.

Table 2 provides a summary of the density of sows with families and their young for the intensively worked portion of the study area. Observed densities for the same characteristics in the extensive portion of the study area generally range from one-quarter to three-quarters of the value for the intensive area. Much of the difference is due to lower effort in the extensive area; some of the difference may be due to variation in habitat quality. If the figures derived from the intensive sub-area are expanded by a factor appropriate to the relation of the size of the intensive sub-area to the size of the

TABLE 1 MINIMUM ESTIMATES OF GRIZZLY DENSITY BASED ON TOTAL STUDY AREA (INTENSIVE PLUS EXTENSIVE PORTIONS), EASTERN MOUNT MCKINLEY NATIONAL PARK, ALASKA.

Year	No. Different Bears	Bears Per		Area Per Bear	
		km ²	mi ²	km ²	mi ²
1957	52	.026	.067	38.5	14.9
1958	66	.033	.085	30.5	11.8
1959	83	.041	.106	24.4	9.4
1973	76	.038	.097	26.3	10.3

TABLE 2 MINIMUM NUMBERS AND DENSITY OF GRIZZLY BEAR FAMILIES IN INTENSIVE STUDY AREA ONLY, MOUNT MCKINLEY NATIONAL PARK, 1957-1959 AND 1973.

	\bar{x}	Range	s^2	s.e. \bar{x}	C.V.
No. females with young	9.0	7-12	4.67	0.735	24.0
Density females with young/ km ²	0.01	0.008- 0.014	7×10^{-6}	0.026	26.3
No. young (total) with females	16.25	13-20	10.92	0.908	20.3
Density young (total) with females/km ²	0.019	0.015- 0.023	15×10^{-6}	0.031	20.3
No. females with cubs	3.75	3-5	0.917	0.489	25.5
Density females with cubs/ km ²	0.005	0.004- 0.006	9.1×10^{-7}	0.015	20.1
No. cubs with females	7.25	5-9	4.25	0.718	28.4
Density cubs with females/ km ²	0.008	0.006- 0.010	4.3×10^{-6}	0.023	25.0
No. females with yearlings	4.0	2-7	4.67	0.735	54.0
Density females with year- lings/km ²	0.005	0.002- 0.008	6.3×10^{-6}	0.025	52.6
No. yearlings with females	7.0	4-12	12.67	0.943	50.8
Density yearlings with females/km ²	0.008	0.005- 0.014	16.3×10^{-6}	0.0317	48.9
No. females with two-yr-olds	1.25	1-2	0.250	0.354	40.0
Density females with two-yr-olds/km ²	0.001	0.001- 0.002	2.5×10^{-7}	0.011	40.0
No. two-yr-olds with females	2.0	1-3	0.667	0.452	40.9
Density two-yr-olds with females/km ²	0.002	0.001- 0.004	15.8×10^{-7}	0.018	56.0

total area in a manner generally similar to the method used by Martinka (1974), the estimates for the characteristics presented in Table 2 are on the average about 36% higher than those based on a summation of the data from the two sub-areas; this average difference would be substantially lower but for the large difference in those estimates associated with yearlings.

As was mentioned earlier, a series of plots was censused during the summer of 1973. The plot on Sable Pass (20.7 km²), a notoriously good bear area, had the highest counts. Means based on five counts were as follows: \bar{x} no. bears/check = 6.57, \bar{x} no. families/check = 1.86, \bar{x} no. bears/km² = 0.32, \bar{x} no. families/km² = 0.09.

TABLE 3 AGE COMPOSITION AND STATUS OF ALL GRIZZLIES OBSERVED AND CONSIDERED DISTINCT, MOUNT MCKINLEY NATIONAL PARK, ALASKA (TOTAL STUDY AREA).

	Adults plus Two-Year or Older not with Sow											
	Cubs		Yearling		Two-Yr-Olds with Sow		Excluding Sows with Young		Including Sows with Young		Total	
	n	%	n	%	n	%	n	%	n	%	n	%
1957	13	25.0	7	13.5	4	7.7	15	28.8	28	53.8	52	
1958	20	30.3	6	9.1	1	1.5	24	36.4	39	59.1	66	
1959	8	9.6	17	20.5	3	3.6	39	47.0	55	66.3	83	
1973	15	19.7	12	15.8	7	9.2	23	30.3	42	55.3	76	
Mean Number & Weighted % of total	14.0	20.2	10.5	15.2	3.8	5.4	25.25	36.5	41.0	59.2	69.25	

Age and Sex Composition and Status

Table 3 presents crude average age composition data for all grizzlies observed in the total study area. The average proportion of cubs and yearlings was similar to the Glacier National Park population (Martinka 1974); the proportion of females with young was slightly lower in Mount McKinley National Park. Due to obvious problems with determining the sex of single adult bears, no attempt has been made to estimate the mature male fraction of the observed population. There is also a distinct possibility that mature males utilize somewhat different range than sows with cubs and are thus under-represented in the observed segment of the population.

At this point there is no possibility of deriving cohort-specific or horizontal life tables from the data; both the lack of multiple sequences and the effect of very small sample sizes preclude this.

Litter Size Relationships

Sixty-three litters were observed during the 4 years of intensive observations. The 4-year mean numbers of young per family at the time of observation was 1.81 for cubs, 1.83 for yearlings, and 1.67 for two-year-olds (4-year averages), suggesting very low mortality during the period of intensive maternal care, i.e. the first 18 months of life. Five litters were seen that each had three young. These McKinley data are well within the range reported by Mundy and Flook (1973) and Martinka (1974) and slightly lower than those in the heavily hunted population studied by Troyer and Hensel (1964).

Martinka (1974) suggested that mean litter sizes might be biased toward larger litters in some positive correlation with age of the young; he felt that larger young were more visible and consequently litters of older young would be more likely to be counted completely. This may be true when vegetation is dense and/or observation time is short, atypical conditions at McKinley. Apparent increases there in mean litter size with increasing age are almost certainly associated with small and rather variable samples and represent artifacts.

The mean proportion of cubs in the McKinley population can only be considered a very tentative estimate of crude birth rate in the absence of firm evidence of population level and age structure stability.

Mating

Grizzly males were observed in close association with females on numerous occasions, and in some cases the same pair was observed over an extended period of time. My seasonally earliest sighting of a pair, 30 May 1959, also involved attempted copulation. In 1959, one pair apparently remained together from 1 June until 12 July, with only one sighting out of eight involving the boar only. This boar maintained a triangular relationship from 28 June until 4 July; the original sow was not recognized after 12 July, and the boar was seen with the second female on 16 and 17 July. This second female was seen several times after that through early August but without the male; apparently either mating had occurred or she had become unreceptive about the third week of July. Other pairs were watched over periods of a few days to a week and a half.

Actual copulation, as determinable from a distance, was seen 16 June 1957 (N.J.Reid, pers. comm.; between 0800 and 0900), 26 June 1958 (seen from

aircraft, 0600), and 7 June 1959 (1331; undisturbed mounting lasted just over 20 minutes). Murie (1944) reports observations of copulation in McKinley Park on 20 May, 2 June, 10 June, and 18 June; he also reports pairs remaining together as long as 23 days.

DISCUSSION

Current Management Problems

The patterns and amount of human use of Mount McKinley National Park have changed drastically over the past 18 years. Prior to 1959, the only way to get a vehicle to the Park was to ship it on the Alaska Railroad. Perhaps three or four cars per day entered the Park and many visitors stayed several days or even several weeks. There was very little use of the country more than 2 km from the road. In 1959, the Denali Highway was connected to the Park road and traffic began a steady slow increase. Most visitors still arrived by train and the hotel at the railroad station at the east end of the Park has operated bus tours for many years, using up to four or more large buses depending on demand. The first summer with the new highway between Anchorage and Fairbanks open was 1972; the major portion of the traffic between those cities began to flow through the eastern end of the Park. Park visitation began to increase very rapidly. 'Back-country' use figures illustrate the general increase in visits to the Park and dramatically highlight the shift in use pattern. In 1972, there were approximately 4,500 person-nights spent in the 'back-country'; this figure jumped to over 12,000 in 1973. The potential for bear-human contacts is increasing rapidly as increasing numbers of visitors arrive and as a larger proportion of the visitors hike and camp off the road. Human injuries are increasing in frequency.

Hunting of grizzlies in the area surrounding the Park has been a rather long-standing practice. The area immediately east of the Park supports a resident population of grizzlies that can probably sustain regular hunting with a very low likelihood of significant effect on the Park's population. North of the Park the habitat appears less suitable for grizzlies, and there seems to be much lower probability that a substantial harvest can be supported without repeated recruitment from the protected population. The long narrow nature of the present Park makes the journey from the Alaska Range past the north boundary well within the range of possibility for a bear. The number of grizzly bears killed near the Park as recorded by the Alaska Department of Fish and Game are: 1969-9, 1970-9 and 1971-41. For the 3 years combined, the cumulative percent of the kill included in the above figures was: within 1.6 km of the Park boundary, 6.8%; 3.2 km, 30.2%; 6.4 km, 46.5%; 16 km, 57.6%; 32 km, 75%. We hope to determine the source of the animals being taken in this boundary strip and any effects that such hunting may have on the Park population. This is an area where the National Park Service and Alaska Department of Fish and Game may need to engage in cooperative management.

The third major management problem currently facing the managers of Mount McKinley National Park results from the Alaska Native Claims Settlement Act which provides for possible extensions of the boundaries of the Park. The National Park Service collected public reaction to the original proposals and presented a final impact statement late in 1974. One possibility is extending the boundary to the north to include areas considered by many to be critical winter range for moose, wolves and other Park animals. Some of these lands may be used by grizzlies during early spring and late fall. The potential

addition would certainly provide considerable buffering from hunting since the proposed boundary is 32 km north of the present one in the eastern half of the Park. The state of Alaska has selected land adjacent to the eastern one quarter of the north boundary and several cabin sites have been leased by private individuals. This area constitutes a major weakness in any attempt to contain the core of the Park's large mammal populations in the present or proposed boundaries.

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Conflicts between Man and Grizzly Bears in the National Parks of North America

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INTRODUCTION

Few Canadians or Americans have ever seen a grizzly bear (*Ursus arctos* L.). Far fewer have been injured by this massive, powerful and potentially dangerous carnivore. Despite a very low probability of injury the possible presence of the bear crowds most people's thoughts when travelling on foot or horseback through grizzly habitat. It does not matter if you fail to encounter a grizzly. A partial foot track set in mud showing claw marks well beyond the toes, or a massive scat full of partially digested huckleberries, is enough to make most backcountry travellers feel the presence of the bear. Where grizzlies exist, they set the mood for many backcountry excursions.

But in National Parks, the grizzly has had another major interaction with man. For example, in Yellowstone as recently as 1967, it was commonplace to be able to see as many as seventy grizzlies standing shoulder to shoulder, foraging amongst garbage at the Trout Creek Dump. In public campgrounds in Yellowstone, grizzlies gradually became accustomed to feed on man's garbage and food became highly dangerous nuisances. Here too people thought of and feared the grizzly, but in response they demanded better management to end the unfortunate mixture of garbage and bears. Similar situations have occurred in other national parks because the omnivorous feeding habits of the grizzly have brought him into contact with omnivorous man.

It is because the influence of the grizzly on the behaviour of human beings extends well beyond its few sightings and statistically insignificant attacks on man that study of conflicts with man is justified. I began this type of research by analyzing the causes and character of grizzly bear attacks on man in the National Parks of North America from 1872-1969 (Herrero 1970a; b). Since then further information has been collected mostly on a standardized form available to wildlife managers in National Parks having grizzly bear populations. In this paper I analyze these data for the period 1970-73 and compare them to my pre-1970 data and to analyses carried out by others. Martinka (1971; 1974) has made the most detailed analysis of grizzly bear and human interactions in a single national park.

ATTACKS- How many? Where? Preceding circumstances? What type of bear?

Table 1 shows that during the period 1970-73 there were 23 persons injured in 18 separate incidents which occurred in 5 of the 13 national parks in Canada and the United States which have grizzly bear populations. One person was injured in each of 13 incidents and 2 persons in each of 5 incidents. A single grizzly bear inflicted all of the injuries in each case, although frequently a female grizzly was accompanied by cubs prior to attack. Crude estimates of the frequency of injury are summarized in Table 1.

TABLE 1. GRIZZLY BEAR INCIDENTS AND INJURIES 1872-1969 AND 1970-73, SHOWING THE NATIONAL PARK IN WHICH THEY OCCURRED.

North American National Parks which have Grizzly Bear Populations	1970-1973		1872-1969	
	Number of Incidents	Injuries	Number of Incidents	Injuries
U. S. A.				
Yellowstone	4	5	45	45*
Glacier	0	0	10	14
Mt. McKinley	4	5	2	2
Grand Teton	0	0	0	0
Canada				
Banff	4	5	2	4
Jasper	4	5	4	8
Waterton	0	0	0	0
Yoho	0	0	2	3
Kootenay	0	0	0	0
Glacier -Revelstoke	2	3	1	1
Kluane	0	0	-	-
Nahanni	0	0	-	-
Totals	18	23†	66	77

* In 1970, when the first analysis was conducted, there were 18 more incidents resulting in 18 injuries listed as 'possibly' due to grizzly bears in Yellowstone. Cole (1972) referred to these 18 cases as 'probable' grizzly attacks. Cole (1974b), after further investigation, refers to these incidents as 12 probable and 6 known. All took place in developed areas and were preceded by camping; none have been included in my analysis.

† Includes 3 incidents and injuries not directly inflicted by grizzly bear.

Table 3 indicates that of the 23 persons injured 10 received major injury and 13 minor injury. Two deaths were included as major injuries, one death being inflicted by an adult female and the other by an adult male. Except for these two incidents the remainder of major injuries and most minor injuries were inflicted by female grizzlies with cubs.

Table 4 categorizes the injured person's activity prior to attack and the age/sex class of the bear involved in each injury. Females with cubs were responsible for a minimum of 74% of all the injuries inflicted during the 1970-73 period. In my analysis of injuries 1872-1969, this age/sex class of bear was responsible for a minimum of 48% of all injuries. This difference is statistically significant because the data describe the entire population of injuries and not a sample, but it is important to note that during 1872-1969 in 42%, or 32 of 77 incidents, the age/sex class of the bear was unknown. During 1970-73 the age/sex class of the bear was unknown in 13%, or 3 of 23 incidents. The 'unknown' age/sex class represent possible major sources of error which could significantly change the percentage of all incidents for which females

TABLE 2. CRUDE ESTIMATES OF THE FREQUENCY OF INJURY INFLICTED BY GRIZZLY BEARS*.

	Total Visitation (No. of visitors/injury)		Back Country Use (No. of backcountry man days/injury)
	1960-1969	1970-73	1970-73
Banff	17,170,465:1	2,019,753: 1	53,200: 1
Jasper	872,839:1	1, 176,714: 1	38, 175: 1
Waterton	4, 742, 100 : 0	2, 149,372:0	15, 187:0
Yoho	6,136, 125:0	4, 032, 260 : 0	78,700:0
Kootenay	6,571,778:0	4,972,459:0	25,050:0
Glacier/Revelstoke	12, 487, 444 : 1	2, 610,511: 1	2,620: 1
Yellowstone	510,000: 1	1, 745, 142 : 1	59,300: 1
Glacier(USA)	500, 000: 1	4, 403, 000 : 0	85,469:0
Mt. McKinley	131,750:1	153,340: 1	5,054: 1

*These figures are only crude estimates of frequency of injury. Data on total visitation in some parts includes persons driving through as well as persons stopping. Data from which backcountry man days were calculated are *very* tentative, especially for the Canadian Parks where errors could be in magnitudes of two or three. More precise data quantifying human use of grizzly bear habitat is needed.

TABLE 3. EXTENT AND NUMBER OF HUMAN INJURIES AND AGE/SEX CLASS OF GRIZZLY BEARS INVOLVED WITH THE INJURY 1970-1973.

Extent of Human Injury	Age/Sex Class of Grizzly Bear				Totals
	Female with cubs	Adult female	Adult male	Unknown	
No. of persons receiving major* injury-	8	1	1		10
No. of persons receiving minor † injury	9		1	3	13

*MAJOR injury included those injuries which resulted in greater than overnight hospitalization or death.

†MINOR injury included those injuries which resulted in overnight or less hospitalization.

TABLE 4. PERSON'S ACTIVITY PRECEDING ATTACK AND AGE/SEX CLASS OF GRIZZLY BEAR INVOLVED WITH THE INJURY.

Age/Sex Class of Grizzly Bear	Activity of Person				Provoking Bear	Total
	Hiking or Riding Back- Country Area	Camping				
		Backcountry Undeveloped Area	Developed Area			
Females with cubs						
Of year	5 ^R			2		7
Older		1				1
Age unknown or unstated	6	2 [†]			1	9
Total all females with cubs	(11)	(3)		(2)	(1)	(17)
Adult female (no cubs)				1		1
Adult male				1*	1	2
Unknown	3					3
Totals	14#	3		4		23

^R Two of the injuries were inflicted in one incident by a female with cubs of the year who had a history of garbage foraging.

Two of these persons were injured when thrown from horses.

[†] These two injuries were inflicted by a female with cubs in what appeared to be a sudden surprise incident in camp. The bears had no known or suspected history of garbage foraging.

*An old male grizzly tried to enter a cabin. A park employee was injured when he jumped through a window.

with cubs were responsible during each period. Despite this, the most probable explanation for the apparent increase in percentage of incidents attributed to females with cubs is that circumstances preceding attacks have changed quantitatively since 1872-1969 (Table 5). During 1970-73 a significantly larger percentage of incidents (61%) were preceded by backcountry hiking-riding than during 1872-1969 (31%) (Herrero 1970a). Conversely, during 1970-73 a significantly smaller percentage of incidents (30%) were preceded by camping as compared to 1872-1969 (61%). During 1872-1969, females with cubs were not found to be disproportionately involved in incidents preceded by camping in developed areas, although the data were incomplete. The percentage decrease in incidents preceded by camping generally reflects better garbage and food management in many of the national parks. Poor management of garbage and human food, especially in campgrounds and developed areas, were tentatively held responsible for 44 out of 47 incidents

TABLE 5. PERCENTAGE OF INJURIES DURING 1872-1969 AND 1970-1973 PRECEDED BY DIFFERENT ACTIVITIES

	1872-1969 %	1970-1973 %
Camping:		
Backcountry Undeveloped Area	5	13
Developed Area	56	17
Total	61	30
Hiking or Riding		
Backcountry Area	31	61
Provoking Bear		
	6	9
Other		
	1	-

preceded by camping during 1872-1969 and for 5 out of 7 such incidents 1970-73. In these areas grizzlies seemed to learn to associate food or garbage foraging with human odour and thus lost some of their avoidance behaviour toward man. After habitually foraging on food or garbage near people, some grizzlies became directly aggressive toward people while others attacked people after they were surprised at close range.

Females with cubs accounted for a much larger percentage of incidents preceded by backcountry hiking/riding (minimum 71%, 1872-1969; minimum 79%, 1970-73) than their typical percentage fraction (17%)* within a population would predict if all age/sex classes were equally likely to be involved in attacks preceded by backcountry hiking/riding.

In summary females with cubs account for most backcountry incidents preceded by hiking/riding. Additionally, the data available do not demonstrate that females with cubs are more likely to be involved in campground foraging incidents than is any other age/sex class. This information, therefore, tentatively accounts for the percentage change in incidents attributed to females with cubs—a minimum of 48%, 1872-1969, and a minimum of 74%, 1970-73.

It is also probable that females with cubs of the year are more dangerous to the backcountry hiking/rider than are females with older cubs. The 1970-73 data show that females with cubs of the year were positively identified as being responsible for five out of eleven backcountry-hiking/riding incidents attributed to grizzly bear females with cubs. In the remaining six incidents the age of the cubs was not determined or was not reported. I advance the hypothesis that, despite individual differences in aggression, there is overall a decrease in aggression by females as their cubs grow older. The hypothesis is tentatively supported by the data trend showing more injuries inflicted

*This figure was calculated using data for the Yellowstone population available in Craighead *et al.* 1969, and Craighead *et al.* 1974.

by females with cubs of the year than by females with older cubs. The data are crude, however. Pearson's (in press) detailed field observations on aggressive behaviour of grizzly bear females with cubs also suggest a decrease in aggression as cubs grow older. This hypothesis is also logically supported by the cubs' increasing ability with age to defend themselves. The evolution and expression of aggressive behaviour in grizzlies is discussed elsewhere (Herrero 1972).

As was found previously (Herrero 1970a; b), sudden surprise at close range was an important variable preceding backcountry-hiking/riding incidents (Tables 4 and 5) which involved females with cubs. In each of 11 injuries inflicted under these circumstances, the attacked did not sight the bear at a distance greater than 100 m (328 ft.). Often the distance was less than 30 m (89.5 ft.). Under these circumstances females with cubs appear to be acting almost reflexively in response to an intrusion into their 'individual distance', Martinka (1968) labelled this type of incident a 'defence reaction'. It is very important to realize that other age/sex classes of grizzly bears are seldom involved in this type of incident. Additional observations suggest that this behaviour is rare even for females with young cubs. They will usually flee in response to an intrusion if sufficient escape space and time are available.

Females with cubs were also involved in six injuries in which backcountry hiking/riding was not a preceding variable (Table 4). Of these, two injuries were inflicted in one incident by a female with cubs assumed (from the presence of fresh scats) to have been living in an area chosen as a backcountry campsite. In this incident the female with cubs apparently came upon two men in their sleeping bags without being aware that the men were there. There was no reason to suspect that this female was foraging for human food or garbage. Sudden surprise at close range was probably the important preceding circumstance. Of the remaining four injuries inflicted by females with cubs, three involved probable foraging for human food or garbage in camping areas, and one involved a photographer up a tree who made a squeaking noise like a rabbit to attract the female with cubs. The bear climbed 3.0-4.6 m (10-15 ft.) up the tree, pulled the man to the ground and inflicted major injury. This incident was classified as involving provocation.

The three incidents involving identified age/sex classes other than females with cubs were unique. They are important and merit detailed description because they resulted in one minor injury and two deaths, the sixth and seventh human fatalities inflicted by grizzly bear in the National Parks since 1872.

The sixth fatality occurred on June 25, 1972, at about one o'clock in the morning. Two young men returned to a technically illegal campsite in the Upper Geyser basin of Yellowstone National Park. In the dark they unexpectedly came upon an old female grizzly (the park's report estimated the age as about 20 years) who was foraging on their inadequately stored groceries. Both men ran and the bear charged, quickly catching and killing one man. Park's records show that the bear had been previously captured and transplanted from the Old Faithful developed area because of nuisance behaviour in 1970. After the attack the bear was killed and appeared reasonably healthy for an older bear. There were no parasites and the kidney fat index was normal. One possible indication of difficulty for the bear was that all canine teeth were broken and worn smooth to the level of the incisors. Several pieces of important data are disputed in this incident. A key issue is whether or not the abrupt closure of Yellowstone's dumps was a proper management strategy to restore and perpetuate natural grizzly populations. This issue has been debated in the literature (Cole 1972; 1974; Craighead and Craighead 1972; Craighead *et al.* 1974).

The National Academy of Sciences, U.S.A., has investigated this issue [National Academy of Sciences (NAS), 1974]. In brief the Craigheads have claimed that abrupt dump closure *increased* (at least for a period) the probability of injury in developed areas, and because of the large number of grizzlies killed, plus natural mortality to grizzlies, has given rise to a situation which, if it continues, will endanger the Yellowstone grizzly population. Conversely, Cole hypothesizes that abrupt dump closure *decreased* the cumulative probability of human injury because habitual campground foraging grizzlies were killed and young bears had less chance to learn this behaviour. Cole further claims that compensatory responses in the population have now restored the population to near carrying capacity. For the purposes of my present analysis the relevant data are clear—a very old bear with a history of some campground involvement killed and partially consumed a young man. My data suggest that very old grizzlies may be over-represented in aggressive encounters and attacks. I will discuss this later.

Sudden surprise of a grizzly bear on ungulate kills or carrion has been the cause of several aggressive encounters with grizzly bears in national parks. Outside national parks, hunters have been severely injured when returning to find cached game which, during the hunter's absence, has been claimed by a grizzly. Superficially the bear involved in the fatal Yellowstone incident behaved as if it were defending food. What is unknown is the extent to which the campground foraging history of the bear, or the abrupt phasing out and closure of dumps, influenced its behaviour.

The seventh fatality occurred in a backcountry area of Banff National Park and involved significant provocation of the bear and poor judgement on the part of the men involved. In late September 1973, a large adult male grizzly, with a well-documented history of numerous aggressive, garbage/human food foraging incidents, was being transplanted by helicopter. A Canadian Wildlife Service (C.W.S.) employee, a professional photographer and the helicopter pilot, accompanied the drugged bear to the transplant site. The C.W.S. employee and the photographer waited to photograph the bear as it came out of the drug. Photographing proceeded for several hours. Despite several clear signs of aggression, the two men continued to film and to move within 28 m (92 ft.) of the bear. The bear finally charged the men, both of whom ran. The bear caught and killed the C.W.S. employee despite attempts by the photographer throwing rocks to scare the bear away. The helicopter pilot flying his helicopter finally scared the bear off the body.

Bears recovering from the influence of drugs may behave strangely. John Craighead (pers. comm.) reported an instance where a female grizzly just recovering from drugging was charged and killed by an adult male. I interpret this to mean that the female's normal signal and defence system was altered, thus predisposing her death. These two incidents serve to suggest that drugged bears can be either dangerous to man or in danger themselves. Grizzlies under these circumstances should be regarded with utmost care.

The third incident involving an identified age/sex class of grizzly other than a female with cubs allows further comment on incidents involving very old bears. In Mt. McKinley National Park, near Wonder Lake Ranger Station, a grizzly 'in excess of 20 years' was involved in repeated break-ins into campers, garbage trucks and finally the ranger's cabin (Mt. McKinley National Park, pers. comm., 1975). At the cabin the bear seemed to be breaking down the front door so a park's employee jumped through the rear window, cutting himself on the broken glass. This is one of several incidents which suggest that very old bears may be particularly dangerous to man. The death and

partial devouring in Yellowstone in 1972 of a young man by a grizzly about 20 years old has been discussed. The August 1967 incident at Trout Lake in Glacier National Park, U.S.A., where a young girl was killed and partially devoured also involved an old female with worn canines and no cubs. This bear had aggressively sought food near humans many times before (Glacier National Park, 1967; Russell 1968). Generally, park wildlife managers often have unusual trouble with this age class. Martinka (1974) reported that 'selective disposal of five bears during 1968-69 involved sub-adult or old-age individuals in each instance'. Similarly in Waterton Lakes National Park, Canada, in October 1972, near Chief Mountain Customs station, a grizzly was reported to be 'obsessed' with breaking into every building nearby. The bear was killed and examination revealed worn teeth characteristic of an old bear. In an incident which occurred outside a National Park near Fort St. John, British Columbia, (Bryan and Jansson 1973), a guide was partially eaten, and presumably killed, by a very old grizzly.

Among the most bizarre of all aggressive encounters with grizzly bears was one which took place in the backcountry of Kluane National Park in August 1973, and involved a very old female accompanied by a 3-5 year-old sub-adult. Autopsy later showed the female to be 'thin' (79.5 kg, 175 lb), and 'in poor shape'. She had broken nasal bones and long claws indicative that she had not been digging very much. A park warden out on patrol first saw these two bears at 137 m (450 ft.). The female charged, followed by the sub-adult. The warden dodged and warded off attack with his rain slicker and a poncho. Ten to twenty charges were endured, each beginning from a distance of 1.5-9.1 m (3-30 ft.). During several charges the old female leaped completely off the ground and launched herself into the air toward the warden. Finally after the bear had grabbed and worried both slicker and poncho, the warden dropped his hat, which was also grabbed and flipped about. At this point the warden was able to separate himself from the bears. He later returned with a companion and they were tracked when the bears apparently got their scent and discovered their camp. While the bears were in the wardens' camp a shout and thrown rock triggered a charge. The bears were shot and later autopsied.

These incidents collectively, while often lacking precision of detail, strongly suggest the potential danger of some very old grizzlies to man. It appears that difficulties in securing adequate food to maintain a healthy body weight may increase foraging motivation so that human food or garbage may be aggressively sought. The possibility that some old grizzly bears under special circumstances may be potential predators of man is also suggested by the data. Bryan and Jansson (1973) report that Corbett in his studies of man-eating leopards and tigers in India found that the only animals which became man-eaters were those prevented from normal hunting by age or injury.

The data should not be interpreted as sanctioning the widespread disposal of very old grizzlies from national park populations. Old females can produce offspring (Craighead and Craighead 1972), and for this reason alone are valuable. The analysis does suggest that old-aged grizzlies may form a difficult management challenge and that specific individuals require careful evaluation if involved in aggressive incidents.

ADDITIONAL CIRCUMSTANCES RELATED TO ATTACKS

The data suggest that sleeping in the open without a tent may be particularly dangerous in grizzly bear habitat, but especially when garbage foraging griz-

zlies exist which are habituated to human odour. During 1872-1969, records show that nine persons were injured while in sleeping bags on the ground without a tent, whereas ten were injured in sleeping bags while in tents. From 1970-73, five of seven persons injured in incidents preceded by camping were in sleeping bags on the ground without tent or other protection. During the same period, no one was injured while in a tent. I do not know what percentage of persons camp without tents, though I suspect that it is only small compared with those who camp using tents. If this assumption is correct, then the data do suggest that 'sleeping under the stars' may increase the probability of injury as compared to using a tent. Martinka (1974) has recommended that in some areas protective sleeping accommodation might be considered.

I have found no records of persons in national parks who were on horseback prior to being directly injured by a grizzly bear. In two incidents which were included in my 1970-73 injury analysis, the persons were injured when thrown from a horse which was startled by aggressive behaviour from a grizzly bear. In these incidents the grizzly did not contact the person.

Making a noise to prevent sudden surprise of a grizzly, or climbing a tree if adequate time exists, are two frequently recommended techniques. These should not be inferred as giving absolute protection as the noise may be masked or the bear's attention focussed sharply on something such as feeding. Mature grizzlies do not commonly climb trees, but with strong motivation and proper spacing of limbs they can climb. During 1970-73, a party of two persons were both injured although they claimed to be making noise prior to attack. In another incident a grizzly climbed 3.0-4.6 m (10-15 ft.) into a tree and injured a man who had been provoking the bear. Grizzlies have previously been reported to climb trees above the level of their reach and then injure people (Herrero 1970a).

Data did not indicate that either menstruation or the use of cosmetics by women were related to any attacks as has been hypothesized (Glacier National Park, 1967). Because of the grizzly's acute sense of smell this hypothesis might merit experimental investigation.

INDIVIDUAL NATIONAL PARKS

Glacier National Park, U.S.A.

The most significant decline in grizzly bear inflicted injury rates from the 1960s to 1970-73 took place in Glacier National Park, U.S.A. (Table 2). Here the dramatic death of two girls in two separate incidents in 1967 sparked a very intensive management programme (Martinka 1968, 1971, 1974). Management actions there have included successful clean-up of garbage and other unnatural food sources both in developed and backcountry areas, an intensified research programme on both grizzly bear ecology and the grizzly's relationship to man, as well as management of human activities in certain backcountry areas. The latter point has included periodic trail closure in areas known to be frequented by female grizzlies with cubs or in areas where grizzlies seasonally congregate for food, or in areas where unnatural food sources attracted grizzlies. In Glacier in 1969-73, there were no grizzly-caused human injuries, despite an increase in number of visitors at a mean annual rate of 4.8 per cent. Also very important is the fact that few grizzlies were captured and transplanted or purposely killed by park personnel during the period, thus indicating that the causes of the grizzly problem were dealt with rather than the symptoms.

Yellowstone National Park, U.S.A.

Evaluating the situation in Yellowstone National Park is more difficult for reasons previously indicated. In Yellowstone the garbage management problem, especially in campgrounds, was far worse than in any other national park. The number of grizzly bear injuries inflicted in man during the 1960s and earlier reflected this (Table 2). Sanitation of campgrounds and successful bearproofing of sanitary landfill sites has improved the situation with regard to danger to the visitor although abrupt phasing out of dumps 1969-70 and abrupt closure of dumps 1970-71 may have temporarily increased the probability of human injury. Yellowstone still has several major campgrounds located in or near prime grizzly bear habitat and this will continue to create special management demands beyond those existing in Glacier National Park, U.S.A., where a comparable situation does not exist. Cole (1974) presents evidence that injuries to humans declined significantly in Yellowstone during 1970-73. He also argues that during this period the grizzly bear population suffered no serious decline despite removal of many grizzlies in management control actions. The Craigheads strongly dispute both points, arguing that after initial dump phase-out and closure the probability of human injury increased at least during 1968-71 (Craighead and Craighead 1972) and that the decline in numbers of grizzlies in the total Yellowstone ecosystem is serious (Craighead *et al.* 1974). The N.A.S. (1964) investigation of the grizzly in the Yellowstone ecosystem concluded that available data were inadequate to settle the controversy over whether or not abrupt closure of dumps increased the probability of human injury. They did conclude that there was no convincing evidence that the grizzly bears in the Yellowstone ecosystem were in immediate danger of extinction, although they reported that during 1968-1973 it was most probable that the grizzly population was reduced substantially. The question of current population status clearly requires further research. Compensatory responses with the Yellowstone grizzly bear population postulated by Cole to have occurred, and considered probable by the N.A.S. team, still require further documentation. Craighead *et al.* (1974) argue that compensatory responses to mortality known to take place in many mammalian populations may not occur within the Yellowstone grizzly population under its present condition. Consistent with this contention, field work done by Knight in 1974 found the average litter size for Yellowstone female grizzlies to be only 1.7 (J. Craighead, pers. comm.).

Banff and Glacier National Parks, Canada

The most serious increase in injury rates from the 1960s to 1970-73 took place in Banff and Glacier National Parks in Canada (Table 2). My understanding of injury data from these parks suggests different causes. In Glacier National Park, Canada, increased injury rates have reflected increases in park and backcountry use. Here there is no reason to suspect serious garbage or human food mismanagement. Rather, sudden surprise encounters at close range were the cause of all injuries. Glacier National Park, Canada, is experimenting with an interesting management strategy to decrease the probability of sudden encounters with grizzlies in backcountry areas. In grizzly habitat where trails pass through densely vegetated areas, and especially where fast-flowing streams create a masking sound, park wardens have made trail cuts up to 6.1 m (20 ft.) wide. The object is to allow hikers to see grizzly bears at a great enough distance to prevent sudden surprise. While such a technique may be effective in preventing injury it obviously should be a last resort after considering trail re-routing, periodic trail closure, and other environmentally and aesthetically less damaging techniques.

In Banff Park, Canada, increases in injury rates reflected both increased overall visitation and backcountry use as well as a continuing inability to solve serious garbage management problems, thus allowing grizzlies to forage unnaturally and become habituated to human odour. For instance in Banff Park 1970-73, four of five injuries were caused by grizzlies with known histories of garbage/camp-ground feeding. In one incident already mentioned, a Canadian Wildlife Service employee was killed. In this incident the man would never have been handling the bear if it had not been necessary to transplant it because of garbage feeding in a developed area. The remaining three garbage-influenced incidents were all probably inflicted by one female grizzly with three cubs of the year with a long and well-documented history of garbage problems in developed and backcountry areas. Two women suffered minor injury from this female grizzly in a brief attack near a backcountry lodge. In the other incident a man was very seriously injured by this same female with cubs when she attacked him while he lay in his sleeping bag at a backcountry campsite. He and his companion's food was properly stored well away from the campsite. This incident, though not fatal, is similar in character to an incident which resulted in death in Glacier Park, U.S.A., in 1967. In Banff National Park serious and immediate effort is needed to improve management, especially with regard to garbage. The extent of the problem is documented by the fact that during 1972-73, wardens in one district alone (District 2, Lake Louise) handled grizzlies 56 times in control incidents, purposely destroying nine and one dying accidentally. During this same period in Glacier Park, U.S.A., only one family of bears was handled in a control incident and one bear was purposely destroyed. Glacier has both a higher population density and greater total population of grizzly bears. There is some indication that the situation may be improving in Banff, since in 1974 only 4 grizzlies were handled in the Lake Louise district, although grizzly bear problems continued in other park areas including a sanitary landfill site near Banff. Detailed scientific assessment of both the grizzly bear population status and the management problems is required to give accurate answers regarding Banff National Park.

Jasper National Park, Canada and Mt. McKinley National Park, U.S.A.

In both Jasper and Mt. McKinley National Parks there was little change in frequency of injury when total visitation during the 1960s is compared to 1970-73 (Table 2). Both parks had 5 injuries during 1970-73. These relatively high numbers of injuries reflect amongst other things significant backcountry human use of grizzly bear habitat in both parks. In Mt. McKinley a garbage problem is not obvious but injury rates are amongst the highest in North America (Table 2). Better trail planning and management of human backcountry use is indicated for both parks. In Jasper in addition to backcountry human use of grizzly habitat there is also a garbage problem needing immediate attention. Here grizzlies occasionally forage in some campgrounds and during the study period they frequently got into the sanitary landfill (Retfalvi, pers. comm., 1973).

Kluane and Nahanni National Park

A challenge is faced in the new national parks having grizzly bear populations. In Kluane and Nahanni of Canada the cumulative knowledge of grizzly bear ecology, and encounters and incidents with man is being used in initial park planning to avoid problems present in established parks.

HOW TO AVOID ATTACKS

There are many ways to reduce to a minimum the small probability of being attacked by a grizzly bear and yet still hike and camp in national parks inhabited by grizzlies. The simplest way is to plan trips into areas where grizzlies are not found or are uncommon. Park Service personnel should be able to provide this information to persons not familiar with seasonal grizzly bear habitat.

If a party chooses to cohabit an area where grizzlies are found, then they and the park service have a joint responsibility. Park officials are responsible for managing and maintaining grizzly bear populations in as near a natural state as is possible. With regard to human safety this means little or no human food or garbage feeding sources. Past failure to control this variable has allowed grizzly bears to become habituated enough to man to forage in developed and backcountry campsites and has thus predisposed grizzly bear attacks on campers. Prompt action and constant surveillance by park officials is required to identify and clean up such areas: their temporary closure may be required while they are cleaned up (Martinka 1974). A special problem is present in areas of good fishing where grizzlies also exist. Both dead fish and fish remains can attract grizzly bears and create danger. Special fishing regulations regarding both the keeping and cleaning of fish may sometimes be needed.

Trapping and transplanting, or 'control kills', of garbage-addicted grizzly bears are inadequate and symptomatic treatment of the garbage and human food problem. Transplants serve to move highly dangerous and human-habituated garbage-feeding bears way from areas of high human concentration into areas of low human concentration. Return rates from most transplants are high. The 'biological success' of transplants has not been studied but is probably low. Bear proof garbage management can nearly eliminate the need for trapping, transplanting and 'control kills'.

Proper garbage and food management cannot stop at park boundaries in areas where acceptable grizzly bear habitat is located adjacent to but outside national parks. Grizzly bears are known to travel long distances in search of food or other needs (Craighead *et al.* 1974; Pearson, in press).

To provide further for human safety, park officials need to know the seasonal distribution of grizzly bears, particularly the approximate location of individual females with cubs. Temporary trail closure or public warnings may need to be employed, or mode of access may need to be regulated. Trail re-routing away from prime grizzly bear habitat may be desirable in some instances. Where re-routing is not practical wide trail cuts may be a partial solution in areas where surprise encounters might take place. Campgrounds located in grizzly bear habitat either require special management or they should be closed. Special grizzly bear preserve areas may be necessary in some cases, with the public seasonally excluded.

The average park visitor is unfamiliar with the characteristics of grizzly bears. Adequate information should be provided to the visitor to alert him to potential dangers. Specific information should be available from park service personnel regarding probable grizzly bear activity in a given area. Park visitors unfamiliar with the bears' habitat and characteristics should be encouraged to make enough noise to warn bears of their approach (Mundy and Flook 1973). Ideally visitors should also learn enough about the grizzly so that their appreciation of the bear outweighs their fear.

Park managers have a broad responsibility to the public for human safety in

grizzly habitat. A thorough scientific research programme is needed to provide information on the bear's ecology and population characteristic in each park. This information is needed by the manager, both to protect the public and also to provide for the long-term survival of the bear populations. Not all biological data collected on one population applies throughout the grizzly bears' range because different ecotypes exist, each adapted to their own local conditions.

Glacier National Park, U.S.A., is a good example of a park which has employed most of these research and management techniques and has as a result greatly decreased both human injury and also handling and control kills of grizzly bears. Their work is well documented (Martinka 1968, 1971, 1974).

The park service cannot, however, guarantee complete safety to the visitor, nor does it have total control over visitors. Visitors can be strongly encouraged to store food and garbage properly, but despite regulations it is their decision whether or not to leave a clean camp. Ironically, refuse left by one of several groups may predispose injury by grizzly bear of some future visitors.

In addition to following rules and suggestions presented by park managers, there are other things that the backcountry park visitor can do to avoid injury in grizzly habitat. Learning about their seasonal habitat preferences, behavioural traits, movement capabilities, food preferences, track and scat characteristics, can assist the visitor in knowing where and when grizzlies might be encountered. Dirty campsites and areas to which garbage bears have been transplanted should be avoided, as should areas of high seasonal natural bear activity.

Knowledge of the grizzly by the visitor, and thorough management activities by parks, can allow the visitor to avoid in most cases the two main causes of human injury—garbage-influenced grizzlies and sudden surprise of grizzlies, especially females with cubs, at close range.

CHARACTERISTICS OF AGGRESSIVE ENCOUNTERS WITH GRIZZLY BEARS. WHAT TO DO IF A GRIZZLY IS ENCOUNTERED OR IF A GRIZZLY ATTACKS.

There are no absolute formulas. The characteristics of individual bears vary as much as do the characteristics of individual people. Nevertheless grizzlies have species-specific patterns of behaviour which are fairly regular. Defense of and care of cubs by a female is a good example of this. The agonistic behaviour signal system is another good example. The grizzlies language of aggression and appeasement has been described by Stonorov and Stokes (1972).

I examined reports of fifty aggressive encounters between people and grizzly bears in North America's National Parks. These incidents did not result in human injury but involved a grizzly (or grizzlies) acting in what was perceived to be an aggressive manner. These data come from park records, written reports (especially Mundy and Flook 1973) and individual responses to my questionnaire. They are only a partial sample of all aggressive encounters. Table 6 categorizes the actions of people prior to the fifty grizzly bear encounters which I studied. These are the actions either before the bear was sighted or before it acted in what was perceived to be an aggressive manner. These actions do not appear to be very different from those which led to attacks in other cases. More revealing are the actions of both people and bear during an aggressive encounter. Single and multiple charges by the bear were common, sometimes to within very close distances such as 1.2-1.5 m (4 or 5 ft.). Grunting, woofing, snapping jaws and laboured breathing were sounds reported

TABLE 6. PERSON'S ACTIVITY PRECEDING AGGRESSIVE ENCOUNTER AND AGE/SEX CLASS OF GRIZZLY BEAR INVOLVED IN THE AGGRESSIVE ENCOUNTER.

Age/Sex Class of Grizzly Bear	Activity of Person					Total
	Hiking or Riding Backcountry Area	Camping or Residing			Driving Car	
		Backcountry Undeveloped Area	Developed Area	Other		
Female with cubs						
Of year	2					2
Older	6	3	2	1	2 ^R .	14
Age unknown or unstated	9		1	2		12
Total all females with cubs	(17)	(3)	(3)	(3)	(2)	(28)
Group	3		1			4
Adult						
Sex Unknown	3			1	1	5
Male	1 [#]				1*	2
Sub-Adult						
Sex unknown	3	1				4
Female					1 [†]	1
Unknown	5		1			6
Totals	32	4	5	4	5	50

* Large male grizzly which had been previously shot.

^R Female grizzly with older cubs charged a crew working on train tracks.

• What was assumed to be a female grizzly with a 3 year old cub chased 4 fisherman at a backcountry lake.

* Adult male grizzly aggressively approached a fish cleaning table and then a boy.

† A three year old female grizzly aggressively approached 3 fishermen at a backcountry lake.

TABLE 7. PERSON'S PREDOMINANT ACTION(S)
DURING AGGRESSIVE ENCOUNTER

Predominant Action	Number of Parties Doing Action
Stand still	6
Talk quietly	1
Shout, bang, clap, scream or growl	12
Run away	13
Walk slowly away	5
Climb tree	10
Slap or hit bear	1
Get into car	1
Fire shot	1
Total	50

in several instances. These sounds and close charges without contact are part of the normal species-specific agonistic display system of the grizzly. What is it then which turns a possible aggressive encounter into an actual attack? The characteristics of the individual bear which seem important are factors such as: has it a history of garbage feeding and habituation to human beings? is it a particularly reactive female with cubs of the year? has it previously been wounded outside the park? is it a very old bear with feeding difficulties? I have already hypothesized that most females with cubs of the year may be more dangerous than females with older cubs. In a given instance, characteristics of the individual bear will interact with the specific situation to produce flight, an aggressive encounter or an attack. Probably 95% of encounters are non-aggressive and result in the bear fleeing. This is an impression for which I do not have accurate data. How important are the actions of the person(s) involved in a confrontation? Certainly sudden surprise at close range should be avoided but if it is not, what then? Table 7 categorizes people's actions during the fifty aggressive encounters which I studied. Particular note should be taken that several behaviours not recommended in park's grizzly bear information pamphlets (Parks Canada, 1974) were common and did not in these instances lead to attacks. Twelve actions by persons involved shouting, screaming, banging, clapping or even growling. Thirteen actions involved running away. This documents that under certain circumstances, with certain bears, these actions by people do not necessarily lead to attack. Conversely my analysis of attacks during 1872-1969 revealed that 13 persons injured while hiking (54% of all persons were injured while hiking) were attacked while fleeing. Five were running away and eight were part way up a tree. I conclude that fleeing does not necessarily trigger an attack, although it certainly may. The documented ability of grizzlies to outrun human beings (Herrero 1970a) is an important variable in this context.

The commonly recommended course of action if actually charged by a grizzly

at close range is to stand one's ground or slowly withdraw while quietly talking to the bear. This action seems to be effective for those people calm enough to pursue it. I also tried to discover whether or not the dropping of an object, such as camera or pack, during the chase might help to distract a grizzly. In the reports which I examined approximately one out of two charging bears seemed to be distracted. Tree climbing was effective prevention if appropriate trees were available and the bear was spotted far enough away.

Clearly, no absolute recommendations can be made regarding human behaviour in close proximity to grizzly bears. Ultimately progress will be made as we begin to better understand grizzly bear behaviour in an evolutionary and ecological perspective. Why grizzly bears occasionally charge and sometimes attack human beings can be understood by knowing grizzly bear ethology. In incidents related to foraging for garbage or human food, specific grizzlies seem to have overcome a reluctance to associate with man and have become willing to forage aggressively near man in campsites. The danger comes either from this aggressive foraging or from sudden encounters with people while foraging. Occasionally it appears that a grizzly will 'explore' a person as a possible food source.

Sudden surprise of a grizzly at close range is the other major category of circumstances preceding encounters and attacks. My data demonstrate that for bears who have not become habituated to man through garbage feeding it is females with cubs which constitute the primary danger. They apparently charge in response to a perceived violation of their individual distance, i.e. they charge in response to a perceived threat. To alter this situation either a person needs to leave, i.e. retreat beyond the individual distance, or needs to allow the female and cubs opportunity to leave. Being sensitive to this situation can suggest different human actions in different specific situations. Age/sex classes of grizzlies other than females with cubs do charge people and will occasionally attack in response to sudden surprise, but these instances are very rare. For further understanding of grizzly bear behaviour the reader should consult Hornocker (1962); Stokes (1970); Stonorov and Stokes (1972); and Herrero (1972).

The final situation to be considered is that where actual attack occurs. What does analysis of actual attacks tell us concerning bear and human behaviour?

Grizzly bears, when attacking people, almost always do so from a position with the four legs on the ground. During 1970-73, only one attack took place while a bear was standing on its hind legs and only minor injury was inflicted to each of the two women involved. The hind-leg stance, however, often preceded attack, and appears to be a reaction whereby a bear is attempting to sense a situation through smell or sight. During attack both jaws and claws are used as weapons although in cases of death it is injuries inflicted by the jaws which are usually fatal. Cattle are also killed with the jaws (Murie 1948). Attacks are almost always of short duration, 30 seconds to several minutes, although in certain instances where major injury has been inflicted attacks have lasted in excess of ten minutes. In incidents preceded by backcountry hiking/riding and sudden surprise of non-garbage/human habituated bears the bear seems to have behaved as if it were responding to a threat. Generally, once the person (threat) is chased away or held still (playing dead, fainting), this category of attack ceases.

In 1970(a), I hypothesized that the extent of injury, once attacked, might in some cases be related to the behaviour of the person during the attack. I further suggested that incidents involving people attacked by garbage-influenced/man-habituated bears might be subject to different rules than incidents involving

non-garbage-influenced bears suddenly surprised at close range. I suggested then, and have further discussed in this paper, that the motivation of the bear was different in each instance. Table 8 presents data which relate to these questions. Here I attempted to analyze attack reports to see whether playing dead or fighting back increased or decreased the intensity of attack after it began. Because of the subjective interpretation necessary for these data, statistical analyses are not valid. The data do, however, suggest that playing dead may be a good strategy if involved in a sudden surprise incident while hiking. Further, in this type of incident, fighting back seemed to increase the intensity of attack. In a few cases the opposite effects were found, so once again absolute rules are not possible. In such sudden surprise hiking incidents the bears' attack was sometimes diverted from one person to another by shouting or running, with the person doing the action receiving the fresh attack. In incidents preceded by camping and involving garbage/man habituated bears, neither fighting back nor playing dead seemed to influence the intensity of attack. Here also the number of instances was small.

TABLE 8. NUMBER OF THE INCREASES OR DECREASES IN INTENSITY OF ATTACK PER PERSON ONCE CONTACT MADE, TABULATED AGAINST ACTION OF PERSON DURING ATTACK, AND CIRCUMSTANCES PRECEDING ATTACK.

	Play Dead or at Least not Resist		Fight Back, (Yell, Kick, Struggle, Knife)		Preceding Circumstances
	1872-1969	1970-1973	1872-1969	1970-1973	
	7	7	2	0	
Decrease	14		2		All incidents preceded by hiking*, or involving sudden surprise in camp of a presumably non-garbage -conditioned grizzly bear.
	1	1	3	4	
Increase	2		7		
	2	0	2	1	
Decrease	2		3		All incidents preceded by camping and all bears presumably garbage-conditioned.
	0	1	3	0	
Increase	1		3		

*In incidents preceded by hiking the bear's attack was sometimes diverted from person to person by shouting or running, with the person doing the action receiving the fresh attack.

LEGAL IMPLICATIONS OF GRIZZLY BEAR ATTACKS

In some cases the question of blame for a grizzly bear attack becomes a legal one. Several persons have attempted to sue and prove negligence on the part of

park managers who are ultimately the Canadian and United States government. Few cases have come to trial and only in one instance have the courts supported the claimants. A 1974 decision in the United States awarded approximately \$87,000 to the estate of the man killed in Yellowstone during 1972. As better information is developed concerning the proper management of grizzly bear populations for human safety (as well as for human enjoyment and local grizzly bear population survival) the issue of liability will become increasingly more clearly defined. This should force the management of every park population of grizzly bears to be of the highest known standards.

THE BIOLOGY OF REMNANT POPULATIONS AND REGIONAL PLANNING IMPLICATIONS

In North America, all National Parks have the statutory obligation to preserve natural ecosystems. The long-term fulfilment of this mandate will be particularly difficult with regard to grizzly bears in several national parks. At one time the grizzly's range in North America was large (Storer and Tevis 1955; Haynes and Haynes 1966; Macpherson 1965; N.A.S. 1974). Today in the contiguous United States and in southern Canada the grizzly exists in remnant populations. The question of what is a minimum population size for grizzlies for their survival is a complex one. Part of the answer depends upon the number of years into the future one wishes to have a high probability that grizzlies will survive in a given park or other area. Diamond's (1972) data on extinction rates in tropical ecosystems can tentatively be interpreted to suggest that, other things being equal, the smaller the population of any species the greater the probability of extinction over time. For species like the grizzly, national parks essentially become island refuges with gene flow to other populations prevented. If we are forced to choose and can only allow certain populations to survive, then the biology of remnant populations tells us to choose the largest populations in the largest areas.

In a genetically isolated remnant population of European brown bear (*U. a. marsicano*), which Franco Zunino and I studied in central Italy, the population was estimated to have numbered only 70-100 (Zunino and Herrero 1972). In a population of this size we can expect in any one year about 5-7 adult females with their cubs of the year. Unusual natural death in this population segment coupled with deaths inflicted by man could in one bad year seriously endanger this population. If further the population is fragmented and its habitat altered, the swing to extinction could be rapid.

Are any of the North American National Park populations endangered? Craighead *et al.* (1974) present evidence that, if present trends continue, this will be the case for the Yellowstone population. Good quality population data are not available for any southern Canadian national park population; however, I believe that three populations require careful study to document their characteristics and to generate long-term planning for protection: these exist in Waterton, Glacier and Revelstoke, and Banff, Yoho and Kootenay National Parks. Waterton is a small park (525 km² = 203 sq. mi.), intensively used. Surrounding land is significantly utilized for cattle grazing and resource extraction. On the British Columbia border of the park a proposed road over the Akamina Pass could remove potentially valuable habitat, cause conflict with human users, and further fragment the population. A hopeful condition exists where the southern border of Waterton Park is continuous with Glacier Park, U.S.A.

A similar problem exists in Glacier and Revelstoke National Parks. Here small

park size, Glacier 1349 km² (521 sq. mi.) and Revelstoke 259 km² (100 sq. mi.), means small park grizzly bear populations, estimated to be 74 grizzly bears for the larger and more densely populated Glacier (Mundy and Flook 1973; Hamer 1974a). The two parks are surrounded largely by B. C. provincial lands. Historically the grizzly has been heavily hunted in these areas as well as being killed when in conflict with men logging, mining or farming (Hamer 1974a; b). In Banff, Yoho and Kootenay, similar conflicts exist in surrounding British Columbia and Alberta Provincial Lands. In parts of Banff Park, population declines have been tentatively attributed to hunting in surrounding British Columbia Provincial Lands (Noble 1972). The situation, no doubt, exists elsewhere but has not been studied. There is, however, evidence that both provinces, British Columbia and Alberta, are well aware of the potential impact of hunting on grizzlies and that their management plans reflect this. Further concern is necessary in Banff, where control kills and stress induced by translocation are high. In addition Banff may soon see development of a new visitor service centre at Lake Louise, very near grizzly habitat. A very large (tentative permanent service population of up to 3700 persons) proposed development was withdrawn only after extreme protest (Herrero 1970c; Omstead *et al.* 1972).

Clearly the potential impact of all proposed developments within these parks must be carefully evaluated with regard to influence on grizzly bear populations. This cannot be done until proper scientific data exist regarding grizzly bear population characteristics and overall ecology. Often we have managed dynamic ecosystems as if they were static. From this view, development might be justified in closed coniferous forest. This habitat type is usually not important for grizzly bear feeding habitat. But if the forest is burned, successional stages can be very productive of food for the grizzly. Martinka (1973) reported a major grizzly bear concentration on huckleberries (*Vaccinium* spp.) in one area forty-four years after a burn. In addition to careful impact assessment for all developments, regional wildlife management plans should be developed with surrounding provincial and municipal jurisdictions. The best example of this regional management approach is in the Yellowstone ecosystem, where coordinated research and management exists for a 69, 930 km² (27, 000 sq. mi.) area, having the 8, 806 km² (3, 400 sq. mi.) of Yellowstone as its core (National Park Service, 1973). This integrated research and management unit is clearly valuable and necessary, but its initial success has been questioned (N. A. S. 1974). If rapid progress is not made in the direction of regional research and management in Canada, several grizzly bear populations could be lost within the 50-year future.

THE GRIZZLY BEAR IN THE MIND OF MAN

Scientific data on grizzly bear ecology and on the interactions between man and grizzly are necessary for management programmes. However, these data are not sufficient to ensure the future of the grizzly in the various North American national parks where it is found. For survival the grizzly needs to become a valued resource to a significant percentage of North Americans. The challenge is to reach, educate, and relate grizzly bears to, the average North American whose life is normally far removed from them. There is hope. For those who appreciate the grizzly it is one of the finest living components and symbols of natural ecosystems. Because it requires large tracts of relatively undisturbed land for survival it is a type of wilderness indicator species where it is found. Monitoring the status of grizzly bears and maintaining their population status usually ensures the integrity of many other ecosystem components (Herrero *et al.* in press).

Ecologically the grizzly bear usually has minor influences. The ecosystem effects of grizzly bears are greatest in the infrequent situation where they function as significant predators, especially if other more specialized predators such as wolves are absent or reduced in numbers. Such a situation exists periodically in Yellowstone Park where Cole (1972) believes that grizzlies through predation help to dampen elk population fluctuations by culling vulnerable animals. The grizzly in this specific circumstance could also influence local elk evolution because predation becomes a selection factor. Further, Cole demonstrated how a grizzly population, through predation and scavenging upon elk, could influence secondary consumers such as coyotes. The same types of relationships would exist where grizzly predation upon salmon is significant (Shuman 1950; Gard 1971). More typically, however, the omnivorous food habits of the grizzly mean that its energy intake sources overlap with many other species. It functions as a browser, grazer, scavenger and predator. Remove a grizzly population from an area and there is no ecosystem collapse. But the grizzly does demonstrate what spectacular beings biological evolution can produce to fill an open niche. The grizzly is a massive and powerful statement of the evolutionary history of circumpolar northern environments. The grizzly symbolizes the power, dynamism and productivity of the ice ages. Grizzly bears are a well-tuned way of capturing and utilizing a broad range of available energy. But the omnivorous grizzly ultimately competes with omnivorous man, and human beings through their technology have what our primitive ancestors lacked—the power to exterminate the grizzly.

We should preserve grizzly bear populations, not because their ecological function is critical, but because of what they can do for human imagination, thought and experience. York Edwards (1970) describes two similar mountains, one which has lost its grizzlies and the other which still has them. On the mountain with the great bears there is suspense, caution, more of the unknown—in a word, mystery. The other mountain, having lost its grizzlies is tamer and somehow depauperate.

Travelling through grizzly country can provide human visitors with a rare opportunity to establish relationships with the natural world. Fernandez (1972) discusses the manner by which human experience with animals was essential for definition of the self in aboriginal human beings. We still have the genotype of our ancestors. Travel in grizzly country can help us to define, understand and appreciate ourselves through appropriate responses to this species which shared Pleistocene evolution with man. In grizzly habitat caution, care and occasional fear and awe, are key elements. These are significant components of the wilderness experience and are elements for which our own genetic heritage is preadapted. But a wilderness experience cannot be had with a grizzly bear tamed and warped by garbage feeding.

I have discussed what the grizzly bear in national parks can become to fortunate and understanding visitors. It should be clear that this is the hopeful and biased opinion of one who appreciates grizzlies.

Public opinion concerning grizzlies is another important source to consider. Mahalic (1974) did a detailed study of the attitudes toward grizzlies of 158 visitors to Glacier National Park, U. S. A. Approximately 65% of all persons surveyed had positive attitudes, 20% were neutral and 15% had negative attitudes. Mahalic had little success in understanding the genesis of their attitudes. An attitude survey done by the Christian Science Monitor of its readers (Cahn 1968), just after two girls were killed by grizzlies in 1967 in Glacier National Park, U. S. A., revealed that only 104 out of 3420 persons (3%) favoured elimination of grizzlies from national parks. Bryan and Jansson (1973) surveyed human

attitudes toward grizzlies, and knowledge about grizzlies, in three Canadian communities in Alberta: they concluded that substantial inaccuracies exist with regard to people's understanding of grizzly bear behaviour, but that improvements in understanding are correlated with familiarity or contact with wildlife. They also predicted that increased injuries would create strong public pressure to destroy potentially dangerous wildlife species such as the grizzly. At least one scientist (Moment 1968, 1969, 1970) has called for the elimination of grizzly bears from the national parks of North America.

Also relevant are the views of those individuals who have actually been injured by grizzly bears in the national parks. Some opinion has been against the grizzly. 'They shouldn't be allowed to exist anywhere near civilization' and 'I can see no reason why grizzlies should be preserved in the national parks' or 'guns should be carried so that aggressive grizzlies can be shot'. But even amongst the group of individuals actually injured by grizzlies the majority of opinions favour the bear. 'We are in complete agreement concerning the preservation of the grizzly' was one comment. 'There is no reason in the name of civilized progress to kill an animal for doing what is natural. I feel no malice toward the bear.' This statement came from a man seriously mauled by a female with cubs.

What influences these different perceptions of the grizzly? How can the grizzly bear become more of a valued resource and less of a liability to North Americans? The formation of our perceptions seems to be imbedded in our lifestyle, education system and attitudes toward nature.

The grizzly bear is worth the strong focus and disproportionate interest which I have suggested, because of its unique place in the mind of man. It alone is the 'beast which walks like a man'. It is similar in some ways to man, yet awesomely more physically powerful and clearly more at home in natural environments. In learning to share some of our national parks with the grizzly we can begin to rediscover and redefine our place in nature.

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SUMMARY

During the period 1970-73, twenty-three persons were injured by grizzly bears in the national parks of North America. Persons were hiking or riding in backcountry prior to 14 (61%) injuries; were camping in backcountry prior to 3 (13%) injuries, and were camping in a developed area prior to 4 (17%) injuries. Two (9%) injuries were preceded by provocation of the attacking bear.

Female bears with cubs were the most dangerous age/sex class of grizzly and responsible for a minimum of 17 (74.9%) of all injuries. Most injuries involved sudden surprise of the female at close range.

Very old grizzlies were another age class disproportionately involved in incidents with man. Careful monitoring is recommended for difficult bears from this age segment.

Examination of the current management programme in Glacier National Park, U. S. A., suggests that management strategies exist which can both encourage the long-term survival of free-ranging grizzly populations and also provide park visitors with a high degree of safety regarding females with cubs, as well as other age/sex classes.

Ways of avoiding attack by grizzly bear point to a joint responsibility of park managers and park visitors. Circumstances which preceded aggressive encounters which did not result in human injury are discussed. In the event of actual attack, especially after sudden surprise of a female with cubs, data suggest that playing dead can help to decrease the intensity of attack.

Garbage and human food disposal continues to be a problem, though in most parks the situation was improved. Grizzlies who forage on human food or garbage in close proximity to people become habituated to man and also more dangerous to visitors.

The effectiveness of management programmes is assessed with respect to human safety and grizzly bear preservation for relevant North American national parks. Human safety is being adequately provided for in many and the remaining problem areas which can be made safer by improved management are identified. However, several park grizzly bear populations appear to be headed for elimination during the next 50 years unless effective regional management plans are adopted soon.

The grizzly bear is worth disproportionate study emphasis compared to other animal species in national parks because it uniquely stimulates human imagination and thought, and can help man relate meaningfully to his own genetic heritage and to natural environments. The grizzly is a wilderness indicator species whose protection encourages survival of many other species and their wild habitat.

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Ecological Role and Management of Grizzly Bears in Glacier National Park, Montana

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INTRODUCTION

Colonization of western North America by modern man led to significant reduction in numbers and distribution of grizzly bears, *Ursus arctos*, during the past 150 years (Storer & Trevis 1955). Response has been classically evident south of Canada where widespread population declines and local extinctions have occurred. Viable populations have persisted only in more expansive wilderness and park areas of Montana and Wyoming where remoteness and land use characteristics contribute to their protection. National parks provide unique refugia where the natural integrity of grizzly bears can be preserved as an ecosystem component by mitigating detrimental effects of modern man.

This paper summarizes current knowledge relating to the ecological role and management of grizzly bears in Glacier National Park, Montana. The park is administered as a natural area within which grizzlies require a spectrum of management considerations. These may be broadly categorized as environmental requirements and relationships to park visitors. Field studies of population biology and ecosystem relationships provide criteria for interpretation of environmental requirements within park ecosystems (Martinka 1972; 1974a). Evaluations of management programs contribute to an understanding of relationships between grizzlies and park visitors (Martinka 1971; 1974b).

HISTORICAL PERSPECTIVE

Evaluation of species evolution permits a more complete understanding of current status since adaptive development can frequently be correlated with changing environments. These changes may occur within established geographic ranges or result from emigration to new areas. In the case of grizzly bears, physical and behavioral adaptations associated with speciation resulted in potentially efficient utilization of a variety of habitats. In contrast, ability to cope with certain associated fauna may have been less pronounced. Current status and relationships in North America reflect a number of traits which developed during the evolutionary process.

Paleontological records suggest that the grizzly bear differentiated from the Etruscan bear, *Ursus etruscus*, in Asia during the middle Pleistocene (Thenius 1959; Kurten 1968; Herrero 1972). Speciation occurred during a time when climatic fluctuations caused periodically extensive glaciation in northern continental areas. Extensive replacement of forests with treeless tundra and steppe accompanied cold phases and glacial maxima (Giterman & Golubeva 1967). Adaptation to the presence of these treeless habitats appears to have been a key element associated with genetic separation of the grizzly from its forestdwelling ancestor (Herrero 1972).

Formation of land bridges during glacial maxima provided opportunities for faunal interchange between Asia and North America. Dispersals were pre-

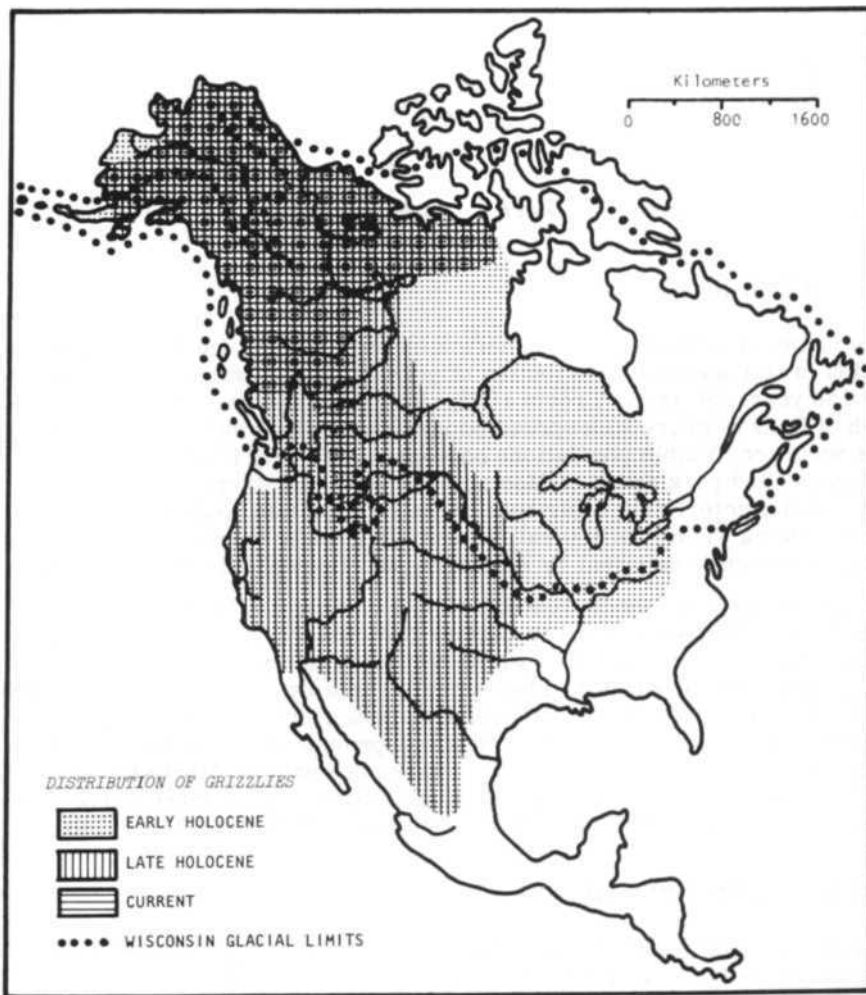


Fig. 1. Postglacial distribution of grizzly bears in North America.

dominantly eastward and generally included species adapted to forest environments during the early and middle Pleistocene (Repenning 1967). Steppe and tundra forms dominated late dispersals and it appears that grizzlies did not successfully colonize Alaska until the Wisconsin glacial period (Herrero 1972). Continued range expansion was temporarily restricted at that point by the merged Cordilleran and Laurentide ice sheets.

Recession of the continental ice sheets opened extensive areas of suitable habitat for grizzly bears in North America (Figure 1). Distribution expanded eastward to Ontario (Peterson 1965), Ohio and Kentucky (Guilday 1968), and southward into Mexico (Storer & Trevis 1955). Distributional recession apparently followed eastward expansion in response to development of unfavourable environmental conditions (Guilday 1968). Populations were present throughout most of western North America during the eighteenth century (Storer & Trevis 1955), but the rapidity of local extinctions suggests that many of these were also of marginal status.

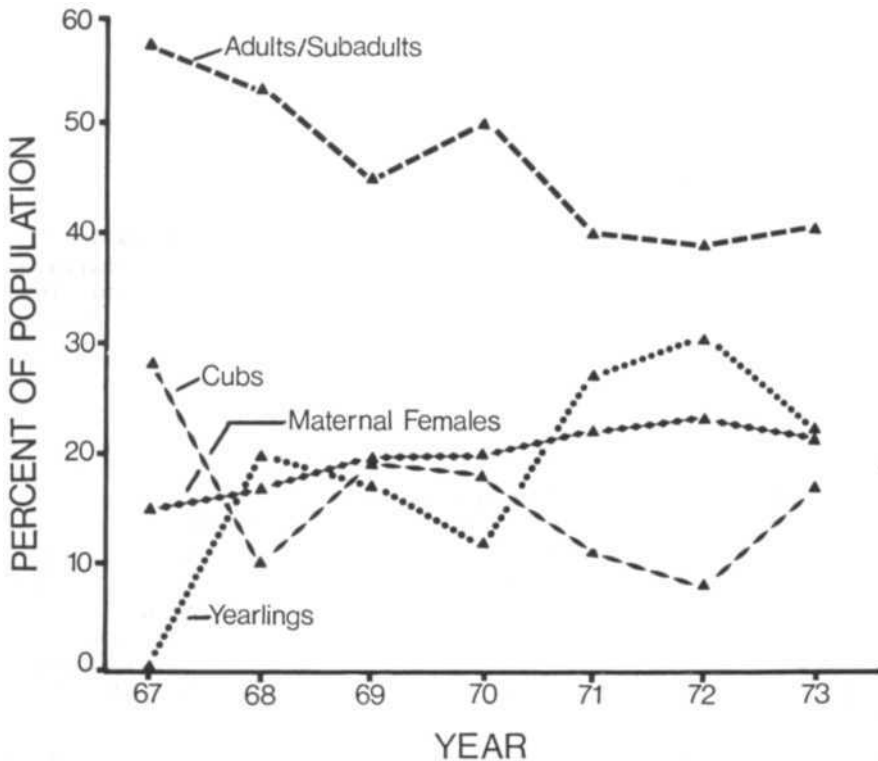


Fig. 2. Composition of the grizzly bear population in Glacier National Park as determined from annual classification of different bears from 1967 through 1973.

Present distribution of grizzlies is largely restricted to the more secure mountain habitats of northwestern North America (Figure 1). It seems likely that postglacial occupancy progressed from midcontinental habitats as mountain glaciers receded and food sources developed. Mosaics of forest, grasslands, and alpine tundra provided a productive habitat for grizzlies but also reintroduced potential competition with black bears, *Ursus americanus*. This closely related species had dispersed to North America during an earlier period and was well adapted to forest environments.

Primitive man and grizzly bears apparently occupied North America in a biologically neutral relationship. In contrast, relatively recent emigration of modern man to North America added a significant dimension to the postglacial history of the grizzly. Protection of human life, depredation control, sport hunting and habitat deterioration were focal points which contributed to population declines. These pressures continue to the present but public expressions have recently added a protective phase to the history of grizzly bears.

Significant developments in the relationship between modern man and grizzly bears are reflected in the history of Glacier National Park. Grizzlies were encountered and shot when railroad survey parties first entered the area in the mid 1800s (Stevens 1860; Pumpelley 1918). Faunal richness attracted sport hunters during the late 1800s (Schultz 1962) and by 1900 commercial trapping of the bears for hides was a common activity (Bailey & Bailey 1918). These

activities undoubtedly influenced grizzly populations until establishment of the park in 1910 provided protection. Limited control continued thereafter but of insufficient magnitude to prevent restoration of a natural grizzly bear population (Martinka 1971; 1974a).

POPULATION STATUS

Glacier is presently inhabited by a wild grizzly bear population which ranges throughout the park under essentially natural conditions. Population estimates determined from density samples ranged from 175-230 and averaged 191 for 7 years of study from 1967-73. Annual fluctuations resulted from deficiencies in the census technique but general trends suggest that population levels were relatively stable. Regulation of numbers is thought to occur naturally through social interaction and associated dispersal and/or death of subordinate bears. Aging of hunter-killed bears and depredation controls beyond the park's periphery provide tentative support for this hypothesis (Greer 1971; 1972; 1974).

The population is characteristically structured as single individuals and family groups (Martinka 1974a). Annual classifications of different bears observed showed means of 46, 20, 16 and 18 percent unclassified adults, productive females, cubs, and yearlings, respectively (Figure 2). Trends toward increasing proportions of maternal females and their offspring correlated with decreasing proportions of unclassified adults observed during the study. Substantial fluctuations occurred in annual production of cubs but combined proportions of cubs and yearlings exhibited a trend similar to that of maternal females.

The mean increment of 16 percent cubs contributed approximately 31 potentially new members to the population each year. Realized recruitment appeared contrastingly low in view of stable population trends and apparent longevity of adult bears (Greer 1971; 1972; 1974; Mundy & Flook 1973). Recruitment probably relates to a replacement function involving displacement and/or mortality of established population members. Surplus subadults likely succumbed to mortality through social interactions, emigrated to vacant habitats, or both.

An average density of 4.6 grizzlies per 100 km² was computed from the mean population estimate of 191 bears. Exclusion of offspring provides a basis for estimating a potential breeding density of 2.9 bears per 100 km². The presence of sexually immature subadults could reasonably reduce effective breeding densities to 2.5 bears per 100 km². This low density requires compensatory movement patterns to assure adequate gene flow and prevent the potential influence of genetic drift on isolated population segments (Wilson & Bossert 1971). The complexity of these patterns is suggested by Craighead & Craighead (1965), Martinka (1970), Mundy & Flook (1973), Murie (1944, 1961) and Pearson (1972).

ECOLOGICAL NICHE

Glacier National Park encompasses 4100 km² of cordilleran terrain in northwestern Montana. Glaciation has created rugged topography which is extensively occupied by coniferous forests at lower elevations and alpine tundra above the timberline. Wildfire and snowslides provide habitat diversity within coniferous forests by maintaining seral shrub and conifer communities. Local

influences of soil and wind on certain sites have contributed to the formation of grasslands. Combinations of terrain and vegetation provide an interspersed array of habitats for the grizzly bear population.

Each of the major habitats was utilized by grizzlies during the May through October period of activity. Frequent use was made of coniferous forests but a distinct preference was apparent for treeless types. Grasslands and tundra provided relatively permanent open habitats while wildfire and snowslides created favorable types within the coniferous forest zone. Movements to higher elevation shrub and alpine habitats occurred during the snowfree summer and early fall season. Bears were most consistently observed in areas of maximum habitat diversity.

Seasonal progression in habitat use was accompanied by a predictable sequence in the predominantly herbivorous diet. Spring and early summer preferences included grasses, Gramineae, horsetail, *Equisetum* spp., and cowparsnip, *Heracleum lanatum*. Ripening fruits of huckleberry, *Vaccinium* spp., supplemented with serviceberry, *Amelanchier* spp., mountain ash, *Sorbus scopulina*, and hawthorne, *Crataegus* spp., formed the bulk of late summer and fall diets. Predation, scavenging, and digging occasionally added variety in the form of mammals, roots and insects.

Food habits reveal that the grizzly is well adapted to efficient utilization of postglacial mountain habitats. An obvious preference for certain herbaceous foods displaced potential use of numerous alternative items which were also present. Food abundance and distribution undoubtedly influence densities to some extent. For example, ample foods have apparently permitted development of a high density potential by coastal populations in Alaska (Troyer & Hensel 1964). Contrasting conditions existed on historic steppe and tundra habitats where herbaceous foods were widely scattered or in limited supply. Foraging by predation, scavenging and digging most likely evolved under these conditions. The population in Glacier seems to be regulated at a point somewhat below the biomass carrying capacity of the habitat.

Seasonally high densities of grizzlies are occasionally observed in Glacier. An area of particular interest includes 22 km² of high elevation seral shrub habitat on the Apgar Mountains which was created by a wildfire in 1929. The relatively dependable huckleberry crops produced on the area each year attract bears when fruit production fails in surrounding habitats. Combined aerial and ground observations in 1967 and 1973 revealed that late summer densities reached as high as 1.3 grizzlies per km² under these conditions (Table 1). Spacing was distinct among the social units present with one agonistic interaction recorded involving an adult chasing a subadult. High concentrations continued for several weeks but the temporary, unpredictable and local nature of the phenomenon reduced potential as a significant influence on overall population levels.

A late summer concentration of black bears also occurred on the Apgar Mountains. The magnitude of observed densities was inversely related to numbers of grizzlies present (Table 2). A low density of grizzlies in 1967 apparently permitted foraging by numerous black bears in spaced distribution. In contrast, a high density of grizzlies in 1973 nearly precluded use by black bears. Those observed were in distinct association with forest edges or isolated stands.

The significance of forest canopies to the evolution of both species has been discussed by Herrero (1972). Highly developed arboreal capabilities by black bears apparently contribute to competitive superiority in forest habitats.

TABLE 1. DENSITY ESTIMATES FOR GRIZZLY BEARS ON A 22 KM² AREA OF THE APGAR MOUNTAINS DURING LATE SUMMER AS DETERMINED FROM COMBINED EVALUATION OF AERIAL AND GROUND SIGHTINGS OF DIFFERENT BEARS IN 1967 AND 1973.

Year	Type of Sightings				Total Number of Different Grizzlies	Bears per Square Kilometer
	Aerial 1/		Ground 2/			
	Adults	Young	Adults	Young		
1967	7	2	1	2	12	0.5
1973	5	7	9	7	28	1.3

1/ One hour helicopter survey plus routine sightings during management flights.

2/ Associated primarily with fire surveillance and/or suppression activities.

TABLE 2. GRIZZLY AND BLACK BEARS OBSERVED DURING 1 HOUR HELICOPTER FLIGHTS IN A 22 KM² AREA OF APGAR MOUNTAINS DURING SEPTEMBER OF 1967 AND 1973.

Year	Number of Different Bears Observed	
	Grizzlies	Black Bears
1967	9	16
1973	20	6

Aggressiveness and extended maternal care provide competitive advantages for grizzlies in open habitats. Interspecies relationships have apparently evolved to a point of mutual avoidance where spacing is maintained. This system permits overlap in habitat use and is an important consideration in determining population levels of both species.

MANAGEMENT OF GRIZZLIES

Current management is directed toward the dual objectives of park visitor protection and maintenance of a natural grizzly bear population. Field management procedures include a visitor information program, control of attractive unnatural foods, opportunity for visitor travel restrictions, and removal of persistently troublesome bears. Annual program evaluation considers number of conflicts and management actions relative to trends in visitation. Results for 1968 through 1973 are presented in Table 3.

Progressive increases in park visitation through 1973 were accompanied by generally low encounter rates between bears and visitors. Those which occurred were predominantly aggressive displays or equipment damages. Increased contacts during 1972 and 1973 correlated with rapid expansion of backcountry use by hikers and campers. Management response through temporary travel restrictions apparently mitigated the potential for human in-

TABLE 3. SUMMARY OF VISITATION, GRIZZLY BEAR CONFRONTATIONS WITH VISITORS, AND MANAGEMENT ACTIONS IN GLACIER NATIONAL PARK, 1968 THROUGH 1973.

Year	Annual Visitation		Grizzly Bear Confrontations		Management Action		
	Total 1/	Overnight Visits 2/ Campgrounds and Hotels	Belligerent Encounter	Personal Injuries	Visitor Restrictions	Transplant	Disposal
1968	936,000	366,000	5	1	6	0	2
1969	1,023,000	337,000	2	0	5	0	3
1970	1,034,000	328,000	0	0	1	1	0
1971	1,081,000	328,000	3	0	7	1	0
1972	1,114,000	326,000	12	0	9	1	0
1973	1,174,000	337,000	7	0	9	0	1

1/ Total visitors passing through gates one or more times, adjusted to exclude those on transient access route.

2/ Visits defined as one visitor for one day in each category.

3/ Includes two chalets.

juries. In addition, bear control was maintained at a biologically acceptable rate for a natural area.

Mutual avoidance appears to be a key element in current relationships between grizzly bears and park visitors. Management design and characteristic shyness of bears are the principal factors contributing to an essentially compatible coexistence. Effects of the relationship on visitors are measurable in terms of imposed changes in activity patterns and travel distributions. Response by grizzlies is more difficult to document but observations suggest that population dynamics and ecosystem role remain nearly unaltered from pristine conditions.

Projections of management needs characteristically identify additional control of human activities as a primary goal (Martinka 1974b). However, it is becoming increasingly apparent that certain ecological phenomena may also require consideration. The potential significance of wildfire seems particularly important as demonstrated by its ability to cause extensive structural and compositional change in park habitats. Temporary reduction or elimination of forest canopies appears to create superior habitat for the grizzly. In contrast, successional advance toward mature forests creates conditions more favorable for black bears. The latter trend has been enhanced by a wildfire suppression policy which continues to the present. Restoration of wildfire to its natural ecosystem role is considered essential to maintaining a natural grizzly bear population within the park.

A wild, free-ranging population of grizzly bears has been shown to present the least conflict with visitors in Glacier National Park (Martinka 1971). Prudent application of facts to management planning is required to assure continued low conflict rates and protect the natural integrity of the bear population.

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Paper 14

Attitudes and Opinions of Persons Experiencing Property Damage and/or Injury by Black Bears in the Great Smoky Mountains National Park'

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INTRODUCTION

As indicated by Stebler (1970), all North American bear species are powerful and dangerous. They are behaviorally little studied, and hence are dangerously 'unpredictable'. It is generally agreed, however, that of the two species which come in contact with man in our national parks, the grizzly bear, *Ursus arctos*, is more dangerous than the black bear, *Ursus americanus*. Statistics indicate that some kind of provocation by man induces a bear to attack. For the grizzly bear the provocations take the form of various human activities (Herrero 1970), whereas for the black bear personal injury or property damage are typically induced primarily by an attraction to human food. Although not nearly as temperamental as the grizzly bear nor as apt to cause serious injury or death, the black bear, because of its greater numbers in association with people in several national parks, accounts for the highest percentage of the injuries and property damage. For example, in the Great Smoky Mountains National Park (GSMNP) a total of 251 incidents involving black bears occurred during the period 1970-1973, for an average of 63 incidents per year. The number of incidents per park visitor during this period was one incident per 119, 000 visitors. In addition, one personal injury resulted per 1, 030, 000 visitors. The estimated cost of property damage for the 1970-1973 period was \$10, 634 or an average of \$2658 per year (National Park Service Records, 1974).

As a solution to the grizzly problem one author advocates extirpation from national parks (Moment 1970). We think most rational scientists and lay people would agree that such drastic measures are not necessary for the black bear (or, in our opinion, the grizzly either). Both Jonkel (1970) and Stokes (1970) emphasized the need to carry out further research on the behavior and ecology of both bears and people where the two interact. We would also emphasize that ultimately the solution to bear-human interactions lies with man and the alteration of his behavior and attitudes through education. One step toward solving the problem is to first determine the present attitudes and opinions of park visitors about bears (Burghardt *et al.* 1972). It would seem especially appropriate to also evaluate the attitudes of visitors who were actually involved in a bear incident. Sometimes these people have irrational and emotional thoughts about what should be done about bears in

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national parks at the time of the incident, in an attempt to vindicate themselves and 'solve their problems'. In retrospect, what are their feelings?

By surveying this group we felt we could be reaching a unique segment of park visitors. Management policies and procedures should not be based on nor tempered by the 'emotions of the moment'; guidelines should be rational, well-planned and carried out in a standardized fashion. A retrospective survey might reveal whether the bad experience of a visitor with bears has been educational and whether the attitudes and opinions of these persons represent an extreme viewpoint in regard to bear management in national parks.

METHODS

A total of 231 names of Park visitors experiencing property damage and/or personal injury between 1968 and 1973 were obtained from records in the GSMNP. A 35-item questionnaire was mailed to these persons. The questions consisted of demographic information, general information on the kind of use visitors made of the Park, attitudes toward bears and their place in the Park, and personal experiences with bears. Most of the questions were identical to those used by Burghardt *et al.* (1972). A cover letter was mailed with each questionnaire explaining the purpose of the study. A stamped return envelope was also enclosed.

RESULTS AND DISCUSSION

Of the 231 questionnaires mailed, 119, or 52 percent, were returned. Sixteen were personal injury responses and 103 were property damage responses. Forty (17 percent) questionnaires were returned by the postal service because of incorrect addresses. Seventy-two (31 percent) of the questionnaires were unaccounted for. Of the questionnaires presumably received by the addressee, 62 percent were returned. Since this is primarily a preliminary survey based on a small sample size, statistical hypotheses are not tested. Sufficient detail is given to allow such calculations by interested readers.

Demographic Characteristics of Respondents

In regard to age, 43 percent of the respondents were age 30 and under. From ages 31 to 50 there is a relatively even distribution, and then a decline in the number of respondents greater than age 50 (Table 1A). There was a greater percentage of male respondents (89 percent) than female respondents (12). However, the questionnaire stated that the head of the household should answer the questions, which thus accounts for this difference. The modal and median family size was four persons (Table 1B).

The greatest percentage category of respondents (24 percent) had completed secondary school of 12 years of education. Over 60 percent of the respondents had completed some education beyond secondary school, and 39 percent of the total number of respondents had completed four years of college or more (Table 1C). Thus, the education level is higher than that found for park visitors as a whole (Burghardt *et al.* 1972).

As mentioned by Burghardt *et al.* (1970), classification of respondents into occupational groups proved to be difficult. Instead of attempting to group

TABLE 1. DEMOGRAPHIC CHARACTERISTICS OF RESPONDENTS (percent)

A. Age								
<26	26-30	31-35	36-40	41-45	46-50	51-55	56-60	Unknown
21.0	21.8	10.1	10.1	10.9	9.2	7.6	4.2	2.4
B. Number in Family								
1	2	3	4	5	6	7	8	Unknown
12.6	16.0	16.8	24.4	15.1	6.7	2.5	3.5	2.4
C. Highest Year of Education Completed								
<5	6-8	9-11	12	13-15	16	17-18	>18	Unknown
0.8	2.5	7.6	24.4	21.8	18.5	14.3	5.9	4.2
D. Occupation								
Military	Unskilled	Low level white collar		Skilled	Housewife	Student		
3.4	4.2	9.2		28.6	3.4	9.2		
Teacher (Sub-college)	High level white collar, executive	Professional	Retired	Unknown				
5.9	12.6	9.2	2.5	11.8				
E. Population of Area of Residence								
< 1,000	1,001–5,000	5,001–20,000	20,001–50,000	50,001–100,000	100,001–500,000			
4.2	10.1	16.8	19.3	10.9	20.2			
500,000–1,000,000	>1,000,000	Unknown						
5.0	8.4	5.0						

certain responses with only limited information, these were classified as unknown (Table 1D).

Rural areas or communities of less than 1000 persons accounted for only 4 percent of the respondents' home communities. Home communities of over 500,000 persons were given by 13 percent of the respondents (Table 1E).

Fifty-seven percent of respondents came from communities of less than 100,000 population. These persons may have a greater opportunity for association with wildlife but likewise may know only enough to make them reckless.

Results of the demographic information do not exhibit many differences from the results of the visitor survey conducted by Burghardt *et al.* (1972). Where differences do exist, they can likely be explained by the approaches used in surveying (e.g. face to face interview versus a mail survey). For instance the 'typical' respondent in this survey was male, less than 30 years old, and a college graduate. The high proportion of male responses (89%) was explained earlier, however; the relatively younger age (43% vs. 26% less than 30 years old) and higher education level (39% vs. 22% completed four years of college) of our respondents, as compared to Burghardt's, may be reflecting a greater interest in and understanding of our survey on the part of the college-educated group. Of the 31 percent of the questionnaires that were unaccounted for, the proportions of respondents who never received the questionnaire or who simply do not respond to mail surveys or who had such an unfortunate experience with bears they refused to answer, will remain unknown. Of major concern to us is the third of the groups just mentioned. However, they may actually be over-represented in that the questionnaire gives them the opportunity to vent their opinions and frustrations.

Of the 16 injury respondents, 12 were injured along the main trans-mountain road through the Park. The other four were in sleeping bags camped outside trail shelters on the Appalachian Trail. Attitudes of the injury group did not differ from the property damage group.

General Information on Park Use by the Respondent

Ten categories were listed in the questionnaire regarding the main reasons visitors came to the Park. The majority came to camp and sightsee, but 42 and 24 percent, respectively, states that one of their main purposes was to observe animals and bears (Table 2).

Sixty percent of the respondents stated that they spent more than ten days/year camping. At the time of their bear incident 84 percent of the respondents were staying overnight in the Park. Tents were utilized by 50 percent of all respondents, while 13 percent used some type of tent camper. Most persons (93 percent) had food with them while in the Park, and 54 percent of these people stored food inside a vehicle other than a tent camper. Over 14 percent of the respondents stated that they stored food in a tent or some kind of camping vehicle (Table 3). Most of the respondents (53%) camped in tents or under less cover and in large campgrounds amidst mobile campers and tent campers.

Over two-thirds of the respondents (68%) stated that they received information concerning possible problems with bears (Table 4A) and almost 38 percent attended Park naturalists' talks, which is one way such information is disseminated (Table 4B). In addition, almost three-quarters of the subjects said that they had visited the Sugarlands Visitor Center, where information concerning bears is readily available (Table 4C). From specific write-ups of incidents, however, it was obvious that most bear victims did not listen, read or heed recommendations, or else misunderstood the material that was provided. Perhaps information to visitors about bears should be more specific and better illustrated.

Numerous respondents stored their food inside their vehicle (54%). However some left windows partly down, exposed food, did not utilize trunk space, or drove a station wagon without trunk space. Also, the mixture of mobile campers and tent campers in similar areas may increase the chances of damage to tent campers because of less precautions taken by mobile campers in regard

TABLE 2. PURPOSES IN VISITING THE PARK (percent)

Camp	Hike	Sightsee	Observe Animals	Fish	Rest, relax	Observe bears	Picnic	Passing through	Other
89.1	65.6	74.8	42.0	18.5	67.3	24.4	22.7	8.4	9.2

TABLE 3. CAMPING EXPERIENCE (percent)

A Days/year Spent Camping										
0	2	3	4	5	6	7	10	>10	Unknown	
3.4	1.7	1.7	2.5	4.2	2.5	3.4	10.1	59.7	10.1	
B. Stay Overnight in the Park?										
Yes										
No										
84.0	15.1									
C. Type of Shelter Used										
Tent	Tent camper	Trailer	Trail shelter	Sleeping bag	Makeshift	Mobile camper	Unknown			
50.4	12.6	7.6	7.6	0.8	1.7	5.9	9.3			
D. Where Food was Stored										
Inside vehicle	Inside tent or camper	In special storage area	In a trail shelter	Other						Unknown
53.8	14.3	3.4	6.7	20.2	1.7					

TABLE 4. USE OF PARK INFORMATION BY VISITORS (percent)

A. Receive Information Concerning Possible Problems with Bears?			
	Yes	No	Unknown
	68.1	30.3	3.4
B. Attendance at Park Naturalist Talks?			
	Yes	No	Unknown
	37.8	60.5	1.7
C. Visit the Sugarlands Visitor Center?			
	Yes	No	Unknown
	72.3	26.1	1.7

to cooking and the presence of better storage facilities for their food. Although car trunks offer good storage for car campers and stringing food on a rope between trees high off the ground is usually good practice for back-country campers, examples of bears getting at both were presented by respondents. A bold, persistent bear can be a formidable opponent to an inexperienced or unwary visitor. Also, many visitors underestimate the abilities of a bear. Concentrations of large numbers of people in relatively confined areas will continue to attract bears and create problems unless food and food refuse is handled properly. Recent attempts at dispersing backpackers from the Appalachian Trail has resulted in establishment of some 100 primitive campsites in the Park. With backpacker use of the Park increasing to over 80,000 in 1973, increased use of some primitive sites may result in increased numbers of incidents at these locations in the future.

Although a higher percentage of visitors indicated they came to camp and sightsee than to observe animals or bears, we wonder how significant a role the presence of a free-roaming bear population plays as a subconscious attractant to visitors. Certainly commercial interests outside the Park have taken advantage of the traditional 'Smoky Mountain Bear' cliché and symbolism are in evidence everywhere: billboards, motel and restaurant names, wood carvings, statues, ceramics, paintings, etc. The black bear is present and used in sundry forms and formats by private enterprise outside the Park.

The fact that 93 percent of the respondents had food with them helps substantiate the fact that incidents with black bears are usually food-related. The 8 percent who indicated they had no food may have been victims of the bears' keen ability to associate certain food-type containers with food, whether they were empty or not. In the case of injury, they may have been innocent bystanders among a group of visitors feeding a bear. Also, some of the respondents may have been trying to give us answers they thought we wanted to have; this is particularly true for questions related to food, where food was stored, etc.

It is apparent from the answers to questions on Park information that most respondents came in contact with the precautionary information being disseminated by the Park about bears. But observations of roadside bears indicate that the urge of visitors to feed bears is very strong, almost appearing

instinctive. However, the anthropomorphic appearance of bears along with exposure from childhood to teddy bears, Gentle Ben, Goldilocks, Smoky Bear, Yogi Bear and pandas likely counters the information and warnings regarding the strength and wildness of bears, especially in relation to bear feeding and food exposure. This means that the educational process must go much deeper than the NPS is responsible for or presently capable of handling; the NPS alone cannot be expected to completely reorient a visitor's thinking during his brief stay in the Park.

Knowledge and Attitudes Concerning Bears

It is interesting to note that a higher percentage of the respondents in this survey (93%) than in the survey by Burghardt *et al.* (1972) (77%) felt that black bears would not make good pets. Perhaps this is an indication that the respondent's incident was truly a learning experience and that the possibly preconceived concept that bears are friendly, gentle or harmless was altered.

Table 5 summarizes three questions asked during both surveys. In regard to what bear behavior is considered to be troublesome, the responses are dif-

TABLE 5. RESPONSES TO QUESTIONS REGARDING BLACK BEARS BY PARK VISITORS INTERVIEWED ORALLY (BURGHARDT *et al.* 1972) AND VISITORS RECEIVING PROPERTY DAMAGE OF INJURY INTERVIEWED BY MAIL, 1973.

Question	Percent responding	
	Systematic visitor Interview (500 responses)	Injury-Property Damage Interview (119 responses)
What bear behavior is troublesome:		
Just being around	3.8	8.2
Coming too close	23.6	29.4
Taking food from where stored	17.6	56.5
Blocking traffic	2.2	9.4
Raiding garbage cans	3.8	22.4
Other—	58.6	29.5
What to do with troublesome bears:		
Remove to other areas of Park	51.2	60.5
Zoo or cage	19.0	2.5
Do nothing	7.6	5.9
Destroy	15.8	4.2
Remove to outside Park	6.0	17.6
Special feeding areas	0.8	19.4
Other —	7.0	16.8
Rules concerning visitors and bears:		
Left as are	66.4	30.6
Left to visitor	3.6	3.5
More strictly enforced	26.0	63.9
Other —	3.0	4.7

ferent in only two major categories. A much higher percentage of our respondents felt that bears taking food from where it was stored and raiding garbage cans (57 and 22% respectively) was troublesome in contrast to the responses to the survey by Burghardt *et al.* (1972) (18 and 4% respectively). This contrasting response probably reflects the altered attitudes of those actually involved in an incident over food.

In regard to what to do with troublesome bears, a majority of both groups agreed that they should be removed to other areas in the Park. However, it is interesting to note that a higher percentage of the respondents to the survey by Burghardt *et al.* (1972) favored destruction or removal to a zoo or cage versus a higher percentage of our respondents favoring removal to areas outside the Park or creation of special feeding areas. In choosing to leave the bears in a wild, free-roaming situation rather than destroying or putting in a cage, one could possibly infer that our respondents' incidents with bears may be reflecting their realization that what they are dealing with is truly a wild animal not necessarily responsible for its actions toward man. Recent exposure to a number of wildlife trapping and removal operations on television may have also influenced the respondents' replies to this question.

In regard to attitudes about rules concerning visitors and bears, there is an interesting inverse relationship. On the one hand 66 percent of the respondents to the survey by Burghardt *et al.* (1972) felt that Park rules about bears should be left as they are versus 31 percent in our survey; only 26 percent of the respondents to the survey by Burghardt felt rules should be more strictly enforced whereas 64 percent of our respondents felt this way. Again, this likely reflects the relatively recent experience of the respondent with bears and the realization that rules regarding them serve a purpose. Moment (1970) felt that the NPS was not strict enough in enforcing regulations about grizzly bears and LaFollette (1974) points out the same problem with black bears in the GSMNP. It appears that those involved in an incident also agree. However, in an area like the GSMNP, how can a very limited professional staff of rangers efficiently handle over 7 million visitors a year when bear problems are only a very small part of the overall responsibilities? Again, the ultimate answer is public education.

Suggestions offered by respondents to solve bear problems were varied. Some included:

1. 'Enforce No Feeding Rules'
2. 'Fence in campgrounds'
3. 'Nothing'
4. 'Provide special feeding areas'
5. 'Provide some kind of insurance to cover damage'
6. 'Stiffer penalties for visitors caught feeding bears'
7. 'Require campers to use air-tight food containers'
8. 'Hang bags of moth balls around as a deterrent'
9. 'Better coverage of campgrounds by rangers'
10. 'Mandatory lecture prior to issuing a camping permit'
11. 'Don't eat after dark'
12. 'Get rid of the bears'

13. 'Keep people from treating bears as a plaything'
14. 'Remove constant offenders (bears) from park'
15. 'Close down the campgrounds for one year and hope the bears forget garbage cans and people as a source of food'
16. 'Provide food storage areas'
17. 'Make it harder for bears and humans to make contact; if someone really wants to see a bear let them go look for one'

Many of these suggestions are either presently unworkable, (e.g. 7, 9, 10, 16), ineffective (e.g. 8, 11), or contrary to the purpose of National Parks (e.g. 2, 4, 12, 15). Some, of course, may be good ideas but are not original (e.g. 1, 6, 10, 13,14,17).

Many of the answers were unclear as to who was at fault in the incident with bears. Therefore, we categorized the respondents as being at fault *only* when they themselves stated clearly they were guilty. Even with this very conservative approach, 42 percent of the respondents fully and openly admitted they were at fault in regard to their incident with a bear. Considering the respondents' rather recent bad experience with bears, it was desirable to know if these people felt that bears posed a serious problem to Park visitors. A majority (64%) felt that black bears did not pose a serious problem, whereas 31 percent felt they did pose a problem. However, when asked whether bears should be allowed in the Park, only one person felt that they should not. In fact, many of the respondents 'reacted' to this question and regarded it as ridiculous, explaining why they felt the bear had as much right to be there as visitors. Bears were mentioned by only 7 percent of the respondents when asked what they like least about the GSMNP; most (27%) listed crowded conditions as being what they liked least. In addition, 91 percent of the respondents stated that they had already returned or planned to return to the Park in the near future.

It seems appropriate to close with a summary of some of the comments of the respondents:

'It is the most beautiful place I know and I always feel physically and spiritually renewed. It belongs to the bears and we are the intruders.'

Injured respondent—"This is their home. If people would read signs and believe them, they would not get hurt.'

'It would be a terrible thing to diminish the population of the black bears in parks due to the ignorance of man.'

'The troublesome bears are no one's fault but the campers!'

'The danger of bears becomes a threat only through ignorance or foolishness of Park visitors.'

'Tourist attitude toward bears often reflects over-exposure to Walt Disney.'

'They were there first; we are the intruders.'

'Some people have never seen a live bear in their natural surroundings.'

'It is a people problem rather than a bear problem.'

'Black bears are not a problem by themselves; people make them a problem.'

'I think it (the Park) is the most beautiful and most unique area in the East. I presume it is the only part where we can see bears. I know bears are unpredictable. They can appear tame and playful yet are capable of anything; they are deceptively quick and awesomely strong.'

'Of course they should be allowed in the Park—they live there!'

'People cause most of the problems with bears by not respecting their rights.'

'Man is the intruder, as usual.'

Injured respondent—'I don't think it would be right to punish a bear for being curious.'

'It is his (bear's) home too!'

Injured respondent—'The bear could hardly be blamed for using his instincts.'

'Their privacy should be respected as well as left alone.'

'We feel that the bears are an essential part of the pleasure of the mountains. Where else can we observe nature without bars and cages?'

'It just wouldn't have been the same without them. Leave them alone.'

'Inconsiderate, troublesome and disrespectful tourists are the main problem.'

'We must be cognizant of the fact that we are invading their territory and are subject to their rules.'

'The Smokies have much to offer to individuals like myself and that includes *BEARS!*'

'Leave them alone. That's the beauty of the wilderness.'

'I would rather forfeit a meal or two than have the bears removed from the Park.'

'The damage we sustained was slight and well deserved.'

'I came to the Smokies to see them and I enjoy every one I see.'

'We do not want to see the bears taken out of the Parks. We enjoy them.'

'They are part of what the Park was established to preserve!'

'Because little children are raised with the thought that bears are cuddly, when they encounter the real thing, they and unthinking parents don't give them the respect due a wild animal. People often don't realize that this huge, strong animal doesn't have the ability to reason.'

Injured respondent—'People have to remember they are wild animals and not house pets.'

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Paper 15

Characteristics and Management of Black Bears that Feed in Garbage Dumps, Campgrounds or Residential Areas

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INTRODUCTION

Many black bears, *Ursus americanus*, in northern Michigan habitually supplement their natural summer diets by feeding in garbage dumps, campgrounds or residential areas. In the past, many of these bears were destroyed as nuisances. To minimize such waste, the Michigan Department of Natural Resources began capturing nuisance bears and releasing them away from areas of human habitation. In conjunction with this program, we estimated the age and recorded the weight, sex and breeding condition of each captured bear in an attempt to learn the sex ratio, age structure, growth rate and fecundity of wild black bears that supplement their diets with garbage. This paper reports and discusses our findings.

METHODS

Data were collected from 126 bears captured between 20 June and 5 September 1968. Forty-two animals were taken with a Cap-chur gun at dumps, and 67 were box-trapped in campgrounds or residential areas. Seventeen cubs that accompanied captured bears were treed and netted. Each animal was immobilized with succinylcholine chloride and anesthetized with pentobarbital sodium as described by Rogers *et al.* (1975).

All bears were sexed, ear-tagged and weighed. A first premolar was extracted from each animal for estimation of age from annuli in the cementum (Stoneberg and Jonkel 1966; Sauer *et al.* 1966; Craighead *et al.* 1970). Tooth sections of inferior quality were prepared from teeth from seven of the study animals; hence, ages of these bears were estimated on the basis of body

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weight, breeding condition and tooth wear features as reported by Stickley (1957), Erickson *et al.* (1964) and Marks and Erickson (1966).

A reference collection of stained first premolar sections from 25 wild black bears captured in Minnesota facilitated interpretation of cementum annuli in study specimens. Teeth in the reference collection were taken from 6 known-age animals 1.5 or 2.5 years old and from 19 older specimens from which premolars had been extracted in successive years to permit determination of annual cementum deposition.

The weights of bears from dumps versus campgrounds or residences were compared where sample sizes of bears of comparable age and sex permitted. Because weight gains by black bears are known to be rapid during summer months (Black 1958; Jonkel and Cowan 1971), comparisons were made only between sex-age groups for which average dates of capture differed by less than a week.

RESULTS AND DISCUSSION

Sex Ratio and Mortality

The sex ratio of the 126 bears captured (85 males: 41 females, 67% males) was significantly ($P < .01$) unbalanced toward males according to analysis using Chi-square (Table 1). Several other workers have reported that the proportion of males at sources of garbage is higher than that found elsewhere (Black 1958; Erickson *et al.* 1964; Rogers 1970). This is partially explained by the fact that males range more widely than females (Erickson *et al.* 1964; Jonkel and Cowan 1971; Poelker and Hartwell 1973) and are more likely to encounter sources of garbage. Additionally Erickson *et al.* (1964) suggested that social factors may influence the sex ratio and age structure at such feeding areas.

The percentage of males was significantly ($P < .05$) higher among bears (excluding cubs) captured at garbage dumps (81% males, $N = 42$) than among those captured at campgrounds or residences (61% males, $N = 67$). Garbage was more abundant in dumps than in campgrounds or residential areas, and widely ranging males familiar with several sources of garbage may have concentrated their feeding where they found the most food.

At all sources of garbage, sex ratios changed markedly with age. The sex ratio among cubs did not differ significantly from a 1 : 1 ratio (59% males, $N = 17$), but the sex ratio among bears 1 through 7 years of age (76% males, $N = 93$) was significantly ($P < .01$) unbalanced toward males. Conversely, females predominated ($P < .05$) among the relatively few bears 8 years of age or older (25% males, $N = 16$), especially among those captured in campgrounds or residential areas (17% males, $N = 12$) (Tables 2 and 3). The reduced percentage of males among older bears probably reflects differential mortality between the sexes from gunshot. Gunshot is a major cause of mortality among bears that feed on garbage, and widely ranging males apparently find and use sources of garbage more often than do the more sedentary females. Bear-hunting pressure during autumn is intense near garbage dumps and campgrounds that attract bears. Additionally, 83 bears were killed as nuisances during the year of this study according to records of the Michigan Department of Natural Resources. Rausch (1961) stated that 'Careless shooting is no doubt the primary cause of injury in bears, at least in populated areas'. The number of deaths from intraspecific fighting is unknown; however, no such deaths of adult black bears have been documented.

TABLE 1. SEX RATIOS AND AGE STRUCTURE OF BLACK BEARS CAPTURED IN GARBAGE DUMPS, CAMP-GROUNDS OR RESIDENTIAL AREAS IN THE UPPER PENINSULA OF MICHIGAN, 1968.

Age in years	Number of males	Number of females	Totals
cubs	10	7	17
1	19	5	24
2	18	5	23
3	14	4	18
4	5	4	9
5	8	2	10
6	5	1	6
7	2	1	3
8+	4	12	16
Totals	85	41	126

TABLE 2. AGES AND WEIGHTS OF MALE BLACK BEARS CAPTURED IN GARBAGE DUMPS, CAMP GROUNDS OR RESIDENTIAL AREAS IN THE UPPER PENINSULA OF MICHIGAN, 1968.

Age in years	Males from campgrounds or residential areas			Males from garbage dumps		
	Weight in kg.			Weight in kg.		
	sample size	Mean	Range	sample size	Mean	Range
Cubs	7	11	7- 14	3	25	23- 27
1	11	45	32- 65	8	45	31- 59
2	10	56	39- 75	8	65	35- 75
3	7	75	66- 83	7	94	58-132
4	4	91	88- 98	1	97	
5	4	92	84-109	4	134	80-168
6	1	153		4	124	97-173
7	2	103	98-108	0		
8+	2	161	129-194	2	196	182-210
Totals	48			37		

TABLE 3. AGES AND WEIGHTS OF FEMALE BLACK BEARS CAPTURED IN GARBAGE DUMPS, CAMPGROUNDS OR RESIDENTIAL AREAS IN THE UPPER PENINSULA OF MICHIGAN, 1968.

Age in years	Females from camp-grounds or residential areas			Females from garbage dumps		
	Weight in kg.			Weight in kg.		
	Sample size	Mean	Range	Sample size	Mean	Range
Cubs	5	11	7-16	2	9	9- 9
1	4	37	28-48	1	35	
2	5	50	34-59	0		
3	2	55	53-56	2	61	56- 66
4	2	72	71-73	2	103	102-104
5	1	55		1	114	
6	1	84		0		
7	1	75		0		
8+	10	76	64-93	2	120	116-124
Totals	31			10		

Reproduction

In spite of the mortality factors associated with feeding on garbage, 24 (28%) of the 85 males and 20 (49%) of the 41 females captured at sources of garbage were 4 or more years of age and were judged to be mature (Table 1).

Rausch (1961) found that black bears fed a rich diet in captivity grew faster and matured two to four years earlier than did wild black bears in Alaska. Bears that supplement their diets with garbage may maintain a higher reproductive rate, on the average, than those that subsist entirely upon wild foods, which periodically are in scant supply. This study was conducted in a year when natural foods were judged to be relatively scarce; nevertheless, the seven litters observed with females at sources of garbage ranged from 2 to 5 cubs and averaged 3.1. Using Student's *t* test, this mean was found to be significantly ($P < .01$) larger than the average of 1.99 cubs per litter reported by Erickson *et al.* (1964) from observations by hunters in the Upper Peninsula of Michigan. The difference remained significant ($P < .01$) even when the unusually large litter of five was omitted. In Montana, Jonkel and Cowan (1971) found that during years when natural food was scarce none of the mature females they captured was accompanied by cubs.

Weights

Bears captured in garbage dumps tended to be heavier than those of the same age and sex captured elsewhere (Tables 2 and 3). Student's *t* tests indicated

that males 4 years or older captured at garbage dumps ($N = 11$) were significantly ($P < .05$) heavier than males of similar age ($N = 13$) captured at campgrounds or residences (Table 1). Two- or three-year-old dump males ($N = 7$ for both 2 and 3 year olds) also appeared to be heavier than other males of the same ages ($N = 10$ and 7, respectively), but in each case these differences in weight were significant only at the $P < .10$ level. Five mature (4 years plus), non-lactating females captured at dumps were significantly ($P < .01$) heavier than 4 mature non-lactating females captured at campgrounds and residences. These findings appear to reflect the fact that garbage was much more abundant in dumps than in campgrounds and residential areas.

Management Considerations

Our observations indicate that bears destroyed as nuisances during the summer usually are not used for food or trophies. However, over 36 percent of the bears killed during autumn hunting seasons in Wisconsin are utilized as food or trophies or both (Dahlen 1959). Our limited observations during autumn hunting seasons in Upper Michigan are consistent with those of Dahlen. It would appear, therefore, that from the standpoint of wise use, the policy of relocating nuisance bears in summer to spare some of them until autumn should be continued.

Recent studies have provided some information on the practicality of relocating bears. Harger (1970) showed that of 164 nuisance bears that were relocated in Upper Michigan, 25 (15%) eventually were harvested by hunters, 27 (16%) were shot or recaptured as nuisances, 8 (5%) were killed by automobiles, 1 (1%) was killed in an undetermined manner, and 103 (63%) provided no further data.

The distance beyond which a bear will not return to its place of capture is unknown. Harger (1970) reported that a bear returned to within 0.5 miles of its original site of capture after being transported a straightline distance of 142.5 miles. However, Sauer *et al.* (1969) reported that in New York only three black bears of 14 that were transported more than 40 miles returned to within 8.6 miles of the original sites of capture. Harger (1970) found that 10 of 27 bears returned after being transported more than 40 miles but that none of the 13 yearlings returned (the distance that the yearlings were transported was not stated). Barnes and Bray (1967) also found that 'Homing behavior was more prevalent among full-grown bears than among young animals.'

Subadult males are particularly prone to wander (Stickley 1961; Jonkel and Cowan 1961), and they probably exhibit less attachment to a particular area than do females and older males. Experiments to determine the homing success of subadult males could provide valuable information for black bear management because subadult males comprise a large proportion of the bears involved in nuisance activity. In fact, 42% of the bears (excluding cubs) we captured in campgrounds or residential areas were males less than 4 years of age.

Observations made during this and other studies suggest that the number of nuisance bears in campgrounds and residential areas probably could be reduced if (1) garbage in such areas were made less available to bears through its prompt removal and by the use of 'bearproof' garbage cans (Barnes and Bray 1967) and (2) if garbage dumps were located at least a mile from campgrounds or residential areas (Rogers 1970).

SUMMARY

One hundred and twenty-six black bears were captured at garbage dumps, campgrounds or residential areas in the Upper Peninsula of Michigan during the summer of 1968. The sex, weight and breeding condition of each were recorded and the age of each was estimated from counts of annuli in the cementum of a first premolar. The sex ratio among cubs (59 males, N = 17) did not differ significantly from a 1 : 1 ratio, but the sex ratio among bears 1 through 7 years of age (76% males, N = 93) was significantly ($P < .01$) unbalanced toward males. Conversely, females predominated ($P < .05$) among the relatively few bears 8 years of age or older (25% males, N = 16), especially among those captured in campgrounds or residential areas (17% males, N = 12). Garbage was more abundant in dumps than in campgrounds or residential areas, and bears captured at dumps tended to be heavier than those of the same age and sex captured elsewhere. Seven litters observed with females captured at sources of garbage ranged from 2 to 5 cubs and averaged 3.1, which is significantly ($P < .01$) more than the average of 1.99 cubs per litter reported for bears in Upper Michigan. Forty-two percent of the bears (excluding cubs) captured as nuisances in campgrounds or residential areas were males less than 4 years of age. Young males may exhibit less attachment to an area than do females or older males, so may be less likely to return after being transported away from human habitation.

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PART III. MANAGEMENT OF BEARS AND TECHNIQUES

Paper 16

Managing Montana's Grizzlies for the Grizzlies!

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The grizzly bear, *Ursus arctos horribilis*, evokes varied reactions in different people, and various values are embodied in this species. It may be viewed as a symbol of a heritage of adventure and freedom; something to be maintained at maximum densities compatible with good forestry practices and recreation, but with optimal annual harvests; a part of the western mountain wilderness concept; a coveted big game trophy; a species that cannot be maintained at former densities; one that is in conflict with human expansion; a potential threat to life; and many other intensely personal images.

National publicity on grizzly bears in Yellowstone National Park since 1968, has resulted in a general doomsday image for this species. Conflicting views of its population status and of management programs within the Park have greatly influenced management of bears in the adjacent areas of Montana, Idaho and Wyoming, as well as of the distinctly separated (and probably larger) grizzly populations in northwestern Montana. While several questions are involved in the management controversy, the basic issue concerns population size. At present, an open conflict exists between scientific information and the view of certain protectionist groups. Strong evidence indicates that the management (and preservation) of grizzly bear populations in Montana is in jeopardy because of the concerted efforts of groups advocating federal laws to eliminate hunting of the species. Decisions pending at the national level could directly affect all grizzlies in the lower 48 states.

In an attempt to clarify the issues, this paper summarizes the present management and control programs, the known mortality data, and the general biological information available on grizzly populations in the various eco-units of Montana, with references to the programs of Yellowstone National Park and the adjacent states of Idaho and Wyoming.

Various concurrent studies are underway in the Yellowstone area, and an extended and intensive program has been initiated for grizzlies in northwestern Montana. Hopefully, better guidelines for management, and reduced kill of bears through control actions will result.

Programs to live-trap and translocate nuisance grizzly bears and orphaned cubs, and to evaluate a 'bear proof fence for the sanitary landfill dump near West Yellowstone, Montana, are also presented.

METHODS

The age of bears was established by examining decalcified saggital root sections for cementum annulations, supplemented by skeletal features and suture closure. Tagging programs in Yellowstone National Park and by the Montana



Figure 1. Administrative areas in the northern and southern grizzly bear populations of Montana.

Cooperative Wildlife Research Unit provided known or assigned ages for some bears (Craighead *et al.* 1974).

All data and analyses were separated into two main categories. Until grizzly bear populations and associated eco-units in Montana are further defined, the two units are construed generally in this report as follows: 1) the northern grizzly populations—including the Bob Marshall and Scapegoat wilderness areas, the Sun River Game Preserve, the Mission Mountains, all drainages of the Flathead River, the Flathead and Blackfeet Indian reservations, and the Cabinet Mountains; and 2) the southern grizzly populations—areas of Montana adjacent to Yellowstone National Park (Fig. 1).

In the enclosure study of a land fill dump, a municipal fence was constructed of 3-m chain-link mesh attached to pipe uprights and surrounded with electrified barbed wire (Greer 1974). The fence was examined periodically to record bear reactions and entry attempts, and its effectiveness in excluding bears from the garbage under a normal maintenance plan was evaluated.

Nuisance bears were trapped and moved and orphaned cubs were held and then moved to measure the effectiveness of this management technique compared to the killing of problem bears.

TABLE 1. ANNUAL KNOWN MORTALITY OR OTHER LOSS OF GRIZZLY BEARS FROM MONTANA AND GRIZZLIES PROCESSED FOR THE ADJACENT NATIONAL PARKS.

	7-Year							Avg.
	1967	1968	1969	1970	1971	1972	1973	
NON-HUNTING								
Illegal	7	4	4	9	6	7	4	
Marauders	4	3	1	4	6	5	2	
Nuisance	0	0	0	1	7	1	1	
U.S. Fish and Wildlife Serv.	2	3	4	2	2	3	0	
Blackfeet Ind. Res.	4	6	3	0	3	1	3	
Flathead Ind. Res.	0	0	3	0	0	0	1	
Live Cubs of the Year	0	0	0	0	0	3	0	
<hr/>								
Total Non-Hunting	17	16	15	16	24 ^b	20	11	119
Total Hunting ^a	24	12	33	13	22	14	15	133
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Total Mortality	41	28	48	29	46	34	26	252
Percent Hunting	59	43	69	45	49	41	58	—
Glacier National Park	4				0	0	1	
Yellowstone National Park	6	12	11	16	7	9	0	
<hr/>								
Total in Parks ^c	10	14	14	17	7	9	1	
<hr/>								
^a All hunting seasons are fall only.								
^b 2 illegal mortalities verified March 1974; changed this total of previously reported 22 to 24.								
^c Specimens received at the wildlife lab.								

DISCUSSION

Surveys conducted since 1947 provide records useful for estimating the annual number of grizzly bear kills. The estimates range from 10 to 60 (mean 37) grizzlies between 1947-1966 (Greer 1970). Since 1967, a special grizzly bear license system has provided a more detailed annual record of the known grizzly bear kill in Montana. Deaths are designated as caused by hunting or non-hunting with several categories in the latter classification. During 1967-73, known grizzly losses ranged from 26 to 48, averaging 36.

Hunting Mortality.

Hunting accounted for an average of 53 percent (range 43-69 percent) (Table 1). Hunters have taken grizzlies in 17 hunting districts (HD) since 1967, but in any one year only 4 to 11 districts have provided grizzlies.

From 59 to 100 percent of the annual hunter harvest for 1967-73 occurred in 12 northwestern Montana hunting districts and 0 to 41 percent in the southern districts, including 5 districts in the Gallatin National Forest (Montana's segment of the Yellowstone grizzly population).

About 57 percent (76 of 133) of the grizzlies killed by hunters during the seven seasons from 1967-73 were taken in HD 150, 280 and 316, which have an early deer, elk and bear season. The early season conventionally opens 15 September and ends in late November; the regular big game hunting season opens with variable dates in mid-October (Greer 1974).

Of these 76 grizzlies 49 were from HD 150, 18 from HD 316 and 9 from HD 280. About 88 percent were taken during the early season, most (53%) in September. Only nine bears were killed during the regular season with no legal kills during the regular season recorded from HD 316.

Non-hunting Mortality.

Other grizzly losses include: 1) illegal kills either by intent or accident; 2) killing of marauders (bears that threaten life or personal property); 3) killing of nuisance bears (repeated visitation to inhabited areas); 4) killing of livestock predators (U.S. Fish and Wildlife Service); 5) killing under treaty rights (Indian Reservations—usually control actions by natives of the Blackfeet and Flathead Indian Reservations); 6) capture of orphaned cubs; 7) transfer to zoos (occasionally an alternative to 1 through 5).

The known non-hunting losses ranged from 11 to 24 grizzlies (mean 17) during 1967-73 and comprised 47 percent (mean) of the total known annual loss. Except for 1971, when a major translocation program of grizzlies was required in the Yellowstone population (Greer 1972), annual non-hunting loss in the southern districts was 20 percent or less, compared to 80 percent in the northern populations.

In the past few years conflicts and confusion have arisen over the annual grizzly mortality in the Yellowstone range. This total includes hunting and non-hunting deaths, and the removal of live grizzlies. When verified by the responsible agencies, they are included in the "official" report by designated representatives of Montana, Wyoming, Idaho and Yellowstone National Park. These data are given in Table 2.

Hunting accounted for only 28 percent of the known man-caused grizzly deaths in the total Yellowstone range during the past 4 years. Records for 1967-70

TABLE 2. ANNUAL GRIZZLY MORTALITIES¹ IN THE YELLOWSTONE ECOSYSTEM (YELLOWSTONE NATIONAL PARK; GALLATIN, CUSTER, TARGHEE, SHOSHONE AND TETON NATIONAL FORESTS) DURING 1970-1973.

National forests									
Year	Gallatin ² and Custer (Mont.)	Targhee ³ (Idaho)	Targhee (Wyo.)	Shoshone (Wyo.)	Teton (Wyo.)	Total ⁴ (Wyo.)	Total Forests	Ynp ⁵	Total Area
1970	7	7	0	8	4	12	26	20	46
1971	21	5	2	8	2	12	38	7	45
1972	4	5	1	3	3	7	16	9	25
1973	3	4	0	5	2	7	14	1*	15
Total	35	21	3	24	11	38	94	37	131
4-Yr. Avg.	8.8	5.3	0.8	6.0	2.8	9.5	23.5	9.3	32.8
Number and (Percent) Mortality by:									
Hunting	14(40)	0(0)	0(0)	17(71)	5(45)	22(58)	36(38)	0(0)	36(27)
Non-Hunting	21(60)	21(100)	3(100)	7(29)	6(55)	16(42)	58(62)	37(100)	95(73)
Total	35	21	3	24	11	38	94	37	131

¹Includes all grizzlies removed from various populations (to zoos, road kills, known natural mortalities, illegals, marauders, nuisance, Indian reservations, and hunting).

²Source by Kenneth R. Greer, from Montana Department of Fish and Game records.

³Source by Frank DeShon, from Idaho Fish and Game Department records.

⁴Source by Larry J. Roop, from Wyoming Game and Fish Department records.

⁵Source by Glen F. Cole (1974), from Yellowstone National Park records.

*Received August 1974—A weathered carcass that was a probable road casualty during 1973.

TABLE 3. TOTAL KNOWN GRIZZLIES KILLED WITH PERCENTAGE OF FEMALES.

	1967		1968		1969		1970		1971		1972		1973		7 Yr. Avg.	
	No.	%F	No.	%F	No.	%F	No.	%F	No.	%F	No.	%F	No.	%F	No.	%F
Hunting	23	35	12	25	33	39	13	54	22	68	14	50	15	60	132	47
Non-hunting	6	17	8	25	8	88	8	63	17	47	16	38	10	30	73	44
Total	29	31	20	25	41	49	21	57	39	59	30	43	25	48	205	46
Glacier National Park	4	100	0	1	3	33	1	100	0	0	0	0	1	100	10	70
Yellowstone National Park	6	50	11	27	11	36	16	69	7	43	9	44	0	0	60	45

TABLE 4. AVERAGE AGE OF KNOWN GRIZZLY BEARS KILLED IN NORTH, SOUTH, AND YELLOWSTONE PARK POPULATIONS.

	1967		1968		1969		1970		1971		1972		1973	
	M	F	M	F	M	F	M	F	M	F	M	F	M	F
Hunting	—	—	4.8(5)	7.0(2)	8.1(16)	5.0(11)	7.3(6)	7.0(6)	5.7(7)	8.5(14)	5.3(7)	9.4(7)	7.8(6)	6.6(9)
Non-Hunting	10.0(5) ^a	16.0(1)	11.1(6)	6.0(2)	1.8(2)	6.4(8)	9.3(3)	7.0(5)	7.8(8)	8.5(6)	8.4(7)	9.3(4)	6.5(6)	4.7(3)
Total	10.0(5)	16.0(1)	8.3(11)	6.5(4)	7.4(18)	5.6(19)	8.0(9)	7.0(11)	6.8(15)	8.5(20)	6.9(14)	9.4(11)	7.2(12)	6.1(12)
North	—	—	—	—	8.5(15)	5.1(8)	7.0(6)	6.9(8)	3.8(4)	8.0(12)	5.9(12)	9.4(11)	7.1(10)	6.1(11)
South	—	—	—	—	2.0(1)	4.7(3)	10.0(3)	7.3(3)	7.9(11)	9.3(8)	12.5(2)	—(0)	7.5(2)	6.0(1)
Total	—	—	—	—	8.1(16)	5.0(11)	8.0(9)	7.0(11)	6.8(15)	8.5(20)	6.9(14)	9.4(11)	7.2(12)	6.1(12)
Yellowstone National Park	3.5(4)	9.5(2)	8.4(8)	5.8(4)	8.4(7)	12.0(4)	7.1(5)	5.8(11)	18.0(3)	13.3(3)	6.9(5)	11.4(4)	—(0)	—(0)

^aAge (sample size)

show that 14 grizzly deaths in the Montana portion of the Yellowstone range resulted from hunting and 8 from non-hunting causes. In the subsequent years of 1971-1973, hunting accounted for 10 of the 28 known deaths in five hunting regions of the Gallatin National Forest. The grizzly bear translocation program, required in the Gallatin National Forest since 1971, led to several non-hunting mortalities that year because of conflicts with livestock grazing allotments in and near transplant sites.

The Idaho Fish and Game Department has not authorized a grizzly bear hunting season since 1946 and, therefore, officially 'protects' the grizzly; however, *official* Idaho Fish and Game Department records recently showed that some grizzly mortalities do occur. In the northern portion of the Targhee National Forest and in the southern portion of the Gallatin National Forest, grizzly mortality has been occurring regularly, with 7, 5, 5 and 4 grizzly mortalities verified during 1970-1973, respectively. Most, if not all, of these losses result from conflicts with sheep ranchers.

The Wyoming Game and Fish Department opened regular grizzly bear hunting seasons in the spring and fall of 1970-1973. Like Montana and Idaho, Wyoming has a significant number of non-hunting grizzly mortalities. An *official* report by the game department indicated that in three national forests (Targhee, Teton and Shoshone) adjacent to Yellowstone Park, only 58 percent of 38 known grizzly losses during 1970-1973 were from hunting (Roop, pers. comm.).

During the same period, Yellowstone National Park *officially* reported that 20, 7, 9 and 10 grizzlies were removed from Wyoming populations inside the Park (Cole 1974).

Sex and Age of Grizzly Bear Mortalities.

Over 95 percent of the grizzlies killed by hunters are taken without considering size, sex or age. Because grizzly bears mature slowly and are irregular in their first or subsequent pregnancies (Craighead *et al.* 1969), females may be a critical component in maintaining numbers. Consequently, close surveillance of female mortality is required to determine the population status of the species.

Although differences occurred in the annual hunting and non-hunting mortality of females, the 7-year averages were nearly identical. Combined, they accounted for 46 percent of the total loss (Table 3). The female mortality by hunting was 25 to 39 percent in 1967-69, and 54 to 68 percent in the following 4 years. Forty-five percent of grizzlies taken in Yellowstone National Park control programs were females.

Consolidating age groups allows comparisons between the two geographic (northern and southern) populations (Table 4). During 1970-73 the average age of all bears ranged from 6.1 to 9.4 years, but males averaged about 1 year older than females in 1970 and 1973, and females averaged about 2 years older than males in 1971 and 1972. In most years, samples of 1-to-3-year-olds are too limited for comparisons between northern and southern populations, but the average ages are not strikingly different for those years of adequate sample size. The average age of grizzlies from Yellowstone National Park—a non-hunted and stable population—is similar to that of the regularly hunted northern populations. If these average ages derived from available samples are considered an approximate representation of the populations, it then appears that age composition has remained uniform.

Complaint-Control-Translocation Programs

Grizzly control has been required since 1967 on the Blackfeet Indian Reservation and since 1971 in the West Yellowstone area.

Conflicts with grizzly bears occurred in as many as seven areas of the state during the past 3 years. Some encounters were resolved immediately when landowners shot the grizzlies. Other bears were reported to Department personnel for live trapping and removal.

In the north, encounters, complaints and control efforts have been made by citizens and Department personnel near Eureka, Polebridge, Big Fork, the Flathead Indian Reservation, Spotted Bear, Choteau, Augusta, Alice Creek, and other settlements. Complaints on the reservations are handled by treaty persons or USFWS personnel. Grizzlies taken by government trappers are forwarded to the Fish and Game Department lab, but grizzly heads from the bears taken by Indians were not available until 1973. With the exception of 1970, from one to six grizzlies were killed on the Reservation in each year from 1967-73.

Grizzly and black bears, *Ursus americanus*, have coinhabited the vicinity of West Yellowstone during spring, summer and fall for many decades. As man's interests and properties have increased, so have complaints about nuisance bears. Community and private garbage dumps in this area were traditional foraging sites for several generations of both species. In most years, an occasional grizzly may appear by late April, but small numbers normally cause no conflict with man. As bear numbers and activities increase during May, June and July, nuisance bears become more numerous, public complaints frequently follow, and control action ensues. The pattern has been repeated from 1971 through 1973. Described below is one study on use of electric fences for bear control. The last open garbage dump at Trout Creek in Yellowstone Park and an open dump near West Yellowstone, Montana, were both eliminated before the 1971 summer season. The West Yellowstone dump was relocated on level ground, and was designed as a bear-proof enclosure including a chain link fence inside an electrified three wire stock fence (Greer 1972). The abrupt relocation resulted in an anticipated increase of grizzly bear complaints. By mid-1971 a control program was required, and a live-trapping program using 230 culvert trap sets and 25 snare sets from 23 June to 22 September, resulted in 23 captures of 19 grizzlies. A few grizzlies continued to visit the dump area during October and November, and one entered the town of West Yellowstone during the first week of November.

During the winter of 1971-72, snow damaged the bear fence around the West Yellowstone dump. Improper construction appeared to be the cause. The fence was reconstructed, but apparently the top edge was not adequately reinforced.

During the second season of operation (1972) it was found that the facility was not completely bear-proof. Bears visited the area throughout the summer, and some entered and exited through the fence at various locations. Although only 3 grizzlies were captured from this area, probably 15 to 25 grizzly bears are involved in over 50 individual entries.

The death of 13 translocated grizzlies (only 3 taken by hunters) during the 1971 management program led us to anticipate fewer troublesome grizzlies around West Yellowstone in 1972. However, live trapping began 23 June, precisely the same date as the previous year, and grizzlies were present during 1972 in the same periods. About 125 culvert trap sets through 15 September resulted in the capture of seven grizzlies. From 5 to 10 additional grizzlies

were also known to be in the vicinity of West Yellowstone (excluding the dump area) for as long as several days during 1972 without causing formal complaints. In total, the trapping effort was about 50 percent less than in 1971, and the number of individual grizzlies captured in 1972 was about 70 percent less than in 1971.

During 1973, minor repairs to the fences of the West Yellowstone dump were again made intermittently but proved insufficient. The fence, although secure at the bottom by being buried 1 m, was attached in only three places at the top to an iron cross bar between uprights. Three strands of barbed wire topped the fence, and three electrified strands were attached to iron posts 0.3 m outside the main fence. This design still did not prevent bears from reaching the disposal pit. Bears were not deterred by the three-stranded electric fence, and upon reaching the main fence they merely crawled up and over, squeezing between the pipe and wire. At each penetration, the wire fence was severely bent. Bears exited in the same or different locations, as none were ever discovered in the enclosure. During the 1973 season, grizzlies made 11 unsuccessful digging attempts to get under the fence.

As evidenced by track size, a minimum of 13 and possibly as many as 24 grizzlies entered the dump. Others may have visited the area without gaining entry. With this many individual bears visiting the area one or several times from May to November, we can assume the total at perhaps 100 visits. A total of 11 trap sets at the dump captured three adult females, and trap sets in nearby areas caught three grizzlies. One male had been translocated 72 airline km the previous year. Trapping effort during 1973 was about 40 percent less than in 1972 and the capture of seven individuals was the same (Greer 1974a). Prior to the hunting seasons of 1971, 1972 and 1973, 17, 4 and 3 grizzlies, respectively, were translocated into Montana hunting districts north of the Park (Greer 1972; 1974). They were moved a distance of 80-100 km, likely into or near areas with which they were familiar (Fig. 2). The relocation of some bears was shortlived for four bears were re-trapped at the original capture site within 19 to 48 days, and three were re-trapped in the vicinity of West Yellowstone in succeeding years.

In 1971, when 17 bears were moved, 9 were killed by hunters in three of five Montana hunting districts adjacent to Yellowstone Park. Among them were a 5-year-old male which was moved 80 airline km on 23 July from West Yellowstone and was killed 28 November at the head of Sage Creek (HD 310), about 16 m north of initial capture. Of seven grizzlies taken by hunters from HD 316 between 16 September and 4 October, two had been translocated from West Yellowstone, two were unmarked, and three held Park Service tags. In 1972, hunters did not kill any grizzlies in these five hunting districts while in 1973 only one bear, a male tagged in the Park, was killed in HD 316.

CONCLUSIONS

Since 1967, regulated hunting, studies of garbage dump closure, and the documentation of man-caused mortalities have been the basis for management recommendations in Montana. Studies reveal that 26 to 48 grizzlies were killed each year, and that 47 percent of the total were taken for reasons other than hunting. The data further show that the average age of bears killed in hunted areas was comparable to that in non-hunted populations in Yellowstone National Park, and that about 45 percent of the annual losses are subadults of 4 years or younger. Closure of some hunting districts, increased license fees

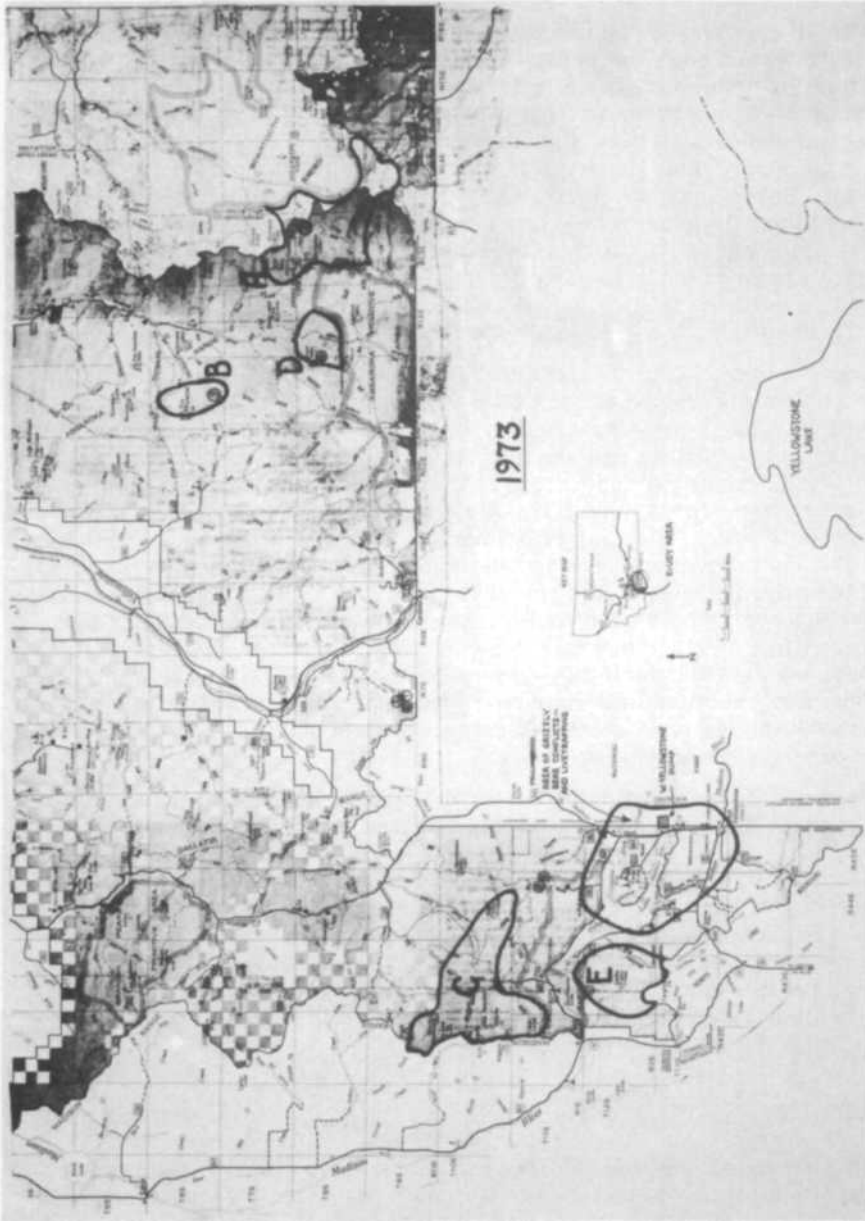


Figure 2. Grizzly bear translocations, and designated areas in the Gallatin National Forest, Montana, during 1973.

and hunting season adjustments can adequately control the rate of the hunter's harvest. With these policies, some grizzly populations appear to be expanding their present range, and the age classes within populations appear to be normal. Although the mortality sample is rather small (20-30) for individual years, it is probably not mere coincidence that the bears killed represent the entire age spectrum in the population.

Apparently, several eco-units of grizzly bears that may form discrete, coexisting or intermingling populations do occur in Montana and provide an annual hunting harvest which is carefully controlled by the State. Other forms of annual mortality are more difficult to curtail.

The major grizzly habitat and populations occur in and adjacent to the Bob Marshall Wilderness area (HD 15). Hunter-killed grizzlies have been well distributed within this one-million-acre area, bears taken ranging from young to old. This area has apparently not experienced a deleterious reduction in resident population numbers or its distribution. Areas adjacent to the South Fork of the Flathead River and the Lincoln-Scapegoat Wilderness Area likewise show no evidence of overharvest. In fact, portions of the population may actually be increasing in a few areas. The various groups of bears should be carefully monitored for changes in their status.

Complaints about grizzly bears around man's dwellings and properties have gradually increased in several locations during the past few years. Only one or two grizzlies were involved in each of 10 areas requiring control action, but a continuous program was necessary, and may be necessary in the future, throughout the range of grizzlies in Montana. The program can be expanded, but, should all hunting cease, considerable additional time and effort may be required. Studies should be made as soon as possible to predict necessary methods and efforts.

The live capture of nuisance grizzly bears introduces the problem of disposal. Relocation within a national forest near the capture site has provided a temporary solution. Some injured or very old individuals are considered poor risks for translocation, and perhaps in the future they should be dispatched. The problem of social impact on resident grizzlies of transplants should be studied further as soon as possible.

In the past 5 years, local and national publicity has amplified the controversy over management of the Yellowstone National Park grizzly population. This controversy, has been extended to other grizzly populations in Montana, Wyoming and Idaho, and several conservation groups have pressed for the reclassification of grizzlies as an endangered species. In their view, further protection will 'save' the species. Their concern, however, is usually restricted to that portion of grizzly mortality which is already under control by licenses, seasons and regulations, while the equally significant non-hunting portion of annual grizzly mortality is generally ignored. With the elimination of legal hunting, it is possible that 'surplus' grizzlies could be involved in incidents and conflicts with man at a greater rate, and many more grizzlies could become casualties, especially in areas where sheep and livestock grazing permits are authorized.

At present, it does not appear that 1,000-2,000 licenses sold annually have significantly affected the rate of harvest; the average hunter success is about 1.5 percent. Grizzly hunting licenses are almost without exception bought as a precaution in case of a grizzly encounter during an elk hunt in areas where both species occur. In fact, a stringent license and quota harvest system for grizzlies could adversely affect grizzly management and, subsequently, the

status of the species. A few possible harmful effects are: (1) a complete loss of the grizzly hunting experience which many persons regard as a cultural and legal right; (2) failure to meet biologically sound quotas; (3) increased encounters between grizzlies and people, resulting in a sudden rise in injuries to people and the non-hunting deaths of bears (of which more may be unreported); and (4) a highly lucrative and illegal traffic in pelts.

Collectively, the *official* reports by the respective state game departments and Yellowstone National Park indicated that 72 percent of the known grizzly mortalities and removals from the Yellowstone area populations were by non-hunting causes during 1970-73. Even when 36 non-hunting mortalities within Yellowstone National Park are deleted, the remaining 94 grizzly losses within the Yellowstone area consist of 38 percent by hunting and 62 percent by non-hunting.

There are strong indications from Idaho that subsequent inquiries and findings will not accurately reveal the number of illegal, marauder or nuisance grizzly mortalities (Frank DeShon, pers. comm.). In subsequent years, lack of verified grizzly deaths in Idaho may not mean none occur, only that they are not reported to agency personnel.

State game departments charged with the control, management and perpetuation of the species must consider the divergent values placed on the grizzly bear, which in turn create serious conflicts. Among management problems are: man's continued intrusion into grizzly range; the conflict of grizzlies with livestock; the economic value of hides to merchants, guides and taxidermists; the population status of the species; role of hunting in grizzly management; size and integrity of grizzly habitats and ranges; recurrent problems at campgrounds, dumps, cabins or other recreational areas, and precautions to be taken to reduce such problems; effects on other populations of controversy and publicity over Yellowstone grizzlies; and differing management approaches taken by State and federal agencies.

The recent move by the Montana Department of Fish and Game to reduce hunting mortalities may stimulate to action those agencies, individuals and organizations which can lessen non-hunting mortalities. For instance, sheep allotments on the Gallatin National Forest in the five hunting regions of Montana have been voluntarily reduced from 18 in 1969 to 11 in 1974, but it is probably unreasonable to expect that *all* public land grazing permits will be eliminated from areas of known grizzly habitation where grizzly hunting has been banned. In the view of the Montana Department of Fish and Game, hunting is not presently jeopardizing the grizzly in Montana. To declare the grizzly an 'endangered' species, thereby eliminating hunting, would in fact be harmful to this species. Although other views are recognized and respected, the State will resist further efforts to ban grizzly hunting. The Fish and Game Commission's grizzly bear policy is, in part,—'to perpetuate and manage this unique wildlife species in suitable habitat of the state for the people of Montana' and in the National interest. Considering the good evidence that substantial populations are present in Montana, hunting seasons and regulations will continue to be based upon sound management and research. With continued effort, any changes in the status of the bears will be recognized and adequate measures will be taken. Continuing studies on grizzlies by the State, in cooperative programs with the U.S. Forest Service, National Park Service, U.S. Fish and Wildlife Service, the Wyoming and Idaho Fish and Game Departments, and the provinces of Alberta and British Columbia, should guarantee survival of the species and a compatible relationship between man and bears.

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Paper 17

**The Dynamics and Regulation of Black Bear
Ursus Americanus Populations in Northern Alberta**

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INTRODUCTION

This paper describes the dynamics of an unexploited black bear population on a 207 sq. kilometer study area in mixed forest type near Cold Lake in north-eastern Alberta. It also reports on a population manipulation designed to examine the regulatory effects that adult males have on the population.

Numbers of black bears on the study area varied little from 1968 through 1971. The removal of 26 large adult males in 1971 and 1972 was followed by an apparent increase in the bear population in 1972 and 1973, primarily in the sub-adult component. Alternate years of high cub production in 1968, 1970 and 1972 probably were solely a function of the number of adult females breeding. Evidence from other studies indicates no significant change in annual litter size. The greater proportion of males in the captured subadult sample was due to their greater mobility during dispersal as evidenced by the fact that seventy percent of the within-year recaptures of males were in excess of 4, 570 meters from the initial point of capture, while 92 percent of female recaptures were less than 4, 570 meters from initial point of capture.

The removal of 26 adult male bears in 1971 and 1972, and subsequent decline in egress of subadult, largely male bears plus possible increased subadult survival, accounted for the estimated population increase to 117 in 1972 and 175 in 1973 from the pre-manipulation mean estimate of 80 animals from 1968 to 1971. This supports the widely held view that bear populations are largely self-regulated. Year to year population changes are largely a function of alternate year synchrony in female reproduction while long term population regulation is a function of adult-male-induced mortality in the subadult cohort.

STUDY AREA AND METHODS

The 207 sq. kilometer study area, located on the northwest edge of Cold Lake, lies in the southern fringe of the Boreal Forest. Approximately 40 percent of the study area is aspen-dominated while 5 percent is spruce-dominated. The remainder is equally dominated by jackpine, brushland, treed muskeg, water and old burn areas. Except for the Martineau and Medley River valleys, bordering the east and west sides of the study area and Primrose Mountain on the north edge of the study area, the topography is generally flat. A few summer residents on the shore of Cold Lake are the only human inhabitants on the study area.

PROCEDURES

A more detailed account of capture and marking procedures than given here is presented by Kemp (1970). All animals were captured in foot snares, per-

manently and individually color-marked and a tooth, usually P_1 or P_3 , extracted for subsequent sectioning and ageing.

During each of the first four years of this project, an incident of mortality of a snared subadult induced by an adult male was recorded. After reviewing the relatively high rates of subadult mortality it was hypothesized that directly and indirectly adult males may be effecting a regulatory influence on the bear population. To test this hypothesis, 14 and 12 adult male bears in excess of 90.8 kilograms were removed from the population in 1971 and 1972. It was concluded that any documented changes in subadult survival or population numbers would, in part, suffice as a test of the hypothesis.

CENSUS TECHNIQUES

Several methods were used to estimate the bear population on the study area. The results of each year's trapping were divided into four equal groups forming the necessary trapping and resampling periods. Tests for homogeneity of trap response indicated that the distribution of total captures did not differ significantly from a Poisson, i.e. they tended to occur at random. We thus feel justified in using retrapping to obtain marked-unmarked ratios for Lincoln index calculations (Table 1). Completion of the O-capture category of each truncated distribution and their subsequent summation yielded additional estimates of population size. The employment of the capture efficiency method (Table 1) followed the technique as described by Meslow *et al.* (1968).

POPULATION ESTIMATES

Population estimates by several independent methods indicated no significant change in the population during the first four years of study from 1968-1971 (Table 1). The mean estimate for 1968-1971 of 80 results in an overall density of one per 2.6 sq. kilometer. In 1972, the second year of the population manipulation, the population increased to 117 and continued to increase in 1973 to 175 animals (Table 1).

REPRODUCTION

The reproductive performance of the black bear population was principally affected by the proportion of the adult female cohort successfully breeding each year (Table 2). Sows with cubs were rarely seen on the study area, hence no average annual litter sizes could be calculated. Data reported by Jonkel *et al.* (1971), however, indicate that average litter size is remarkably constant from year to year and thus would not importantly affect changes in the size of the cub cohort. Litter sizes as reported by Jonkel for other areas of North America range from 2.0 to 2.5.

The effect of the changing proportion of adult females breeding is reflected in the age composition of the population (Table 3). Unless the litter is lost prior to the breeding season adult females generally breed only every second year. The data (Table 3), however, suggest an element of synchrony when it would normally be expected that about 50 percent of the adult females would breed in any one year. Loss of a litter, age at sexual maturity, age composition and failure to breed every two years would result in asynchronous breeding. This

would indicate that some agent(s) in the environment induce this synchrony by either uniformly stimulating reproduction or impeding it. Our hypothesis at this time is that reproduction is uniformly impaired.

TABLE 1. BLACK BEAR POPULATION ESTIMATES FOR COLD LAKE STUDY AREA, 1968-1973.

Mean Date	Numbers Estimated	Basis ¹
July 31 1968	108	A
	38 ²	B
	76	C
	— x 84 (50-118) ³	
July 29 1969	72	A
	59	B
	108	C
	— x 71 (65-86)	
July 20 1970	99	A
	82	B
	94	C
	— x 92 (77-107)	
July 4 1971	72	A
	77	B
	90	C
	— x 75 (47-103)	
July 6 1972	120	A
	88	B
	87	C
	— x 117 (85-150)	
July 16 1973	188	A
	64	B
	158	C
	— x 175 (106-244)	

¹ Numbers estimated based on:

- A. Lincoln index; retrapping of marked individuals.
- B. Modified capture efficiency.
- C. Completion of O-capture category using a 'maximum likelihood' technique.

² Each Lincoln index and modified capture efficiency estimate is mean of one or more individual estimates.

³ Confidence limits are at 95 percent level.

TABLE 2. THE ANNUAL NUMBER OF FEMALE BLACK BEAR WITH CUBS CAPTURED ON THE COLD LAKE STUDY AREA, 1968-1973.

Number of female bear with Cubs					
1968	1969	1970	1971	1972	1973
13(16) ¹	2(13)	5(11)	1(6)	6(11)	3(4)

¹ Total number of adult females present on the study are in parenthesis.

TABLE 3. AGE DISTRIBUTION OF INDIVIDUAL CAPTURES OF BLACK BEAR ON COLD LAKE STUDY AREA, 1968-1973.

Age (in years)	1968	1969	1970	1971	1972	1973	Total
cubs	10	3	5	3	8	3	32
1	0	12	3	10	6	6	37
2	2	0	12	1	23	12	50
3	1	4	4	9	10	19	47
4	0	1	3	6	5	2	17
5	29	22	22	15	21	13	122
Total	42	42	49	44	73	55	305

AGE COMPOSITION

The summer age composition of the black bear population was determined from the capture of known-age animals (Table 3). A pre-molar was extracted from animals one year and older and later sectioned to determine the exact age.

The lack of subadults in the 1968 age distribution is probably the result of several years of successive reproduction failure. The strong cub crop of 1968 can be seen in the strong succeeding age cohorts of 1969-1971. The subadult (including cubs)/adult age ratio changes progressively from 0.45 in 1968 to 0.83, 0.96, 1.14, 1.80 and 2.4 in 1969 to 1973, respectively.

As will be shown later, the dramatic increase in the subadult/adult age ratio in 1972 and 1973 is, at least in part, a function of the removal of adult males from the study area and the subsequent increase in subadult male ingress on to the study area.

MORTALITY

Calculation of mortality rates from life table analysis was precluded because the population was neither stationary (Table 1) nor age stable (Table 3).

Average annual subadult (to 2 yr. old) survival as calculated from a survival series (Ricker 1958) was 0.42, 0.43, 0.30 and 0.55 in 1968 to 1971, respective-

TABLE 4. SEX RATIOS OF BLACK BEAR NEAR COLD LAKE, ALBERTA. SAMPLE SIZE IN PARENTHESIS.

Percent Males						
1968	1969	1970	1971	1972	1973	Total
52 (46)	61 (28)	71 (35)	58 (24)	76 (38)	81 (31)	66 (202)

TABLE 5. DISTANCES MOVED BY BLACK BEAR IN THE SAME YEAR AS INITIAL CAPTURE ON THE COLD LAKE STUDY AREA, 1968-1973.

Sex	Total Recaptures	Percentage of Recaptures at Various Distances from Point of Initial Capture			
		914 m	914-4, 570 m	4, 770-18,280 m	>18,280 m
Female	24	33.3	58.3	8.3	0
Male	43	11.6	18.6	39.5	30.2

ly. The removal of adult males in 1971 and 1972 precluded the calculation of adult survival rates in this manner.

The low survival in 1970 probably reflects the presence of a large dispersing cohort of 2-year-olds born in 1968, with a normal number of adult males present on the study area. It is felt that the relatively high survival of 1971 is a result of the removal of 14 adult males from the study area.

SEX RATIOS

The overall sex ratio of the black bear population (133 : 69) differed significantly from the theoretical 50 : 50 (Table 4). The sex ratio of 25 : 10 in 1970, 29 : 11 in 1972 and 25 : 6 in 1973 were significant departures from the expected ratio ($P < .05$). Yearling, 2-yr old and 3-yr old cohorts show a substantial departure from the 50: 50 sex ratio (Table 5). Since the cub and adult age cohorts are close to the expected sex ratio and since we have no evidence of sex specific mortality, the resultant high proportion of males reflects the increased mobility of dispersing subadult males and in the post 1971 period, the ingress of subadult males onto the study area.

MOVEMENTS

Bear movements are examined in this paper for two reasons: (1) seasonal and/or annual changes in movements may bias the estimation of numbers of bears on the study area; and (2) movements and dispersal are population phenomenon which may importantly affect survival.

Tests for homogeneity of trap response have indicated that the frequency of capture does not differ significantly from the expected random. Captures per trap-night remain constant until the latter part of September at which time the

TABLE 6. DISAPPEARANCE OF MARKED INDIVIDUALS FROM THE COLD LAKE STUDY AREA, 1968-1973.

Number Marked and Recovered in the Succeeding Years						
Year	1968	1969	1970	1971	1972	1973
1968	46	14	7	5	5	1
1969		28	10	6	6	3
1970			15	12	10	4
1971				25	13	6
1972					38	10
1973						31

TABLE 7. DISAPPEARANCE OF MARKED ADULTS (≥ 3 YRS) FROM THE COLD LAKE STUDY AREA, 1968-1973.

Number Marked and Recovered in the Succeeding Years						
Year	1968	1969	1970	1971	1972	1973
1968	33	11	5	5	5	1
1969		12	9	5	5	3
1970			14	7	6	2
1971				8	2	2
1972					7	2
1973						4

TABLE 8. DISAPPEARANCE OF MARKED SUBADULTS (1-3 YRS) FROM THE COLD LAKE STUDY AREA, 1968-1973

Number Marked and Recovered in the Succeeding Years						
Year	1968	1969	1970	1971	1972	1973
1968	13	3	2	1	0	0
1969		16	1	0	1	0
1970			21	5	4	2
1971				17	11	4
1972					31	8
1973						27

onset of hibernation results in reduced mobility. This evidence strongly suggests that seasonal movements do not bias the estimation of numbers.

Ninety-two percent of the captured female population moved less than 4, 570 meters from point of initial capture to subsequent capture in the same year (Table 6). Likewise, 70 percent of the male population moved more than 4, 570 meters. Preliminary analysis indicates that the bulk of the males moving more than 18, 280 meters are dispersing subadults.

Relative disappearance rates may also be indicative of mobility and/or mortality combined. For the period 1968-1973, 34 percent (n = 172) of the animals marked in one year were recovered the following year (Table 6). The overall recovery rate for adults was 42 percent (n = 74) (Table 7) while that for subadults was 29 percent (n = 98) (Table 8). A further examination of the subadult recovery rates indicates that 18 percent (n = 50) of the subadults were recovered in the pre-manipulation period prior to 1971 while 40 percent (n = 48) were recovered in the post manipulation period of 1972 and 1973. Although the data is admittedly crude, it is felt that the increased recovery rates in the post-manipulation period reflects the lack of adult males and the increased desirability of these vacant areas to subadults.

DISCUSSION

Population regulation is here defined simply as the dampening of numerical fluctuations by density-dependent processes. Evidence presented in support of the hypothesized regulatory effect of adult males on the bear population is:

- (1) the population increase from 80 in the pre-manipulation period to 175 in the post-manipulation period; and
- (2) the increased recovery rate and hence possibly survival of subadults in the post-manipulation period.

The fact that snared subadults were killed by adult males indicates that adult males are capable, if given the opportunity, of inflicting outright mortality. It is not suggested that this occurs in significant instances in free-ranging animals. Whether or not directly induced mortality by adult males is significant, or whether mortality is from other causes resulting from aggressive behavior and subsequent increased dispersal of subadults, remains to be tested in 1974 and 1975.

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Paper 18

Polar Bear Den Surveys in Svalbard, 1972 and 1973

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DEN SURVEY IN 1972

An effort to estimate the abundance of polar bear (*Ursus maritimus*) dens in Svalbard was made in 1972. Because most polar bear females with cubs leave their dens over a relatively short period of time (Uspenski and Kistshchinski 1972), large areas must be surveyed simultaneously. The purpose of the pilot study in 1972 was primarily to define the relative importance of various regions as denning areas rather than to try to determine the absolute number of dens. Studies from other parts of the Arctic have demonstrated the feasibility of fixed wing aircraft in polar bear den surveys (Uspenski and Kistshchinski 1972). Fixed wing aircraft were used in Svalbard in 1972, both for den surveys and for transport of field groups and supplies. With fuel depots established in Tjuvfjorden, Freemansundet and Sorgfjorden, and with bases in Longyearbyen and in Ny-Ålesund, the aircraft were able to survey the entire archipelago (Fig. 1). Two Cessna 185's with ski/wheels and cargopacks were used in the surveys. The cruising speed was between 130 and 150 km per hour. Observations were made from altitudes between 70 and 100 meters. On most surveys, the planes worked together; they either searched one side of a fjord each, or a mountain at different altitudes, or one surveyed a shoreline while the other checked islands, riverbanks, etc.

Some areas of particular importance were patrolled repeatedly, while others were surveyed only once, due to great distances or bad weather conditions. About 200 hours were flown on surveys between 25 March and 13 May. Field parties simultaneously searched possible denning localities on foot or on skis frequently using binoculars and spotting scopes. If dens were discovered, efforts were made to determine whether it was a maternity den or temporary den, mainly on the basis of tracks around the den. During aerial surveys it was often difficult to classify dens. Tracks and other signs were studied through binoculars, and they were photographed whenever possible. Pictures were then examined afterwards. The islands Edgeøya and Bartentsøya were surveyed several times during late March and throughout April. Not until 27 and 28 April did the aircraft find a group of eight and one single den in the eastern and northern part of Edgeøya. The northern coast of Nordaustlandet was surveyed from the air 8, 15 and 16 April. Prior to the last two surveys, there had been more than a week of very calm weather on Nordaustlandet (E. Nyholm. pers. comm.). One could assume, therefore, that dens which had been opened during the first week of April, would still be visible on the surveys. Twenty-six dens were located during 30 hours of effective flying (Fig. 1). On Kong Karls Land, ground surveys were made between 31 March and 18 April by two field parties. The western massif of Kongsøya was surveyed by a three man group between 31 March and 10 April. Thirteen dens were found in four effective days, and an additional nine were discovered during a three hour aerial survey on 10 April. On Svenskøya, a two man field party found 21 dens between 12 and 18 April, in six effective days. Another six dens were found during a two hours aerial survey on 18 April (Figs. 2 and 3).

The northern and eastern coast of Spitsbergen were surveyed repeatedly, but no dens or evidence of denning was found. There was, however, a relatively high degree of bear activity in some areas.

Of a total of 84 polar bear dens found in Svalbard in 1972, 54 were spotted from the air, while 30 were found by the field groups. Air observations could not be



Fig. 1. Polar bear dens recorded on Nordaustlandet and Edgeøya during aerial surveys in April and May 1972. X: Fuel depots. O: Single dens. Concentration of dens are given by bigger circles and a number.

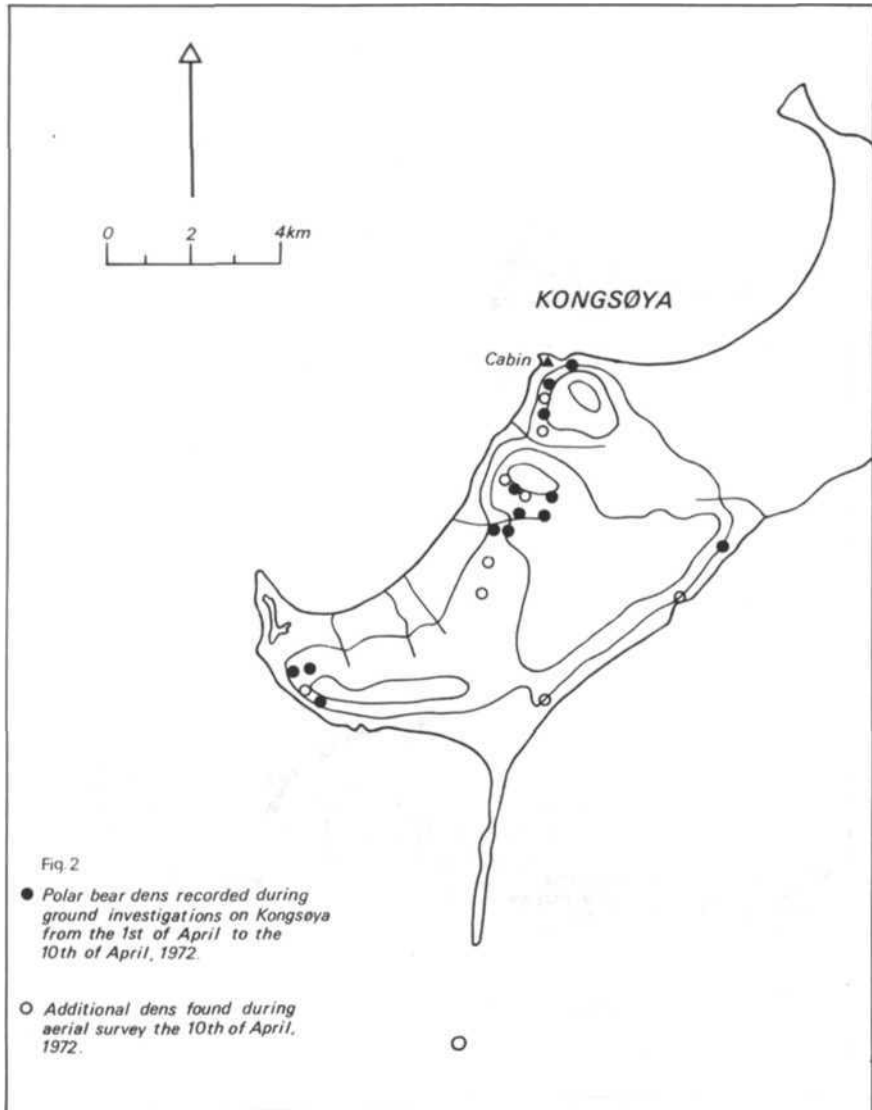


Fig. 2. Polar bear dens recorded during ground and aerial surveys on Kongsøya, Svalbard, April 1972.

proved to be more effective than ground surveys, or vice versa. Ground observation success depended upon topography, weather and light conditions. Drifting snow might fill up and cover dens shortly after they were abandoned. By the use of aircraft, observation success was dependent upon cruising speed and altitude, light conditions and the observer's skill and experience. The comparative air and ground counts on Kong Karls Land indicated that about 50 percent of the dens present in an area may be seen from the planes. Track observations and other signs indicated that about half the number of dens were maternity dens.

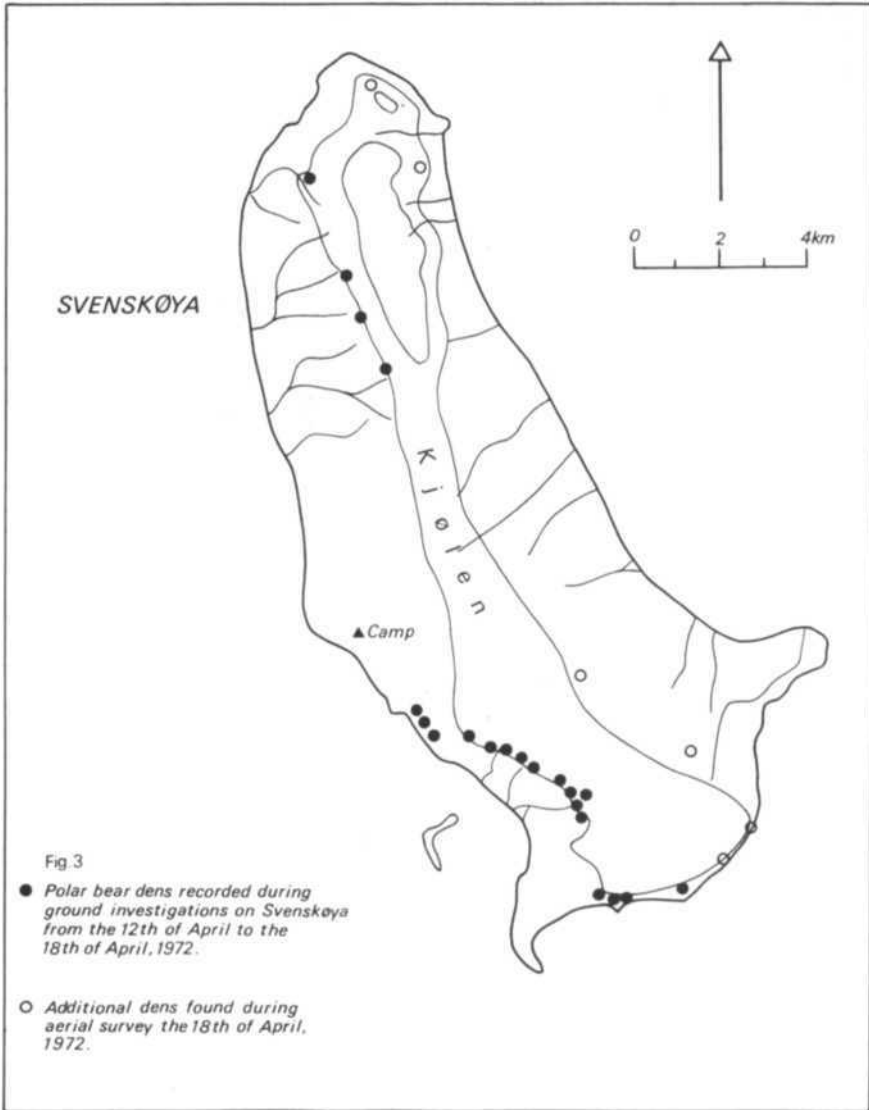


Fig. 3. Polar bear dens recorded during ground and aerial surveys on Svenskøya, Svalbard, April 1972.

DEN SURVEY IN 1973.

Studies of polar bear dens in 1973 were concentrated on Kong Karls Land. The purpose was to try and determine the absolute number of dens on the islands, to distinguish between den types whenever possible, and to describe den sites and den construction. Two field groups, each consisting of two men, carried out ground surveys on Kongsøya and Svenskøya between 15 March and 29 April and between 17 March and 28 April respectively. Each group surveyed the islands as often as possible in an effort to make absolute den counts. Each den found

was marked with bamboo sticks and monitored repeatedly. Efforts were made to distinguish between maternity and temporary dens. When abandoned, dens were in some cases dug out and described. The field groups also made observations of single bears and family groups and their activities. Bad weather conditions hampered the work for both groups. On Kongsøya, 26 days were considered effective days for observations, during which time 49 dens were found. Forty-six dens were found between 16 and 26 March. Nineteen dens were classified as maternity dens, six as temporary dens, while in 24 cases, the den type could not be determined. Of the unclassified dens, some were in accessible, while others were filled and covered by snow during storms, so that they could not be located afterwards. Five maternity dens and one temporary den were dug out and described. In most of the maternity dens, the observers found that changes had taken place during the winter. In many cases, the female had repeatedly dug out snow from the roof, and packed it under her on the floor. Thus, tunnels and chambers could be drastically changed and elevated half a meter or more, sometimes necessitating a new tunnel to be dug out when the family emerged in the spring. When the floor of the dens was excavated, several layers of urine and much feces were often found; in some cases, two kilos or more of feces were found. In many cases, urine and faeces were found in the vicinity of the den after it had been opened. Some dens were elaborately constructed, with two or more tunnels and several chambers or caves. Sometimes, digging had evidently been done by the cubs. A few maternity dens were rather simple, consisting of a tunnel and a chamber only. Most temporary dens consisted of a short tunnel, and in some cases also a chamber.

On Kongsøya, the majority of dens were oriented southwards, between west and southeast. Altitudes varied between 30 and 250 meters above sea level, and the angle of the den site varied between 20 and 65 degrees. The majority of the dens were located less than one km from the coast. Most of the dens were abandoned shortly after they had been opened, and the female bear and her cubs headed straight out into the pack. Only in three cases did the families stay in their dens for 12, 17 and 17 days, probably because the weather became bad shortly after they opened the dens for the first time.

Thirteen single bears were observed on Kongsøya, in addition to five females each with one cub, three females each with two cubs, and two females, each with one yearling.

On Svenskøya, 23 days were considered effective days for observation, during which time 16 dens were found. Ten dens were found between March 18 and 26 March. Two dens were assumed to be maternity dens, six to be temporary dens, while in eight cases, the den type could not be determined. Eight dens were dug out and described. The changes which had taken place in some of the Kongsøya dens were also observed in some on Svenskøya. The majority of the dens were facing southwest, on the lee side of a ridge running northwest to southwest along the island. Altitudes varied between 40 and 150 meters, and the angle of the den site varied between 20 and 40 degrees. Nineteen single bears were observed on Svenskøya, in addition to two females, each with one yearling. The locations of the dens on Kongsøya and Svenskøya are shown in Figs. 4 and 5.

DISCUSSION

The polar bear den surveys in Svalbard in 1972 and 1973 show that Nordaustlandet and Kong Karls Land must be considered as particularly important



Fig. 4. Polar bear dens recorded during ground surveys on Kongsøya, March and April 1973.

denning areas. In Kong Karls Land there were 0.3 and 0.4 dens per square km in 1972 and 1973 respectively. On Kongsøya alone, there were 1.5 dens per square km of habitat suitable for denning, in 1973. There is a marked difference in climate, temperatures and ice conditions between northern and eastern Svalbard and the rest of the archipelago, which may explain the choices for den sites. There are also noticeable differences in the topography.

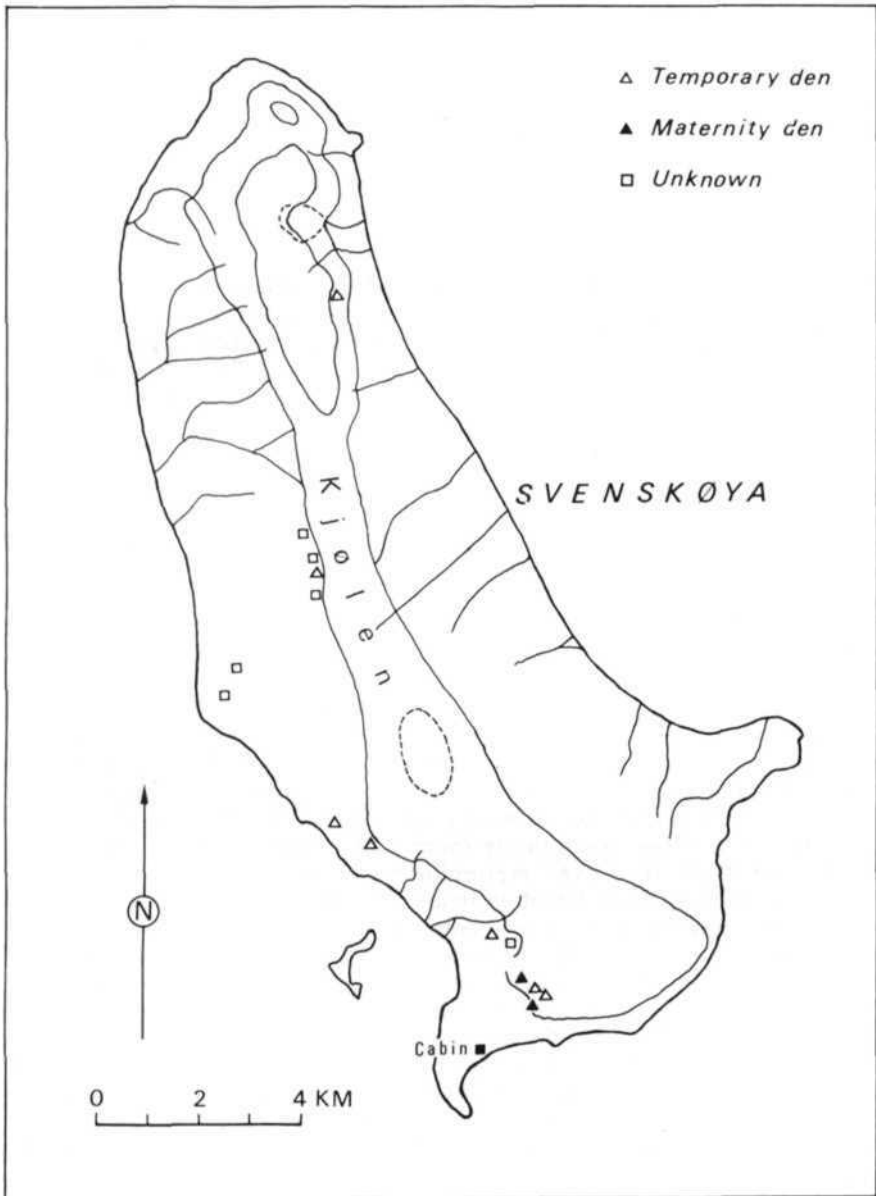


Fig. 5. Polar bear dens recorded during ground and aerial surveys on Svenskøya, March and April 1973.

The location of den sites in 1972 and 1973 seemed to coincide with the amount of snow which had accumulated in various areas throughout the year. Most dens were found on slopes where they were protected from prevailing winds from the north and northeast, and the den openings were normally facing away from the wind. Polar bear dens in the Hudson Bay area are sometimes dug out in the earth as well as in the snow (Jonkel *et al.* 1972). In Svalbard, earth

dens were not found, which coincides with observations from other parts of the high Arctic (Harington 1968; Uspenski and Kistshchinski 1972).

Only ten den sites occupied in 1972 on Kong Karls Land were used again in 1973. Even in these cases, the site may have been moved 100 meters or more, which however, could not be controlled. Uspenski and Kistshchinski (1972) state that the same den sites are not necessarily used again every year in Wrangel Island. It is reasonable to assume that wind and precipitation may alter denning conditions in an area from one year to another, thus affecting the bears' choice of den sites.

In Wrangel Island and in the Canadian high Arctic, most dens are found within 8 km from the coast, but some are located as much as 25 km inland (Harington 1968; Uspenski and Kistshchinski 1972). In the Hudson Bay area, two major den sites are located 20 and 70 km inland (Jonkel *et al.* 1972). Most of the dens in Svalbard have been found less than one km inland. This is partly due to the small sizes of the islands and peninsulas which may be suitable for denning.

Harington (1968) and Lønø (1972) state that polar bears depend upon the drift ice to get ashore and den. According to Vibe (1967), the drift ice is the major factor which determines where and when polar bears will appear along the coast of east Greenland. Lentfer (1972) states that unfavorable ice conditions may prevent the female bears from coming ashore, so that they are sometimes forced to den on the sea ice. On Wrangel Island, female polar bears will come ashore to den from mid September onwards, and in years with normal ice conditions, the majority will den up during October (Uspenski and Chernyavski 1965). According to Parovshchikov (1964), polar bears on Franz Josef Land will den up during October and November. In 1971, northern Svalbard and Kong Karls Land were embraced by the ice by early October. The ice edge probably reached Barentsøya and Edgeøya by the end of October (Vinje 1973 and pers. comm.). Compared with information from other parts of the Arctic, the ice conditions should therefore not have prevented the female bears from going ashore in any of these areas to dig their dens. In 1968, the ice was surrounding Edheøya and Barentsøya even earlier in the autumn (Larsen 1971). But very few signs of the denning were found on those two islands both in 1969 and 1972, in spite of relatively intense surveys both springs. It is unlikely therefore, that the ice conditions account for the lack of dens on Barentsøya and Edgeøya. In 1972, the edge of the loose ice (i.e. about 3/10 ice cover) was found at Kvitøya, 200 km north of Kong Karls Land, by late October. By 4 November, the loose ice had reached Kong Karls Land, while the more consolidated ice did not reach the islands before mid November (Vinje 1974 and pers. comm.). Polar bear dens were as abundant on Kong Karls Land in 1973 as they had been in 1972. If we assume that the drift ice determines when polar bears may come ashore, they could not have reached Kong Karls Land before the first week of November at best, in 1972.

Lønø (1970) states that most polar bear family groups leave their dens in Svalbard between 10 and 25 April. But the observations from Nordaustlandet and Kong Karls Land in 1972, indicated that most of the dens had been opened and abandoned before 1 April. Some females with cubs stay in their dens well after that date. When our data disagree with Lønø's findings, it may be explained by the fact that most of his information was based upon observations of family groups which were already out and may have abandoned their dens some time before the records were made.

The den surveys in Kong Karls Land in 1973 were quite extensive, and probably few dens were overlooked by the field parties. Almost four-fifths of the dens

found on Kongsøya, which were monitored, were maternity dens. But probably only one-fourth of the monitored dens on Svenskøya were maternity dens. The data from 1972 and 1973 indicate that about 40 maternity dens can be found on Kong Karls Land in a normal year. The comparative air and ground counts from Kong Karls Land in 1972 indicate that about 50 per cent of the dens were overlooked from the air. Thus, an evaluation of the observations from Nordaustlandet indicate that an estimated 20 to 30 maternity dens may be found there every winter. It is most probable that the total number of maternity dens in Svalbard in a normal year is well below 100.

It is questionable whether den counts can serve as a basis for accurate population estimates of polar bears. The accuracy of both ground and air surveys is limited by several factors. Ground surveys require a massive effort over a relatively short period of time. Data collected by different observers cannot immediately be compared, as observation techniques and efficiency vary. The ratio between maternity and temporary dens require close examination of almost every den found, which is impossible because some of them are inaccessible and because such inspection is time consuming. But information about the relative abundance of dens can be obtained through repeated counts over several years, and this may reveal changes in polar bear abundance and population composition. Combined air and ground surveys will probably give the best results, and the use of helicopters will probably be more effective than fixed wing aircraft. Surveys must be extensive during the period when the majority of polar bear females with cubs leave their dens. In Svalbard, surveys and den counts may be more easy than in many other areas, because so many of the dens are concentrated close to the coast.

ACKNOWLEDGEMENTS

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Paper 19

Polar Bear Management in Alaska

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INTRODUCTION

In the brief period since 1972, there have been major changes in polar bear, *Ursus maritimus*, management practices and authority in Alaska. This paper discusses past and present programs and what may happen in the future.

Polar bear management authority was vested in the Federal Government before Alaska became a state in 1959. The State of Alaska then had management authority until 1972, when control was returned to the Federal Government under provisions of the Marine Mammal Protection Act of 1972. There have been four eras of hunting under these two jurisdictions: native subsistence hunting, guided hunting with aircraft, guided hunting from the ground, and hunting under the Marine Mammal Protection Act of 1972.

NATIVE SUBSISTENCE HUNTING

Polar bears traditionally have been important in the subsistence economy of Alaskan Eskimos. Meat was used for food and skins for robes and clothing. Skins could be sold and bartered, an exchange that became especially important after commercial whaling began in the 1850s. Polar bears had a cultural significance; Eskimo ceremonies and dances were related to the harvest of bears, and a hunter's prestige was enhanced considerably by his success in taking bears. Alaskan Eskimos most commonly took bears when they came ashore to feed on beach carrion after freezeup in the fall. Hunters used dog teams for transportation, and most often hunted on foot. Occasionally trained dogs were used to bring bears to bay. Bears were also killed throughout the winter and spring, often while Eskimos were seal hunting and whaling. They were taken to a limited extent in the summer when walrus and bearded seals were hunted along the edge of the ice pack from boats. Harvests were greatest in years when heavy ice drifted close to shore early in the fall. The estimated annual harvests for 1925-53, based on records of skins shipped from Alaska, averaged 120 bears (Brooks & Lentfer 1966).

GUIDED HUNTING WITH AIRCRAFT

Trophy hunting of polar bears with aircraft began in the late 1940s. Most hunters took bears with the aid of a relatively few pilot-guides operating mainly from six coastal Eskimo villages. Bears were hunted from February to May when their tracks could be followed and light aircraft could be landed on the sea ice. Most often two planes flew together, and when a bear was located, the plane with the hunter was landed, and the bear was driven to him with the other plane. The skin was taken as a trophy and the meat was usually left on the ice. Males formed 70 to 80 percent of the harvest because young and females with young

were protected, and hunters often selected the larger animals, which were males. The average annual kill during the first decade of airplane hunting (1951-60) was estimated to be 150 bears (Brooks & Lentfer 1966); the average annual kill for the second decade (1961-72) rose to 260 (Lentfer 1973).

Native harvests decreased to about 25 percent of previous levels during the period when airplanes were used for hunting. This was partly because Eskimos were hunting less as they were changing from a subsistence toward a cash economy and partly because hunting with airplanes reduced the number of bears close to villages used as bases for hunting with planes. There was still an incentive for Natives to hunt, however, because hides not taken with the aid of aircraft could be sold. The annual Native kill averaged 13 percent of the total harvest for 1961-72 (Lentfer 1973).

State hunting regulations became more restrictive as pilot-guides became more efficient in taking bears and more people desired to hunt. Restrictions designed to limit harvests included seasons, bag limits, a permit system, limitation on the number of hunts individual guides could participate in each year, and complete protection for young and females with young.

As the demand for skins increased, both by trophy hunters and as a saleable item, some guides started taking bears illegally. Because these were not entered in harvest statistics there was a possibility of overharvest. The Alaska Department of Fish and Game, after close scrutiny of all aspects of polar bear guiding and hunting with aircraft, recommended to Alaska's game regulatory body, the Board of Fish and Game, that hunting polar bears with aircraft not be allowed after 30 June 1972. The recommendations pointed out that hunting with aircraft could be replaced by the much more acceptable method of hunting from the ground, and that illegal hunting with aircraft and a possible overharvest could not be controlled without a complete ban on hunting with aircraft. Public opinion in Alaska, the other states, and throughout the world strongly favored that hunting of polar bears with aircraft be stopped.

GUIDED HUNTING FROM THE GROUND

As a replacement for hunting with aircraft, the Alaska Board of Fish and Game adopted regulations effective 1 July 1972 to promote recreational hunting from the ground. Natives with dog teams and snow-machines were encouraged to start guiding trophy hunters. The regulations permitted hunting during late fall, winter and spring after pregnant females were in winter dens. Hunting pressure, degree of success and the total harvest were anticipated to be much lower than when aircraft were used, but most hunters that participated in a ground hunt would obtain a more aesthetically satisfying and memorable experience than from an airplane hunt. Hunters would be less selective, and would take a higher ratio of females. However, with the reduced hunting pressure, the total number of females harvested would be smaller.

From an economic standpoint, guided hunting from the ground could benefit Arctic coastal villages more than hunting with planes because guide fees would remain in the villages. Because the new regulations were in effect only from 1 July to 21 December 1972, when they were superseded by the Federal Marine Mammal Protection Act of 1972, the recreational ground hunting program did not become established.

HUNTING UNDER MARINE MAMMAL PROTECTION ACT OF 1972.

Polar bears, although not generally considered marine mammals, were nonetheless included in the more than 20 bills and resolutions introduced in the United States Congress in 1971 and 1972 for protection of ocean mammals. The general feeling among legislators, including Senator F.R. Harris of Oklahoma, Representative D. Pryor of Arkansas, and Senator H. A. Williams, Jr. of New Jersey, who introduced original ocean mammal protection bills, was that marine mammals should be completely protected without provision for management programs and utilization. Preservationist organizations, well represented in Washington, D.C., exerted considerable influence to have all hunting of marine mammals, including polar bears, stopped. The Marine Mammal Protection Act of 1972 (Public Law 92-522), as passed, placed a moratorium of unspecified length on the hunting of all marine mammals. Compromises reached before passage exempted Alaska Natives from provisions of the moratorium and provided for waivers of the moratorium and management programs under certain conditions.

The Department of Commerce is responsible for implementing the Act for certain species and the Department of Interior for the others, including polar bear. Regulations pertaining to polar bears are included in Interior Department regulations for the entire Act (U.S. Department of Interior, 1974).

The Act allows Alaskan coastal Eskimos to take polar bears at any time for subsistence or to obtain skins for manufacture into traditional items of handicraft or clothing without restrictions on the number, sex, age, or method of taking, other than that waste shall not occur. Current regulations providing for subsistence are more liberal than the previous State regulations which allowed subsistence hunters to take only three bears a year and did not permit taking of young and females with young. State regulations had also allowed any Alaskan resident to hunt for subsistence, rather than only Natives.

Allowing young and females with young to be taken is not in accordance with recommendations of the International Polar Bear Specialist Group that young and females with young be protected throughout their range. It also causes Alaskan Natives to question the credibility of game regulations and managing agencies. The Alaska Department of Fish and Game for a number of years said that it was necessary from a conservation standpoint to protect young and females with young. The Act now allows these bears to be hunted by Natives. One might argue that before and during part of the aircraft hunting era, Natives took bears without restriction and in greater numbers than today probably without harm to the population. The two periods are not comparable, however, because oil and gas development along Alaska's north coast could now be disturbing bears in denning areas and lowering productivity. If so, it is necessary to fully protect young and females with young.

The Marine Mammal Act prohibits interstate commerce in skins taken by Natives. Regulations to implement the Act, however, prohibit all transfer and sale of skins to non-Natives by Natives. Also, as an aid in controlling traffic in hides, a regulation published 25 February 1974 requires tanneries to be registered before they can tan polar bear skins. Thus far only one tannery has asked to be registered and has not yet received final approval. Few or no Natives have started manufacturing traditional Native articles for sale from polar bear skins. Because of this and because skins cannot be sold or transferred to non-Natives or yet tanned commercially, some have been handled poorly, others have spoiled, and some now in storage may also spoil. Skins from bears taken in the future may also be wasted.

The Marine Mammal Act has sharply reduced the number of bears harvested. Seven were taken in 1973, and 40-50 were taken in 1974. The number of bears along the Alaskan coast increased during the winter of 1973-74, possibly because the Marine Mammal Act had sharply reduced harvests for two seasons. Some residents are now concerned that polar bears may become numerous enough to develop into a nuisance or hazard in some areas. The Marine Mammal Act has also affected the United States polar bear research program, both beneficially and adversely. Increased research funds are now available, but the involved procedures for issuing a permit required for research have caused delays and caused preservationist groups to attempt to have research stopped through court action.

INTERNATIONAL ASPECTS

Management agencies in other countries are concerned that passage of the Marine Mammal Act could generate support for similar acts in their countries. They feel they now have the authority and the ability to effectively manage their bears without the constraints imposed by legislation similar to the Marine Mammal Act.

There are also international aspects of polar bear management not related to the Marine Mammal Act. Polar bears occur on the high seas and cross international boundaries necessitating international agreements for research and management. The International Union for Conservation of Nature, with technical assistance from the affiliated Polar Bear Specialist Group, was instrumental in drafting an international agreement. Representatives from the five polar bear nations, Canada, Denmark, Norway, the USSR and the United States, met at Oslo, Norway, in November 1973, to prepare a final draft of the agreement. This Agreement on Conservation of Polar Bears was signed by four of the delegations at the conclusion of the Oslo Conference; the fifth nation has since signed it. The agreement becomes effective when ratified by three of the five nations.

The agreement is based on the premise that polar bear nations have the ability to manage populations occurring on and adjacent to their coasts. It creates a *de facto* 'high seas' sanctuary for bears by not allowing them to be taken with aircraft, large motorized boats, or in areas where they have not been taken by traditional means in the past. The agreement states that nations shall protect ecosystems of which polar bears are a part and emphasizes the need for protection of habitat components such as denning and feeding areas and migration routes. The agreement also states that countries shall conduct national research, coordinate management and research for populations that occur in more than one area of national jurisdiction, and exchange research results and harvest data. Resolutions appended to the agreement state that delegates to the conference favor establishment of an international hide marking system to control traffic in illegal hides, protection of cubs and females with cubs, and prohibition of hunting in denning areas when bears are moving into these areas or are in dens. The agreement allows hunting as it was conducted in 1973. In the United States, the management program that was in effect immediately preceding the Marine Mammal Act could be reinstated; i.e. recreational and subsistence hunting from the ground.

FUTURE

One of four actions could provide needed protection to young and females with

young: (1) new legislation could be enacted in response to the resolution of the Oslo conference which calls for protection of cubs and females with cubs; (2) the Marine Mammal Act could be amended; (3) the moratorium could be waived, and a management program with appropriate restrictions put into effect; (4) polar bears could be declared depleted under a certain provision of the Act and restrictions then applied to Native taking. Polar bears cannot be considered depleted from a biological standpoint nor, in my opinion, can they be declared depleted according to definitions in the Act. Furthermore, an arbitrary designation of polar bears as depleted might weaken support for declaring other species depleted, threatened or endangered when there is a real need to do so.

Polar bears are a renewable resource, and certain numbers can be harvested without jeopardizing populations. Subsistence and recreational hunting from the ground are uses acceptable to large segments of the hunting and even the non-hunting public. The Marine Mammal Act provides for waivers of moratoriums and enactment of State management programs compatible with the Act. The State of Alaska has applied for management authority for species it formerly managed, including polar bears in territorial waters. Alaska's proposed management plan is basically the same as the management program in effect after airplane hunting was stopped and before the Marine Mammal Act was enacted; i.e. recreational and subsistence hunting from the ground. The application and management proposal will be reviewed by the public, the Department of the Interior, and the Marine Mammal Commission and its Scientific Advisory Committee created by the Act. Preservationist groups are expected to strongly oppose waiver of the moratorium and return of management authority to the State. The final outcome is difficult to predict. In my opinion, the State of Alaska is the logical managing authority for bears along its coast and the Federal Government should remain involved because of international agreements covering animals that cross international boundaries or occur in international waters.

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Paper 20

The Black Bear in Pennsylvania—Status, Movements, Values, and Management

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The black bear, *Ursus americanus*, in Pennsylvania is a trophy that is sought by as many as 130,000 hunters each year. The heavy hunting pressure and other factors are causing increased concern for the welfare and survival of huntable populations of bears in the state. Records of annual harvests since 1915, demonstrate the productivity of the range, the long-term value of the resource and the interest of the hunters in this animal. There have been only two closed hunting seasons, 1934 and 1970. The 1970 closure occurred when annual harvests were less than 300 animals (Table 1). The season was closed to allow the bear population to increase and maintain itself without the pressure of hunting losses.

With the bear on the endangered list in Maryland, nearly extirpated from New Jersey, and possibly over-harvested in the Catskill Mountain section of New York, any indications of a decline in the Pennsylvania bear population are cause for increased concern to hunters and the general public. Thus, when the legal harvest during a one-day season declined from 370 in 1972 to 299 in 1973, a decline in the population was suspected. In view of the heavy hunting pressure on the bear and the general interest in its welfare, a more sensitive management program for Pennsylvania's bear population is needed.

The bear population in Pennsylvania is widely distributed on good-quality range. Individual animals are healthy, the population is productive, and most

TABLE 1. AVERAGE AGE OF HUNTER-KILLED BEARS 1967-1973.

Year	Season Length (Days)	Legal Kill ¹ for Season	Sample Size	Average Age ² in Years
1967	6	568	30	4.18
1968	6	218	None	Unknown
1969	2	295	56	4.00
1970	Closed	None	None	—
1971	2	488	120	3.00
1972	1	370	149	3.72
1973	1	299	246	2.59

¹ Reports of Pennsylvania Game Commission.

² Includes both males and females. Excludes illegal cub kills.

bear range is occupied, although apparently below carrying capacity. Forest areas are composed largely of mixed-oak, *Quercus*; oak-hickory, *Carya*; beech-birch-maple, *Fagus-Betula-Acer*; and transition zones (Ferguson 1968). Spruce-hemlock, *Picea-Tsuga*; tamarack, *Larix*; and blueberry, *Vaccinium*, swamps are a small but important type in the north-east (Eveland 1973; Kordek 1973). Centers of bear populations (in the north-central and north-east portions of the state) coincide generally with commercial forest areas which have low human population.

Many important problems are associated with management of the bear population. In some localities, populations are low, and sex and age class imbalance may exist in parts of the range. Increasing recreational pressure from metropolitan areas is encroaching on much of the bear's range (Anon. 1969). It is obvious that both bears and humans must make adjustments if bear populations are to be maintained. The fact that more than one of every 12 people in Pennsylvania buys a hunting license indicates the potential support for intensified programs to manage the black bear.

The great variety of foods available throughout the year makes the Pennsylvania range potentially productive for bear. This range has supported average annual legal kills of 456 bears from 1915 to 1944 and 382 bears from 1944 to 1969. The productivity of the range is further enhanced by relatively mild winters during which food is available, thereby permitting some bears to stay active and feed for the entire winter (Matula 1974).

A wide variety of high-quality bear foods are produced on the range. Blueberry, juneberry *Amelanchier*, and blackberry *Rubus* fruits are important summer foods; fall mast and fruit allow further weight gains before denning and deer carrion is a regular supplement during winter and spring. The high quality of the range is demonstrated by cubs weighing 36 kg in the fall (Eveland 1973; Kordek 1973; Matula 1974) and by bears leaving dens in the spring in good to excellent condition.

Pennsylvania's 130,000 hunters can pursue bears on approximately 3.64 million hectares of range. Even though dogs are not legally used for bear hunting, the scores of hunters afield are very effective in moving the bears about. Thus, the large number of hunters results in heavy harvests of available animals. Experienced hunters familiar with bear retreats and trails are relatively few but highly successful. Even with the many hunters, some localities have a relatively low hunting pressure. The continued survival of huntable bear populations appears related to three factors: the presence of swamps and similar retreat areas in the primary range that is not penetrated by the hunter; private and public refuge areas closed to hunting; and peripheral bear range that regularly contains a few bears but which receive relatively light hunting pressure. These areas significantly increase the overall survival rate of the breeding-age stock.

The Pennsylvania Cooperative Wildlife Research Unit began studies in 1967 to obtain data for the development of a contemporary management plan. A series of studies by wildlife graduate students, assisted by Pennsylvania Game Commission biologists and game protectors, have played a major role in gathering field data. However, more data are needed to permit analyses to meet the following research objectives:

1. To characterize the black bear population in Pennsylvania by examining the age and sex of animals killed and by capturing, marking and releasing free-ranging animals.

2. To determine movements of black bears in relation to age, sex, season, food supplies, behavior, human disturbance and other factors. (Movements of black bears in and around northern Pennsylvania frequently take them into New York. Research is, therefore, coordinated between the two states to evaluate this interaction.)
3. To establish baseline data on blood parameters of black bear that may relate to changing disease or parasite loads or physiological or behavioral changes in the population.
4. To determine the productivity of the black bear population in Pennsylvania by records of cub production, examination of female reproductive tracts, and reconstruction of bear population data.
5. To develop or adapt a computer program to permit simulation of the population dynamics of bear in Pennsylvania and provide a basis for the utilization of data on kill, age and location, and other information to predict population trends and to guide management.

REPRODUCTIVE SYNCHRONY

In Pennsylvania, harvest and observational data indicate an apparent reproductive synchrony in which a majority of cubs are produced in alternate years. This synchrony is apparent from cub observations obtained in Pike County, Pennsylvania (Table 2) and is similar to the situation reported in New York (Free & McCaffrey 1972). Female black bears producing cubs that survive into the summer months do not mate until the following year. Thus, female black bears usually produce a cub or cubs every second year. The majority of females give birth for the first time in the same year that their mothers are producing another litter. If, by some as yet unexplained circumstance, an age class is severely depleted, the result will be that the majority of cub production will occur every other year with alternate high and low numbers of cubs produced in successive years.

Differential cub production in alternate years is also suggested by the number of hunter-killed cubs and yearlings (Table 2). Although the killing of cubs is illegal in Pennsylvania, it does occur, especially in years of high cub production such as 1972 when 52 were killed. The percentage of yearlings in the kill increased during years following high cub production, as in 1973 when 50 percent of the kill were yearlings. In contrast, only nine percent of the legal harvest had been yearlings in 1972.

In years following high cub production, the yearling age class is an important segment of the total kill as noted above. The total kill in this case usually exceeds the kill during the years when most cubs are produced (Table 2). Thus, larger legal kills have usually occurred in odd-numbered years than in the preceding even-numbered or cub-producing year. For example, in 1968, 218 bears were killed; in 1969, 295; in 1970, the season was closed; in 1971, 488; in 1972, 370; but in 1973, only 299. The decline in 1973 is believed to be the result of low population and the tendency of bears to move extensively and thereby elude hunters during years of natural food shortages.

The apparent synchrony that existed from 1958 until 1966, during which time the legal bear kill was higher in the even-numbered years than in the preceding odd-numbered years, was reversed during 1966 and 1967 with two years of exceptionally heavy kill (605 and 568, respectively). This reversal occurred in 1967 when many cubs were lost (138 bears illegally killed, mostly cubs);

TABLE 2. CUB OBSERVATIONS AND HUNTER HARVESTS, 1970-73.

Year	Cubs Observed ¹ in Pike County, Pennsylvania	Cub Kill Statewide During Season	Percent Yearlings in Harvest Statewide	Statewide Harvest	Size of Sample of Kill for Age Determination
1970	28	None	Hunting Season Closed	0	0
1971	2	41	23	488	120
1972	37	52	9	370	149
1973	10	19	50 ²	299	246

¹ Cub observations reported for Pike County only because this was the one area where a worker was present to record observations.

² This percentage seems unusually high and may reflect an overharvested population with relatively fewer older bears present.

subsequently, more cubs have been produced in even years. It is unlikely that the complicated combination of factors that precipitated this reversal can be completely explained, but the combination of heavy loss to the 1967 age class, with high kill and consequent possible loss of pregnant females in 1966, was probably important.

AGE

Data have been collected on ages on harvested animals, bears killed in other ways, and live-trapped bears. The sample of bears examined has increased from 30 in 1967 to 246 in 1973. For harvested bears, a downward trend was found in the average age from 1967 to 1973, excluding 1968 when insufficient data were available and 1970 when the hunting season was closed (Table 1). As the sample size increased from 30 bears examined in 1967 to 246 in 1973, data became more meaningful. Although a general decline in average age is shown from 4.18 in 1967 to 2.59 in 1973, 1972 does not appear to follow the pattern (Table 1). This is believed to be the result of the hunting season closure in 1970 and the unusually high (34%) representation of 2¾-year-old animals in the 1972 harvest sample. These age data, information on the declining legal harvest (from 1915 to 1944, annual harvests averaged 456 bears; and from 1945 to 1969, the average was 382 bears), and the smaller proportion of adult bears in the kill (42% over 3¾ years of age in 1972 and 16% over 3¾ years in 1973) suggest that the Pennsylvania population is overexploited.

MOVEMENTS

The movements of bears are important to management programs because of the critical influence they have on harvests, nuisance and damage problems, losses on the highways, and utilization of available foods. In addition to the usual marking and recovery methods, radio telemetry techniques have been employed to obtain data needed for management. Detailed data on the extent of movements in north-eastern Pennsylvania were obtained by radio-tracking bears with the aid of fixed-wing aircraft (Matula 1974). One male bear, trapped and moved because he was raiding cabins, traveled 80.5 km north from his release point into New York and then returned almost to the original capture site approximately one month later. Another male was tracked for two winters and apparently remained active during both, although he utilized a winter nest in a swamp during part of the second winter. Two females equipped with radio collars were tracked to determine their home range and later to locate their winter dens.

Home range data obtained for seven instrumented bears (Table 3) suggest two items of management importance: (1) females are less mobile and can, once located, be given protection by refuge or closed areas; and (2) the more mobile males can be harvested outside of the female ranges or cub production areas.

On the average, nuisance animals ranged farther than non-nuisance animals, 19 km compared to 10.2 km, respectively (Table 4). The fact that nuisance bears were transplanted from the nuisance site undoubtedly affects these bears and may lead to the greater movements recorded. From the management standpoint, alternative techniques for nuisance animal management are needed because nuisance bears are capable of extensive moves and may return to the original site. As was also indicated in telemetry studies, males moved on the average farther than females, 15.2 km compared to 5.4 km, respectively.

TABLE 3. HOME RANGE CALCULATED FOR SEVEN BEARS IN NORTHEASTERN PENNSYLVANIA AS DETERMINED BY RADIOTRACKING AND TRAPPING.

	Bear Numbers						
	192-193	215-216	221-222	245-246	272-273	274-275	276-277
Sex	M	F	M	M	F	F	F
Age at Time of First Capture	2+	4+	3+	2+	5+	3+	3+
Time Period Observed	05/27/72- 01/19/74	09/12/72- 09/10/73	10/24/72- 10/04/73	04/09/73- 10/12/73	08/28/73- 12/19/73	09/04/73- 10/28/73	09/04/73- 11/14/73
Number of Observations	90	12	12	17	49	25	37
Home Range Estimates* km ²	-1	9.81	41.49	571.98	44.39	77.75	26.62
	-2	14.71	62.24	857.97	66.59	116.63	40.09
	-3	10.81	93.75	880.48	50.01	338.55	27.17
	-4	16.22	140.62	1320.73	75.02	507.82	40.75
	-5	3.19	13.49	228.79	39.07	40.43	18.71
	-6	1.98	8.38	121.26	12.25	17.73	6.73

*cf. Jennrich & Turner 1969.

1 and 2 — Based on the co-variance matrix of capture loci at the (1) 95% and (2) 99% confidence region.

3 and 4 — Based on the mean recapture radius at the (3) 95% and (4) 99% confidence region.

5 — Based on the estimated convex polygon method.

6 — Based on the estimated minimum polygon method.

TABLE 4. RECORDED MOVEMENTS OF BLACK BEARS FROM TRAPPING TO LAST RECAPTURE OR KILL, 1967-73.

Number & Category of Animals	Age in Years		Km Moved from Nuisance Site		Km from Original Capture to Final Location		Period of Observation (Months)	
	Ave.	Range	Ave.	Range	Ave.	Range	Ave.	Range
<u>Nuisance</u>								
10 Males	2.4	(.75-4+)	44.6	(0-130.4)	21.4	(0-40.2)	9.0	(1-48)
6 Females	4.3	(1-10)	44.4	(9.7-112.6)	14.6	(0-67.6)	4.5	(1-13)
16 Total Nuisance	3.2	(.75-10)	44.6	(0-130.4)	18.9	(0-67.6)	7.1	(1-48)
<u>Non-Nuisance</u>								
32 Males	2.1	(.75-4)		None	12.9	(0-104.6)	7.0	(.2-33)
16 Females	3.1	(.75-6)		None	4.0	(0-14.5)*	9.2	(.2-48)
48 Total Non-Nuisance	2.47	(.75-6)			10.1	(0-104.6)	6.2	(.2-48)
42 All Males	2.24	(.75-4)			15.2	(0-104.6)	7.5	(.2-48)
22 All Females	3.43	(.75-10)			7.0	(0-67.6)	8.3	(.2-48)
64 All Bears	2.65	(.75-10)			12.4	(0-104.6)	7.8	(.2-48)

*Six of these bears had no movements recorded.

Data collected in northeastern Pennsylvania indicate that Pike County is an important cub production area (37 cubs in 1972) for this part of the state (Table 2). Other data showing movements of Pennsylvania bears to the Catskill area of New York indicate the potential importance of the Pike County area to this New York population. Therefore, closure of bear hunting season in Pike County would be expected to benefit a large area of Pennsylvania and the southern Catskill area of New York.

RANGE AND KILL

Our studies, which showed that a high percentage of young bears were being killed, suggest that bears in part of the north-central range were over-harvested by 1968 (Wakefield 1969). In a 6, 883 ha study area, previously the site of much hunting activity and good harvests, only two young males were located and tagged during extensive snaring efforts in 1967. During the 1967 hunting season, eight legal bears and three cubs were killed. Although four of the 1967 legal bears were females, 64 to 69 kg dressed weight, there was only one small female among the nine bears killed in 1968. Since 1968, annual kills in the area have been limited to a few young male bears.

On a state-wide basis during 1973, the average age of male bears killed was only 2. 19 years, and one-half of all bears harvested were yearlings. When considered with other data from trapping records and previous hunting seasons, this suggests that the young, inexperienced males are more mobile and, therefore, more susceptible to harvesting. It also suggests, because the total 1973 harvest was only 299 bears, that there were few older bears available to the hunters.

PROBLEMS

Bear population losses from all causes except legal kill are high, ranging from 21 to 38 percent of the legal kill between 1969 and 1973 (Table 5). The apparent increasing trend in road kills from 19 in 1969 to 77 in 1973 reflects the increased highways and higher traffic speed in bear country and is of great concern because there seems to be no ready solution by management. The high total of 'other' losses in 1972 reflects the high illegal cub kill (52) in a year of high cub production.

TABLE 5. TOTAL BEAR LOSSES OTHER THAN HUNTING.

Year	Road Kill	Total all Losses Other than Legal Hunting	Percent of Legal Kill
1969	19	65	22
1970 ¹	42	59	—
1971	40	102	21
1972	54	139	38
1973	77	110	37

¹ No legal hunting season.

The movement of bears appears to be at least partially related to food availability as demonstrated by the influx of animals into areas of high acorn (Wakefield 1969), berry and apple production. It suggests that bears, particularly males occupying large ranges, visit these areas with some regularity and will remain there for undetermined periods if food is available. During years of extreme natural food shortages, males may concentrate in cornfields and even females may cause considerable damage within their more limited ranges.

The general mobility of the bear population presents a difficult problem for management. Occasionally, this mobility results in heavy legal kills because hunters learn where bears concentrate to feed, and they, in turn, concentrate their efforts there. In years of food shortage, bears may not be concentrated where hunters traditionally seek them and consequently the kill may be low. However, in 1973, a year of bear food scarcity, a reduced legal kill was offset when increased numbers of bears were killed on the highways and shot because of crop damage.

Major changes are occurring in much of the Pennsylvania range, but the changes and the problems they create are particularly critical in the prime bear range in the glaciated northeast. Here, entire towns are developing around the swamps and lakes which are important retreats for bears. The net result of this disturbance and loss of habitat has yet to be measured, but carrying capacity is being reduced. Conflict between suburbanites and bears who raid garbage cans, frighten children and enter cabins, required further reductions in the populations. The problem is further heightened by individuals who feed bears, thereby setting the stage for damage in other areas and adding to the bear-people problem.

SOME MANAGEMENT ALTERNATIVES

With the broad interest in bears by hunters and non-hunters, the implications of a decline in the bear population of Pennsylvania and the increasing problems with them, a perceptive, flexible management program is necessary. It has been demonstrated that the bear, although extremely powerful and potentially dangerous, is basically timid and can live in reasonable proximity to man if the proper food and cover situations are maintained and if people have some understanding of bear behavior and requirements. Obviously all the data are not yet at hand to develop a contemporary management program, but some actions based on present knowledge appear desirable: (1) a broad public and hunter information program is required; (2) the needs of the bear in a developing Pennsylvania must be understood and accepted by the public and hunters; and (3) artificial feeding by the public, which creates problems of bear-people contact, should be eliminated.

A further important management opportunity exists in the recognition of high cub production areas such as Pike County. Closure of such cub producing areas during bear season may be a feasible means of helping to assure a viable population of bears. Where it is demonstrated that larger numbers of cubs are born in certain years, as in Pike County, it is possible to close these areas during 'cub years' and reduce the high loss of cubs.

With over 100,000 hunters seeking to bag a bear annually and the other pressures that are being placed on the population, a permit system to limit the number of bear hunters may be needed.

The ultimate management tool available for protecting and increasing the population is season closure until it is determined that the population is reproducing at a rate equal to its losses. The practical problem arising under this system is the potential for high nuisance and agricultural damage before the desired equilibrium is obtained. It would seem more desirable, therefore, to use a hunting system that would permit controlled numbers of hunters to harvest animals in specified areas to minimize crop damage while assuring the protection of female bears and cubs in other areas.

The success of any system will be closely tied to the public relations program noted earlier and to the availability of adequate data on which to base management decisions.

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Paper 21

Use of M99 Etorphine and Antagonists to Immobilize and Handle Black Bears

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INTRODUCTION

A research study of the black bear (*Ursus americanus*) in the Catskill Region of New York was initiated in 1970 by the State Department of Environmental Conservation in response to declining bear harvests and increasing human use of previously wild areas. The continuing study was designed to determine the present status of the Catskill bear population with respect to population size and dynamics, extent of occupied range, reproductive potential, and basic relationships of bears' and man's influence on bear habitat.

As part of the study, bears were live trapped and handled to obtain data on age, sex, reproductive success, physical measurements, and to mark for later identification. This paper reports the results of using the narcotic drug M99 Etorphine with its antagonists, M50-50 Diprenorphine and M285 Cryprenorphine, for immobilizing black bears during June, 1970 to May, 1974.

Earlier immobilizing techniques for black bears utilized ether, sodium pentobarbital, and succinylcholine chloride (Erickson 1957; Black 1958; Black *et al.* 1959). More recent black bear studies have used the drug phencyclidine hydrochloride (Pearson *et al.* 1968) or a combination of phencyclidine hydrochloride and promazine hydrochloride (Seal *et al.* 1970).

Because of the narcotic properties of M99, its use as an immobilizing agent has been restricted, although it has been used for polar bears (Flyger *et al.* 1967; Larsen 1971) and for other big game. Other wildlife agencies in the United States are presently employing M99 for black bear investigations (R. Ernst, M. R. Pelton, J. Raybourne, J. Rieffenberger; personal communications).

MATERIALS AND METHODS

Both culvert (or barrel) traps and Aldrich foot snares were used to capture black bears. Culverts were set at garbage landfills, homes, campgrounds or apiaries where bears had been previously observed. The procedure of culvert trapping has been described by Black (1958). During 1970, ether was used to immobilize bears captured in culvert traps (Black *et al.* 1959). Bears trapped in culverts after 1970 and all bears trapped in foot snares during the present study were processed with M99, delivered by means of carbon dioxide propelled syringe darts, fired by handgun projector (Palmer Chemical and Equipment Company, Douglasville, Georgia).

Because of a relatively low density of bears in the Catskills, trapping with foot snares has proven to be an appropriate technique (Miller *et al.* 1973). Most bears were trapped using the snare in isolated areas. Trapping success using foot snares was approximately 200 trap-nights per capture.

TABLE 1. BLACK BEARS IMMOBILIZED SUCCESSFULLY USING A SINGLE INJECTION OF M99 ETORPHINE.

Number ^{1/}	Snare(s) or culvert(c)	Sex	Age class	Weight (kg)	Dosage (mg/kg)	Immobiliza- tion (min.)	Recovery ^{2/} (min.)	Remarks
70-14	s	M	1	39.5	.0152	11	15	
70-17	s	M	1	35.5	.0141	10	2	
71-10	s		6	67.0	.0180	10	2	
71-11	s	M	1	34.0	.0147	6	9	Captured in company of year- ling male Very wet; actual weight probably less
71-12	s	M	6	157.0	.0112	9	2	
73-1	c	M	2	81.0	.0154	13	3	
73-3	s		9	74.0	.0134	6	4	
73-1 r ^{3/}	s	M	2	(81.0)	(.0154)			Recapture from previous year
73-6	s	F	1	est. 31.0	est. .0194	7 6	3 14	Not weighed
73-7	s	F	5	56.0	.0178	6	3	
73-8 r1	s	M	8	158.0	.0110	10	4	
73-9	s		7	71.0	.0141	7	4	
73-11	s	M	1	29.5	.0119	6	2	
73-18	s	M	2	98.5	.0143	8	2	
73-20	c	M	2	95.0	.0220	11	14	Recapture from previous year

73-21	s	M	3	103.5	.0097	9	2	
73-22	c	F	7	105.0	.0134	10	2	
73-20 rl	s	M	2	94.5	.0158	10	2	Recapture, same year
73-28	s	M	1	60.0	.0167	6	2	
73-18 r	c	M	2	(98.5)	(.0143)	11	1	Recapture, same year; not weighed
73-20 r2	c	M	2	est. 92.5	.0152	8	19	Recapture, same year
73-8 r2	c	M	8	211.0	.0132	11		Recapture, same year
73-34	s	M	1	48.5	.0143	4	17	
73-23 r	s	M	3	153.5	.0163	20	5	Recapture, same year
73-31 r	c	M	1	64.0	.0218	12	2	Recapture, same year
73-32 r	s	M	2	104.0	.0167	14	1	Recapture, same year
74-1	c	M	11	152.0	.0125	17	4	
74-2 rl	s	M	2	66.0	.0158	9	11	Recapture from previous year
74-3	s	F	4	54.0	.0185	5	7	
74-2 r2	s	M	2	73.0	.0136	7	15	Recapture, same year
74-4	s	M	1	23.0	.0238	6	1	
74-5 r	s	M	4	105.0	.0200	11	3	Recapture from previous year
74-6	s	M	1	30.0	.0167	11	2	Wet and caked with mud
74-7	s	M	2	77.0	.0183	15	1	

1/ Bears are listed chronologically, in order of capture. First number indicates year of capture (e.g., 70 for 1970).

2/ Time, from injection of antagonist drug M285 or M50-50, to complete recovery and departure of bear from trap site.

3/ Recapture of a bear previously handled and ear-tagged.

TABLE 2. BLACK BEARS REQUIRING MORE THAN ONE INJECTION OF M99 ETORPHINE.

Number ^{1/}	Snare(s) or Culvert(c)	Sex	Age Class	Weight (kg)	Dosage Initial	Dosage Total	Immobiliza- tion (min.) ^{2/}	Recovery (min.) ^{3/}	Remarks
70-11	s	M	15	127.0	.0079	—	24	15	Ether used to complete handling
70-12	s	M	6	189.0	.0079	.0158(2) ^{4/}	41	27	Initial dose had no effect
70-13	s	F	4	52.0	.0077	—	42	20	Ropes and ether used to complete handling
70-15	s	M	3	91.0	.0110	—	24	13	Ether used to complete handling
70-16	s	M	3	88.0	.0099	—	30	3	Ether used to complete handling
70-31	s	M	12	149.0	.0051	.0152(2)	21	20	Ether used to complete handling
71-2	s	M	6	172.5	.0101	.0200(3)	113		Weight under-estimated
72-2 r ^{5/}	s	M	7	177.0	.0119	.0152(2)	57	22	Recapture from previous year. Weight under-estimated
73-2	c	M	12	233.5	.0055	.0268(5)	300	2	Dart pistol misfired, only partial dose received.
73-19	s	M	6	188.5	.0075	.0202(3)	62	3	Dart pistol misfired, only partial dose received.

73-23	c	M	3	158.0	.0132	.0200(3)	67	1	Initial dose made bear drowsy but not manageable, dogs barking near
73-31	c	M	1	67.0	.0209	.0262(2)	33	2	At 24 min. bear was nearly immobilized
73-32	c	M	2	113.5	.0123	.0242(3)	66	1	Additional .35 mg given with hand syringe. Weight initially underestimated; additional doses needed to immobilize.
73-33	s	M	1	51.5	.0097	.0165(2)	51	5	Weight initially underestimated.
73-35	c	M	—	(113.5) est.	(.0154) est.	.0220(3) est.	—	—	Bear never fully immobilized; pulled away and escaped; not weighed.

1/ Bears are listed chronologically in order of capture. First number indicates year of capture.

2/ Time, from injection of initial dosage of M99 to complete immobilization.

3/ Time, from injection of antagonist drug M285 or M50-50, to complete recovery and departure of bear from trap site.

4/ Parentheses denote number of doses of M99 required for immobilization in those instances when additional doses were given.

5/ Recapture of a bear previously handled and ear-tagged.

As a narcotic, the drug M99 Etorphine (American Cyanamid Company, Princeton, New Jersey) is subject to regulations of the Bureau of Narcotics and Dangerous Drugs of the United States Department of Justice. It was supplied in concentrations of 1 mg/cc distilled water. Drugs used to antagonize the effects of M99 included Cyprenorphine (M285) and Diprenorphine (M50-50) and were supplied in concentrations of 2 mg/cc. Following processing of a bear, the antagonists (M285 in 1970, M50-50 thereafter) was injected by hand syringe into the femoral vein at twice the concentration of dart-delivered M99.

Trapping was carried out from June to October in 1970, and thereafter during April, May, June, part of July and during September and October. In 1972, no major trapping effort was undertaken because of budgetary restrictions.

A bear caught in a foot snare was distracted by one crew member, while another fired the syringe dart into the upper hind leg muscles. In the case of culvert-trapped bears, the door was raised and a flashlight used to observe the bear's size. Again, one crew member attempted to draw the bear's attention towards the far side of the trap, while a second crew member fired the syringe dart through the partially raised door.

Dosages of M99 were based on an estimate of body weight. Originally, an intended dosage of .008 mg/kg body weight (.35 mg/100 lbs) was used at the manufacturer's suggestion. Subsequent field experience with the drug led to an increase in this dosage.

RESULTS

Thirty-six individual bears were immobilized and handled on 49 different occasions with M99 and its antagonists, M285 or M50-50. No cubs were trapped during this study. Foot snares accounted for the capture of 38 bears, while 11 were taken in culvert traps.

Handlings were divided into (1) those that were 'successful' in the sense that the bear became immobilized with a single dart containing M99, and (2) those that required additional doses of M99 or, in five instances, where ether was used to finally subdue the animal.

Bears 'successfully' handled with M99 are listed in Table 1. Average dosage of M99 required to successfully immobilize 34 bears with a single dart was .016 mg/kg body weight (.72 mg/100 lbs). Times for immobilization ranged from 4-20 minutes after injection and averaged 9.5 minutes. Time needed to recover from the effects of M99 after administering the antagonist ranged from less than one to 19 minutes, and averaged 5.5 minutes. Weights of bears successfully immobilized with M99 given in a single dose averaged 82.6 kg (range, 23.0-211.0 kg).

On fifteen other occasions, more than a single dose of M99 was required to complete immobilization (Table 2). One of these bears (73-35) never did become completely manageable even after receiving three separate doses of M99 within an hour. This was the only instance of failure of the drug to take effect among the 49 handlings experienced. Even in this case, the crew did manage to insert ear tags before the bear escaped into a swamp without receiving the antagonist drug.

For handlings requiring additional doses of M99, immobilization times averaged 66.5 minutes (range, 21-300 minutes). The longest handling involved the

TABLE 3. DOSAGES AND EFFECTS OF M99 ETORPHINE ON 46 WEIGHED* BLACK BEARS CAPTURED IN FOOT SNARES OR CULVERT TRAPS, BY SEX.

Type of trap	No.	Immobilized with initial injection			Not immobilized with initial injection			Totals		
		Mean wt. \pm SD (kg)	Mean dosage \pm SD (mg/kg)	No.	Mean wt. \pm SD (kg)	Mean ^{1/} dosage \pm SD (mg/kg)	No.	Mean wt. \pm SD (kg)	Mean dosage \pm SD (mg/kg)	
<u>Snare</u>										
Males	19	78.4 \pm 44.3	.0153 \pm .0033	9	137.1 \pm 50.4	.0090 \pm .0021	28	97.3 \pm 53.3	.0133 \pm .0042	
Females	8	58.8 \pm 15.8	.0169 \pm .0025	1	52.0 \pm 0	.0077 \pm .0	7	57.9 \pm 14.7	.0156 \pm .0041	
Total	25	73.7 \pm 40.0	.0157 \pm .0032	10	128.6 \pm 54.6	.0089 \pm .0020	35	89.4 \pm 50.5	.0137 \pm .0042	
<u>Culvert</u>										
Males	6	115.9 \pm 55.2	.0167 \pm .0042	4	143.0 \pm 70.9	.0130 \pm .0063	10	126.8 \pm 59.7	.0152 \pm .0052	
Females	1	105.0 \pm 0	.0134 \pm 0	0	—	—	1	105.0 \pm 0	.0134 \pm 0	
Total	7	114.4 \pm 50.6	.0162 \pm .0040	4	143.0 \pm 70.9	.0130 \pm .0063	11	124.8 \pm 57.0	.0150 \pm .0049	
<u>Combined</u>										
Males	25	87.4 \pm 48.7	.0156 \pm .0035	13	138.9 \pm 54.3	.0102 \pm .0041	38	105.0 \pm 55.8	.0138 \pm .0045	
Females	7	65.4 \pm 22.6	.0164 \pm .0026	1	52.0 \pm 0	.0077 \pm 0	8	64.1 \pm 20.9	.0153 \pm .0039	
Total	32	82.6 \pm 45.0	.0158 \pm .0033	14	132.7 \pm 57.1	.0100 \pm .0040	46	97.8 \pm 53.7	.0140 \pm .0044	

* Although 49 bears were handled with M99, weights were not obtained for three bears excluded from this table.

^{1/} Based on initial dosage given; multiple dosages have not been included.

largest bear captured during the study (233.5 kg). For fourteen bears for which weights were obtained, initially ineffective dosages averaged .010 mg/kg (.50 mg/100 lbs). Total dosages received, in from two to five doses, averaged .020 mg/kg (1.0 mg/100 lbs). Weights were significantly higher ($P < .01$) than for those bears successfully immobilized with single darts, averaging 132.7 kg (range, 51.5-233.5 kg). Recovery times averaged 9.7 minutes (range, 1-27 minutes), significantly ($P < .05$) greater than that for bears immobilized with single doses of M99.

For all bears handled, no statistical differences (for the 95 percent confidence level) were observed in mean dosages of M99 required by males versus females, or by bears caught in foot snares versus those taken in culvert traps. A summary of dosages and effect of M99 on bears captured, for which weights were obtained, is provided in Table 3.

The 'typical' response of bears to M99 varied somewhat depending on the dosage received. When a bear was immobilized with one dart, within five minutes after injection the animal became lethargic, its head would drop and, over the next four or five minutes, it would fall to one side losing consciousness. Some bears, particularly when underdosed (below .016 mg/kg), exhibited a brief (less than a minute) excitation period, during which the bear would paw the ground, perhaps climb a tree (if snared), and show considerable agitation. Bears that required multiple doses would become drowsy and inactive, but when approached or otherwise disturbed by noise or movement, became alert, often showing agonistic behavior.

During immobilization, breathing was very pronounced, with respiratory rates of from two to five deep breaths per minute. One bear respired at 27 breaths per minute, yet remained immobilized.

Recovery time for all bears handled was very rapid when the antagonist was injected into the femoral vein. Recovery took place in less than three minutes for 54 percent of the sample, with the bear's respiration increasing dramatically less than a minute before complete alertness returned. Occasionally, recovery was delayed, possibly because the antagonist was not injected fully into the vein.

One bear (71-12) appeared to be in respiratory difficulty when only three very deep breaths were observed over a two-minute period. A partial dose of M50-50 was administered; breathing increased and processing continued without further incident.

DISCUSSION

M99 is a thebaine derivative chemically related to morphine but perhaps 6,000 times as potent (Burkhart 1968) as an immobilizer and analgesic. The mode of action of M99 is believed to involve the quantity of acetylcholine released from postganglionic elements (Dieterich 1968). High dosages of the drug may cause a decrease in respiratory and heart rates of polar bears as well as a depression of deep body temperature due to peripheral vasodilation (Øritsland 1967). Larsen (1971) points out that these complications may prove fatal in an arctic environment and recommends administration of the antagonist immediately after handling. For these reasons, more recent studies requiring capture of polar bears have relied on phencyclidine hydrochloride.

During initial use, M99 was given in the dosage recommended by the manufacturer—a dosage of .008 mg/kg body weight (.35 mg/100 lbs). Following poor

results at this dosage and at .011 mg/kg (.50 mg/100 lbs), satisfactory results were achieved at the presently employed .016 mg/kg (.72 mg/100 lbs) base rate.

Our experiences with M99 would seem to suggest, however, that it is more efficient to give 'overdoses' initially rather than attempt to give minimum effective doses. Underdosing may cause excitation as well as a delay in the entire handling procedure. Mean effective dosage was .016 mg/kg for 34 bears handled with a single injection. Because of difficulty in estimating body weights greater than 90 kg (see Miller *et al.* 1973), it is suggested that higher dosages, from .018 to .020 mg/kg (.8-.9 mg/100 lbs), be given when bears are judged to be of large size. Four of five bears receiving as much or more than .020 mg/kg unintentionally during this study were immobilized without difficulty within ten minutes. The fifth bear actually required a second dose before he could be processed.

A major advantage of M99 over other immobilizing drugs presently in use include the ability to antagonize its effects almost immediately after processing a bear, so that the animal can be observed until safely away from the trap site. New York's experience with M99 has indicated a very wide safety margin between effective and lethal dosages. During this study, minimum effective dosage for bears immobilized with a single injection was .010 mg/kg, while a yearling male received the maximum single dosage of .024 mg/mg without any discernible harmful effects. Other biologists working with M99 report non-lethal dosages up to 2.5 times the maximum dosage used in New York (M.R. Pelton, unpublished).

Other than an observed marked decrease in breathing rate which appears typical of M99's action, no ill effects of the drug have been noted. Of 49 handlings of bears with M99, all left the trap site immediately after regaining consciousness. We had no further indications of drug relapses occurring. Sixteen were subsequently recaptured at periods of five days to fourteen months later, and another fifteen were killed by hunters from one month to 38 months after their release. Therefore, 63.3 per cent (31 of 49) of the bears handled were known to be alive at a later date. One bear (73-35) did escape before being given the antagonist drug and no record of its fate is available. An additional seventeen handlings have not yet resulted in recovery records (as of December, 1974). There appears to be no reason to relate this lack of recovery data with other than normal bear activity and a relatively low success in both the trapping and hunting of Catskill bears.

When M99 was administered at or above a dosage of .016 mg/kg in a single injection, immobilization time was rapid and the induced state of unconsciousness deep and persisting. With the injection of the antagonist, full recovery was extremely rapid. Although we have not had experience with phencyclidine hydrochloride, this drug does not appear to provide any advantages as an immobilizer for black bears over M99 and, in fact, one wildlife researcher reports mortalities due to its use (J.D. Henry, pers. comm.). M99, with its antagonists, appears to be an improvement over previous handling techniques used on black bears in New York.

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Preliminary Management Implications for Black Bears, *Ursus Americanus*, in the Catskill Region of New York State as the Result of an Ecological Study

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INTRODUCTION

New York State has three distinct black bear ranges (Fig. 1). The Adirondack range in northern New York is the largest containing 24,043 square kilometers (9,283 square miles) and an estimated population of 3,500 bears. The smallest is the Allegheny range containing 1,168 square kilometers (451 square miles) and is a peripheral area of a major range centered in northwest Pennsylvania (Sauer and McCaffrey 1965). The Catskill bear range contains 3,280 square kilometers (1,270 square miles) and an estimated 200 bears. This range is located in southeastern New York between 95 and 160 kilometers (60 and 100 miles) from metropolitan New York City and is within easy access of its 16 million people.

A decline in the average hunter take in recent years prompted an assessment of the harvest statistics by town which revealed the possible existence of two sub-populations. The northern population centering in western Greene and Ulster Counties (Fig. 2) appeared isolated from the southern population by a series of towns where there was no take or a sporadic take. When the take was separated into two areas and examined, it appeared the majority of the decline occurred in the northern area. The southern area, while yielding a smaller take, appeared to maintain its population rather than to decline. This area is also contiguous with a larger area in Pennsylvania which has always supported bear populations.

A study was planned to determine the present status of the Catskill black bears and to prepare a policy for future management.

MATERIALS AND METHODS

Each hunter taking a bear during the regular big game hunting season (held during late November and early December) was required to report his bear to the New York State Department of Environmental Conservation via a toll free telephone answering service within 48 hours (Miller 1971). Upon notification of a Catskill kill, a Department employee interviewed the hunter and whenever possible examined the bear carcass for basic biological data. This included removing a premolar, normally a first upper premolar, for sectioning and aging by cementum layering (Sauer *et al.* 1966). These examined bears were considered the 'legal take' for 1970 through 1973. The 1969 'legal take' was by hunter reports only.

Aldrich foot snares and culvert box traps were used to trap, tag and release a substantial proportion of the Catskill bear population (Miller *et al.* 1973).



Figure 1-Location of New York State, Black Bear Ranges, and Catskill Study Area.

Etorphine (M99) and its antagonist Diprenorphine (M50-50) (Miller & Will 1973) were used for immobilization. Most bears were released at the trap site. A first upper premolar was extracted from each captured bear. Trapping was conducted from June to October in 1970 and from April through October in 1971 and 1973.

An appraisal of the economic effects of bears was determined by: (1) damage assessed by investigated nuisance bear complaints and (2) aesthetic qualities such as trophy value and non-hunter interest from interviews with sportsmen and others.

Determination of the current and future land use patterns, human population pressures and other socioeconomic factors that would influence a bear management policy were compiled from *The Land Use and Natural Resource Inventory of New York State, Manual for The Use of The Legislature of The State of New York 1971-72*, and *Deer Habitat Area in New York State* for comparisons.

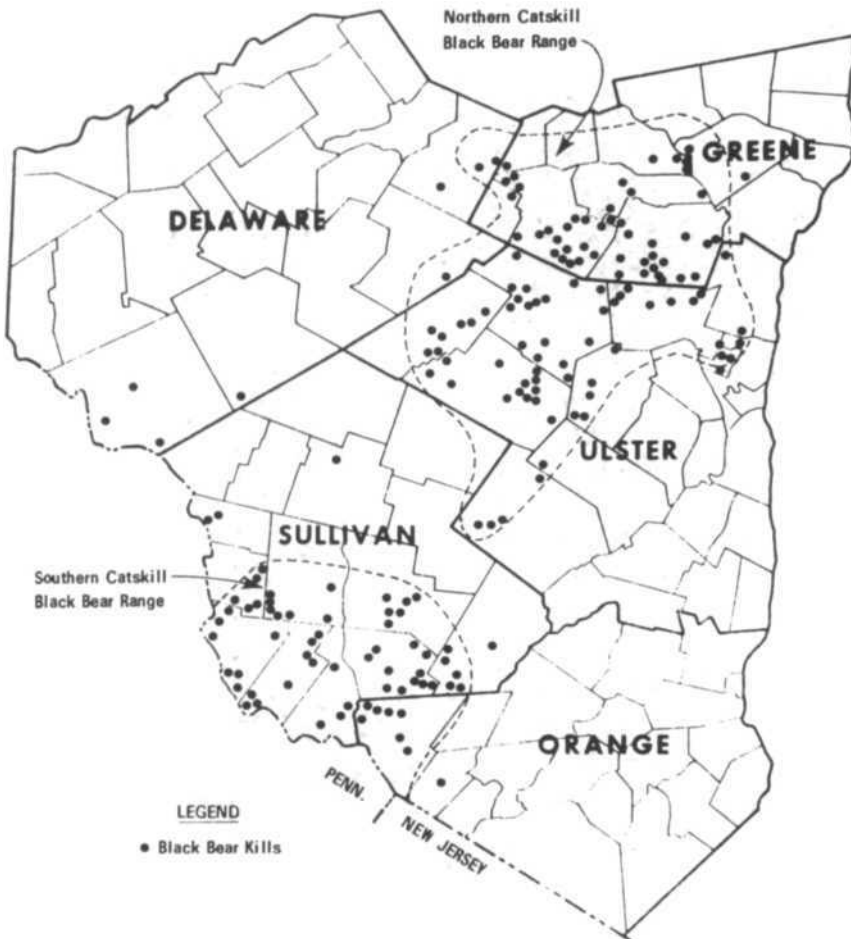


Figure 2 Black Bear Kills in the Catskill Region 1970-73, Inclusive; and Location of Northern and Southern Black Bear Ranges.

The initial study was planned to last from three to five years depending on the number of bears examined and/or captured. Funding difficulties prevented the study from reaching even half its planned expenditures and thus severely hampered the successful completion of the objectives.

Study Area

For the purpose of this study the Catskill Region is described as Delaware, Greene, Sullivan, Ulster and Orange Counties, an area of approximately 13,200 square kilometers (5,100 square miles) between $42^{\circ}31'$ and $41^{\circ}08'$ north latitude and $75^{\circ}25'$ and $73^{\circ}47'$ west longitude (Fig. 3). Elevations range from sea level in the Hudson Valley to 1,281 meters (4,004 feet) on Slide Mountain in the Town of Shandaken, Ulster County. Most of the land in the northern and western Catskills has elevations between 300 and 900 meters, while most of the land in

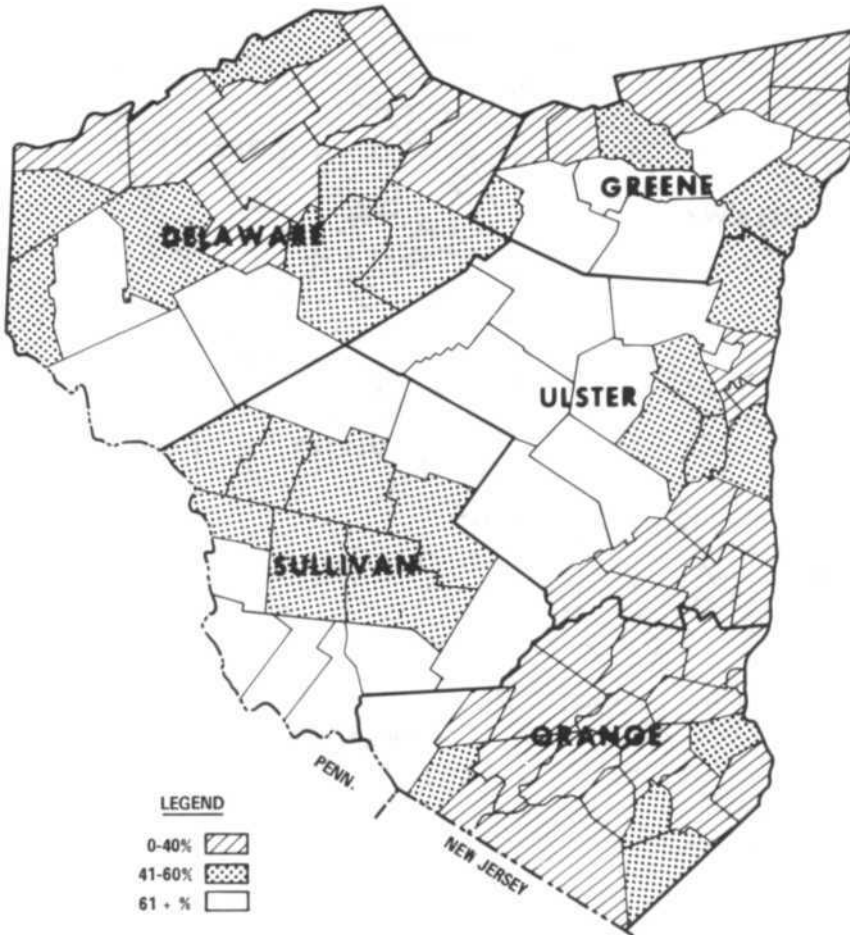


Figure 3 Per Cent Forest and Brush in Towns in the Catskill Region.

the southeast lies between sea level and 300 meters. The western portion of those lowlands is cut by the Shawangunk Ridge which rises between 600 and 900 meters throughout most of its range. Those areas above 900 meters are located in the north central Catskill Region.

Soil types in the Catskills are poor to moderately productive soils of glacial origin derived from sandstone and conglomerate (Howe 1935). The highlands support little or no agriculture. Lower elevations with slightly more fertile soils support numerous farms, most dairies. In the Hudson Valley, the alluvial clay soils support a large apple industry. The Delaware and Hudson River watersheds provide the major drainage for the Catskills. January mean temperatures range from -7°C to -4°C and July mean range from 18°C to 21°C . The minimum temperature ranges from -26°C to -29°C . Annual precipitation ranges from 100 to 125 centimeters with about half of this occurring during the 120-125 day growing season. Annual snowfall ranges from 100 to over 150 centimeters (Smith 1954).

Much of the land is in forest and brush. A large portion is in old field succession and second growth forest re-establishing itself since the extensive clearing for agriculture and lumbering throughout the nineteenth century. Changes in forest composition were effected by large cuttings of hemlock (*Tsuga canadensis*) for tanbark in the late 1800s, and almost total decimation of American chestnut (*Castanea dentata*) by the chestnut blight in the early twentieth century. Native vegetation of the lower elevations consists of various species of oaks (*Quercus* spp.) with some tulip 'poplar' (*Liriodendron tulipifera*).

Mountain laurel (*Kalmia latifolia*), great laurel (*Rhododendron maximum*), low-bush blueberry (*Vaccinium angustifolium*) and highbush blueberry (*Vaccinium corymbosum*) are also locally predominant in the understory. On the excessively well drained soils of the Shawangunk Ridge this flora grades into oak (*Quercus* sp.) and pitch pine (*Pinus rigida*) forest. Throughout the rest of the Catskills, white pine (*Pinus strobus*) and hemlock (*Tsuga canadensis*) combine with northern hardwoods, especially sugar maple (*Acer saccharum*), beech (*Fagus grandifolia*) and yellow birch (*Betula alleghaniensis*).

At higher elevations, mountain maple (*Acer spicatum*) and striped maple (*Acer pensylvanicum*) and finally red spruce (*Picea rubra*), black spruce (*Picea mariana*) and balsam fir (*Abies balsamea*) appear. These last three species also occur sporadically throughout lower elevations of southern Sullivan County in swamps and bogs—remnants of Pleistocene glaciation (Smith 1954; Harlow and Harrar 1958).

Within the Catskill Region, human population densities are highest along the Hudson River, the major branches and tributaries of the Delaware River, and along New York Route 17 and U.S. Route 209. Summer and early fall population densities increase substantially when transient populations move into summer cottages, resorts and hunting camps throughout the Region. Large tracts of land in the northern Catskills are under State ownership while virtually all the land in the southern portion of the Region is privately owned (NYSOPC, 1969; NYS DEC, 1957).

RESULTS

Mortality

Records were maintained on all recorded black bear mortality from April 1970 through March 1973 (Table 1). Hunters accounted for 189 out of 198 bears

TABLE 1. CATSKILL BLACK BEAR MORTALITY, 1970-73 INCLUSIVE.

	Northern Range			Southern Range		
	Hunter Killed	Other Deaths	Percent Killed by Hunters	Hunter Killed	Other Deaths	Percent Killed by Hunters
1970	27	2	93.1	14	2	87.5
1971	38	0	100.0	24	2	92.3
1972	9	1	90.0	12	1	92.3
1973	44	0	100.0	21	1	95.5
Total	118	3	97.5	71	6	92.2

known to have died during this period. There were five killed on highways, two trap mortalities, one found dead during the hunting season and one shot after it damaged an apiary. The distribution of mortality by area (Table 1) indicated a greater number recorded as 'other deaths' in the southern Catskills. This is probably due to a greater effort on the part of the summer trapping crew in making contacts and also a greater road network causing four of the five highway deaths. Both trap mortalities occurred in the northern Catskills and should not be considered as normal mortality since they would not have occurred without the study.

There is no doubt that other mortality has gone undetected. It is unlikely, however, that these deaths would exceed the hunting mortality. The legal hunting take is essentially complete although a few may have gone unreported.

Variable hunter harvests are due to availability rather than fluctuating bear populations. This is indicated by the extremely low take in the northern Catskills in 1972, which was accompanied by unusually early cold weather and deep snows just prior to the opening day of the season. The combination of possible early denning and restricted hunter access lessened hunter-bear contacts and reduced the legal take.

The age and sex composition of the hunter take 1970-73 inclusive (Table 2) reveals substantial differences between the northern and southern Catskill population structures. The northern Catskill sex ratio is about equal, and only about 25 percent of the take are yearlings. Females survive longer than males with 53.1 percent of the females being of the assumed breeding age of three years and older (Free and McCaffrey 1972). The southern Catskill bears on the other hand had a sex ratio of 1.48 males/females and between 60 and 70 percent of the take were yearlings. Older age (3+) males outnumbered females and only 14.8 percent of the take were breeding age females. Annual variation in the sex ratios of the hunter take is extreme. For instance, in the southern range in 1970 there were 12 males and only one female in the take. The other extreme occurred the next year when eight males and 15 females were taken.

TABLE 2. SEX AND AGE COMPOSITION OF CATSKILL BLACK BEARS LEGALLY TAKEN BY HUNTERS, 1970-73 INCLUSIVE.

		Age at Death						Total Bears Harvested
		Cub	1	2	3	4	5+	
Northern Range								
Male	number	5	13	20	7	3	3	51
	percent	9.8	25.5	39.2	13.7	5.9	5.9	100.0
Female	number	4	12	7	9	3	14	49
	percent	8.1	24.5	14.3	18.4	6.1	28.6	100.0
Southern Range								
Male	number	2	24	7	5	1	1	40
	percent	5.0	60.0	17.5	12.5	2.5	2.5	100.0
Female	number	1	19	3	0	0	4	27
	percent	3.7	70.4	11.1	0.0	0.0	14.8	100.0

TABLE 3. MINIMUM 1969 CATSKILL BLACK BEAR POPULATION AS DETERMINED FROM KNOWN EXISTING BEARS.

Year	Age	Male			Female			Total
		Dead	Tagged	Total	Dead	Tagged	Total	
Northern Range								
1969	0+	28	0	28	16	0	16	44
1970	1+	19	2	21	9	1	10	31
1971	2+	11	0	11	13	0	13	24
1972	3+	1	0	1	3	0	3	4
1973	4+	6	0	6	11	0	11	17
Minimum 1969 Population		65	2	67	52	1	53	120
Southern Range								
1969	0+	14	0	14	6	0	6	20
1970	1+	13	1	14	1	0	1	15
1971	2+	4	1	5	1	1	2	7
1972	3+	1	0	1	1	0	1	2
1973	4+	1	3	4	4	4	8	12
Minimum 1969 Population		33	5	38	13	5	18	56

TABLE 4. 1969 CATSKILL BLACK BEAR POPULATIONS CALCULATED FROM KNOWN MORTALITY AND AGE COMPOSITION.

	Bears Alive in 1969 But Killed from 1969 to 1973	Percent Population Four Years or Younger	Calculated Population	Minimum Population
Northern Range				
Male	65	.941	69	67
Female	53	.741	73	53
Total	117		142	120
Southern Range				
Male	33	.975	34	38
Female	13	.852	15	18
Total	46		49	56

Sex ratio variations occurred in the Northern Zone also, but not in such extreme proportions. Cubs are represented in the legal take despite the fact that they were technically illegal. This subject will be discussed later.

The high recovery rate of Catskill bears is indicated by the recovery rate of tagged bears. In the southern Catskills where the most tagging took place, 10 out of 27 bears died during the first fall following tagging (37.0 percent). Of those that were yearlings when tagged, seven out of nine died during the first fall (77.7 percent). Decreased mortality among older bears was also apparent. Three of nine bears aged two and three years old died (33.3 percent) and all nine bears five years old and older survived the first fall after tagging. Only six bears were tagged in the northern Catskills and one of these died during the first fall (16.7 percent). Hunters killed 91 percent of the tagged bears. These mortality rates depend on the assumption that all bears not recovered survived the first fall.

Population Size

Table 3 presents the minimum 1969 bear population. All known mortality regardless of age in 1969 was used as the base. Bears in appropriate age categories killed since 1969 were added to the table. Finally, tagged bears at least four years old in 1973 and not recovered by then were added to the table. Minimum 1969 figures for the Southern Range were 38 males and 18 females for a total of 56 bears. The Northern Range contained at least 67 males and 53 females for a total of 120 bears in 1969.

Realistic populations were calculated (Table 4) by assuming that the dead bears in the minimum 1969 population were in proportion to the frequency of bears 4½ years and younger in the observed age composition (Table 2). The realistic population should then account for bears alive in 1969 and yet to be recovered. Some, but not all, would be the tagged bears used in the minimum population calculation (Table 3). Calculated population for the southern Catskills of 49 actually fell below the known 1969 minimum population of 56. Observed hunter take frequency of five-year old and older bears was not sufficiently high to account for those bears actually known to be alive. The actual 1969 population was undoubtedly larger than the 56 bears determined as the minimum 1969 population. The occurrence of older bears which did not show up in the hunter harvest is difficult to explain. Perhaps insufficient observations of hunter killed bears invalidate the observed age composition, or these older bears have survived because they have home ranges which coincide with areas of low hunting pressure or where bear hunting is prohibited. The majority of trapping effort was on private lands with these restrictions.

The calculated 1969 population for the northern Catskills of 142 exceeded the minimum population of 120. For this area, the calculated population is undoubtedly closer to the actual 1969 population.

Bear Density and Range

Positions of hunter killed bears were plotted on United States Geological Survey Quadrangle maps and superimposed on maps of the Catskill Study Area with human population densities and land use patterns plotted (NYSOPC, 1969). As expected most of the bear kill locations were in those towns with greater than 60 percent forest and brush and less than 3.9 people per square kilometer (10 people per square mile) (Fig. 2 and Fig. 3). For unknown reasons several towns in southeastern Delaware County which fell into this high forest density-

low human population category showed few bear kills indicating little or no resident black bear population.

Occupied bear range was considered to be those areas with a high density of hunter kills. Outlines of the Northern Range and Southern Range were made using plots of the kills and excluding areas with high human populations or intensive farming (Fig. 2). Bears killed outside the range thus defined were considered occupying marginal range or as transient animals. Within these broad ranges there may be areas without resident bear populations, but the extent of these areas cannot be determined without data on where forested land exists within each town.

To determine the actual size of the occupied bear ranges an estimate was made of the percentage of each town within that range. Thus determined, the Northern Range constitutes about 2,250 square kilometers (870 square miles) with calculated 1969 population (Table 3) of 142 bears. This is 15.8 square kilometers (6.1 square miles) per bear or 0.06 bears per square kilometer (0.16 per square mile). The Southern Range constitutes about 1,030 square kilometers (400 square miles) with a minimum 1969 population (Table 3) of 56 bears. This is 18.4 square kilometers (7.1 square miles) per bear or 0.05 bears per kilometer (0.14 per square mile).

Besides the primary ecological constraints the bear ranges are maintained by the secondary effects of land ownership. In the Northern Range an estimated 40 percent of the land is owned by New York State as part of the Catskill Forest Preserve. Land in the Southern Range is in private holdings, but an estimated 30 percent is in the hands of only 15 owners. Both these ownership patterns have effectively reduced human development and encouraged forest succession.

The Cub Law

In the course of the Catskill Bear Study, it was discovered that 7.0 percent of the hunter harvest were cub bears despite a 1938 law which prohibits the shooting of 'bears less than one year old'. This figure is considered low because of documented claims that hunters shoot cubs or small bears and leave them in the woods for fear of prosecution.

Interviews with hunters revealed a problem with field application of this law. Most hunters attempted to identify cubs on a weight basis, usually considering all bears less than 45 kilograms (100 pounds) to be cubs. Field dressed weights taken of bears killed during the study showed this kind of estimate to be unreliable. The weights of the six cubs weighed, three males and three females, ranged from 20 to 34 kilograms (44 to 76 pounds). Both the lightest and heaviest cubs were females. The heaviest cub was 25 kilograms (55 pounds) less than the mean weight of yearling males, but heavier than three yearling females and only 1.7 kilograms (4 pounds) less than the lightest two-year old examined. Because of this overlap in weights among the various age classes it is understandable that hunters found it difficult to identify cubs in the field.

Mortality rates of the Catskill bear population show the futility of attempting to protect cubs. Mortality in young bears is high, despite the law. As stated, cubs make up 7.0 percent of the harvest which, compared to 11.0 percent of the Adirondack harvest where the cub law was repealed in 1956, proves the inadequacy of this provision. Once breeding age (3 years and up) is reached, mortality drops substantially. If the aim of the law is to increase the bear population, a more reasonable approach would be to protect the breeding age females, perhaps protecting sows with cubs. The cub law which casts doubt on the legality of possessing dead animals should be eliminated.

DISCUSSION

This paper has presented the interim findings of the Catskill Bear Study and has attempted to draw some tentative conclusions about population dynamics, population size and geographic extent. The future of the Catskill black bear populations will depend upon future management action. There appear to be two major courses of action which may be used for effective management: (1) promotion of land use patterns which perpetuate wild land and minimize disturbance by man; and (2) promulgation of hunting regulations which will reduce the effect of hunting on bears if it is established that a higher population is desirable. The negative socioeconomic qualities of bears are not currently a major problem in the Catskills, probably because of the relatively low bear population densities and restricted human development in bear range. If bear populations are allowed to increase without suitable wild land available, bear-human conflicts are bound to increase.

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Population Characteristics of the Arctic Mountain Grizzly Bear

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INTRODUCTION

The reduction in numbers and in the range of the grizzly bear in North America has been well documented (Stebler 1972; Cowan 1972; many others). Viable populations unaffected by man occur only in the remote mountains of western and northern Canada, and in Alaska. Concern for the future of those remaining populations precipitated the ecological studies that started in the early 1960s. No studies were made or even planned on the Arctic populations until the threat of a major development scheme focused attention on that area. Preliminary studies have expressed concern for the species while attempting to calculate distribution and abundance within the region (Calef & Lortie 1971; Renewable Resources, 1971, 1973; Watson *et al.* 1973).

The specific objectives of this study were to obtain more precise information on the population parameters of the Arctic Mountain grizzly in a representative study area in northern Yukon. The number of animals, their movement patterns and seasonal habitat utilization, productivity, and food habits were investigated to assess the impact of the construction and operation of a pipeline facility through the area.

It has been speculated that denning sites could be a limiting factor for grizzly bears, particularly in areas with high permafrost (Pearson 1972). It has also been observed in other areas that grizzly dens are sometimes concentrated on specific sites (Hensel 1968; Pearson 1968). In this study special emphasis was placed on locating active grizzly dens and describing their site characteristics.

STUDY AREA

The study area consisted of approximately 3367 sq. km (1300 sq. miles) in the Barn Mountains of northern Yukon (Figure 1). The area was selected as representative of the Arctic mountains which supported relatively dense grizzly populations (Watson *et al.* 1973).

The study area contained parts of four physiographic units: Arctic Coastal Plain; Arctic Plateau; Richardson Mountains; and British Mountains (Bostock 1948). The rugged area of the Arctic Plateau, standing midway between the British and Richardson mountains, provided the core of the study area.

The Arctic Coastal Plain, and similar lowlands extending up river valleys into the mountains, are poorly drained and thus very wet during the summer (Wahrhaftig 1965). Large fields of cotton grass (*Eriophorum angustifolium*) occur on those marshy meadows along with various other sedges (*Carex* spp.).

River, stream and lake banks supported dense thickets of willow (*Salix* spp.). Willows also occurred in shallow depressions at higher elevations where

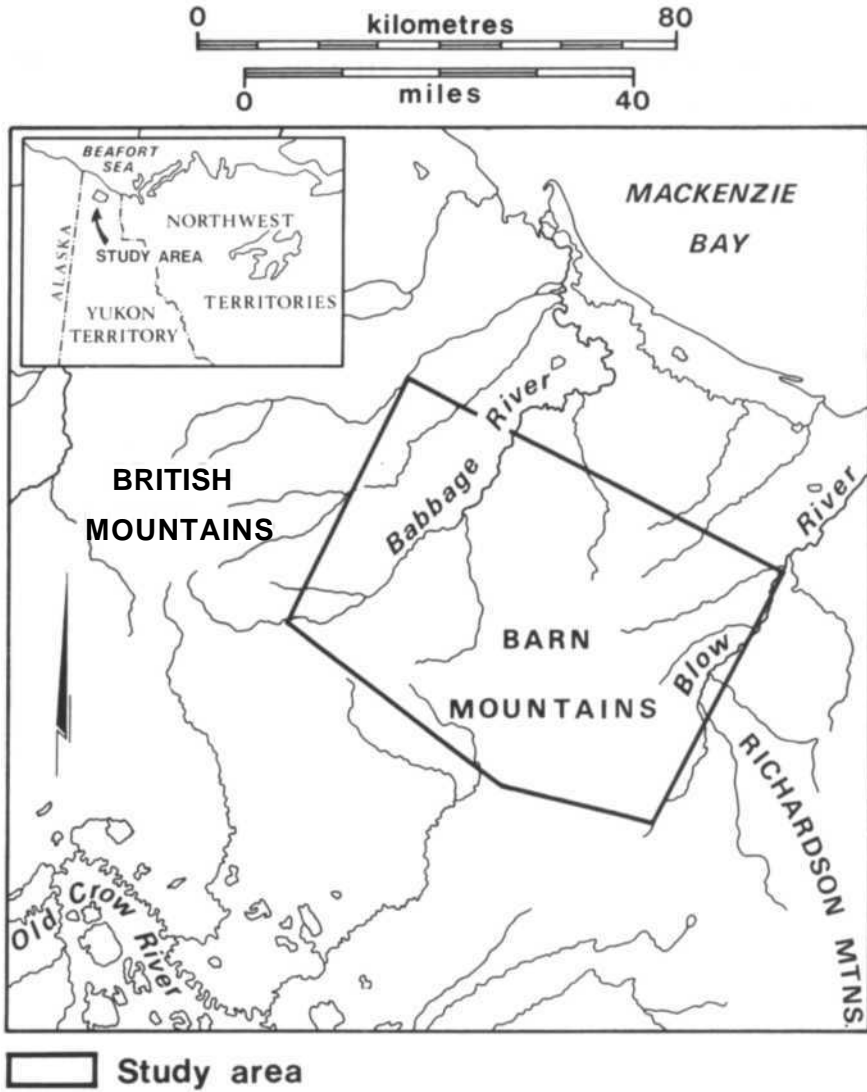


Fig. 1 Study area in the Barn Mountains (Arctic Coastal Plateau) of Yukon Territory.

snowpatch communities were developed. Higher, better drained areas supported a variety of grasses, herbs and shrubs, prominent among which were crowberry (*Empetrum nigrum*), blueberry (*Vaccinium* spp.), dwarf birch (*Betula glandulosa*) saxifrages (*Saxifraga* spp.), poppies (*Papaver* spp.), louseworts (*Pedicularis* spp.), vetches (*Oxytropis* spp.), and grasses (*Calamagrostis* spp.).

METHODS

The population was studied by marking individual bears with specific coloured

tags that facilitated subsequent visual identifications (Pearson 1975). An immobilizing drug, Sernylan (Parke Davis & Co.), was administered to each animal by a Capchur dart fired from a pursuing helicopter (Pearson 1975). Both the Bell 47G3-B2 and 206B helicopters were used for the tagging operation.

Transmitter collars were affixed to selected animals. The signal was in the 40.680 MHz frequency range with 10 KHz between units. Pulsed transmissions between 1 and 6 per second were emitted. Transmitting devices, receivers and accessories were prepared by the Bio-electronics Section, Canadian Wildlife Service, Ottawa (Pearson 1975). A survey grid was established to monitor the entire northern Yukon. A variety of airplanes was used. Flight lines were 8.045 km (5 miles) apart and the initial tracking was done at 1219-1524 meters (4000-5000 ft) altitude. When a signal was received the exact location of the animal was established by low level search until a maximum signal or a visual sighting was obtained. The area was covered at least once a week and all sightings marked on 1 : 250,000 scale topographic maps. Minimum home range polygons were drawn for animals for which four or more sightings were obtained (Pearson 1975)

Den sites were located by searching the area for radio signals in November after the animals were established in their den chambers. Den sites were recorded on maps, photographs of each area were taken and, wherever possible, markers were established.

Any faeces that could be accurately dated were collected and dried for further analysis. The dried faeces were segregated into component parts in the laboratory and the contents recorded.

The occurrence of tagged female grizzlies were plotted on a map of the area. Observations of other identifiable females (e.g. sow with young groups) were also recorded and a preliminary population estimate calculated for the area (Pearson 1975).

Immobilized animals were weighed and measured and a premolar tooth was removed from each. The teeth were sectioned and stained and the cementum annulations counted in order to determine the age of each animal.

RESULTS AND DISCUSSION

Drug Dosages and Reactions

A noticeable difference was observed during the course of the season in the amount of Sernylan required to immobilize the animals. Table 1 shows the average dosage used and the average time for the drug to take effect for each of the four capture periods. Seasonal differences in the reaction of grizzlies to Sernylan have been recorded previously (Pearson 1975). It is not known whether the differences were caused by a seasonal change in physiological tolerance or by a change in the animal's rate of absorption of the drug. Although the 3.81 cm (1.5 inch) needles were used in the September period, there was a chance that the drug could still have been injected into adipose or other poorly vascularized tissue.

Weights and Measurements

The body weights of grizzlies increased dramatically from spring to fall. The average weights of grizzlies handled during the four capture periods can be seen in Table 1. Examples of individual increases in weight of animals handled

TABLE 1. AVERAGE DOSES OF PHENCYCLIDINE HYDROCHLORIDE WITH TIME TO TAKE EFFECT AT DIFFERENT SEASONS OF THE YEAR FOR GRIZZLY BEARS IN BRITISH MOUNTAINS, Y. T.

Month	Sex	Sample Size	Mean Body Wt. (kg)	Average Dose (kg)	Time to Take Effect (min)
May	X	11	72	3.1	5.0
	W	10	153	2.4	6.6
July	X	3	110	2.6	5.7
	W	3	142	2.2	8.8
August	X	6	120	3.3	18.4
	W	2	157	2.6	11.0
September	X	11	145	4.2	35.0
	W	10	195	3.5	17.5

both in spring and fall were: adult W-83 kgs in 110 days; imm. W-65 kgs in 112 days; imm. X-51 kgs in 104 days; adult W-60 kgs in 110 days; imm. W-16 kgs in 35 days; adult X-35 kgs in 62 days while lactating. The Arctic Mountain grizzly was capable of assimilating energy from the tundra ecosystem and converting it into what was likely adipose tissue. The autumn weights of the Arctic Mountain grizzlies were greater than weights found in Northern Interior grizzlies of the same age (Pearson 1975). However, spring weights, which would more closely represent actual body size, were nearly equal. It is hypothesized that natural selection in the Arctic Mountain grizzly has favoured animals that add extra fat in the fall enabling them to survive more rigorous winter conditions.

Food Habits

Thirty-nine faeces samples were collected from the study area in 1973. Ten were collected in late May, five in mid-July, eight in mid-August, and sixteen in mid-September. Table 2 presents the results of identification of food items in faeces during each of the four collecting periods. If a food item was present only in trace amounts it was not included in the listing.

TABLE 2. PERCENTAGE BY FREQUENCY OF OCCURRENCE FOR FOOD ITEMS IDENTIFIED IN 39 GRIZZLY SCATS FROM THE NORTHERN YUKON

Date	n	Food Item			Animal Matter
		Berries	Grass	Roots	
May	10	50	30	50	0
July	5	0	100	0	0
August	8	75	87	0	25
September	16	69	38	31	31

During the late May period grizzlies utilized berries, roots and some grasses. The berries were from crowberry and the roots from eskimo potato (*Hedysarum alpinum*). In mid-July all the faeces collected were composed of 100 percent grasses. In August crowberries and grasses occurred in about equal amounts. The animal matter found in two samples consisted of the remains of ground squirrels (*Spermophilus undulatus*). In September berries were still the most common food item. Crowberry was found exclusively in 73 percent of the samples containing berries, soapberry (*Shepherdia canadensis*) was found exclusively in 20 percent and the two were found together in the remaining 7 percent. Grasses were the second most common food item in September, followed closely by roots and animal matter. Surprisingly, most of the animal matter identified was from ground squirrels, with caribou material noticeably absent. Unknown bird remains were found as a trace occurrence in one faeces.

Two food items were prominent by their absence. The nearly complete lack of caribou remains was unexpected and obviously not precisely representative of the situation. It is postulated that caribou meat would be ingested and digested rapidly by the bears. A bear would remain near a carcass until all of the meat was consumed and faeces containing the caribou remains would be concentrated around the carcass. Most of the grizzlies we captured were not near carcasses and a greater preponderance of vegetable matter would be expected in the faeces.

The absence of berries of *Vaccinium* in the faeces is also difficult to explain. Tissue slides were made to try to determine whether some *Vaccinium* remains had been incorrectly identified as crowberry but none was found. Although quantitative measurements were not made, there appeared to be a low production of *Vaccinium* berries in 1973. Whether *Vaccinium* forms an important food source for the Arctic Mountain grizzly will be known only after further investigation of the food habit patterns during other years.

No indications of grizzly bears fishing for arctic char (*Salvelinus alpinus*) were found in any of the Yukon coastal rivers used by that fish.

Movements and Home Range

During 1973, radiotelemetry collars were affixed to 23 different grizzly bears. There were 152 subsequent locations recorded which provided information on movements and on the calculation of minimum home range sizes.

The data do not substantiate the suggestion made by Watson *et al.* (1973) that the movements of the Arctic Mountain grizzly bears are related to the movements of the barren-ground caribou (*Rangifer tarandus*). In fact, during the June period when the caribou were moving as a unit to the north and west, some adult grizzlies were moving east and south. The movements may have been more nearly related to the breeding behaviour of the bears than to their utilization of the caribou herds. It is believed that the presence of a grizzly near concentrations of caribou could be ascribed to the local attraction of a food source within the bear's home range. That observation does not, however, discount the possibility that some bears, particularly males, have learned to feed on carrion or even prey on caribou and are dependent upon the caribou herds as a year-round food source. The larger home ranges of the male bears would allow them to remain with a caribou herd for many days and still not desert their traditional movement patterns.

Although logistical problems and the unreliability of the telemetry equipment

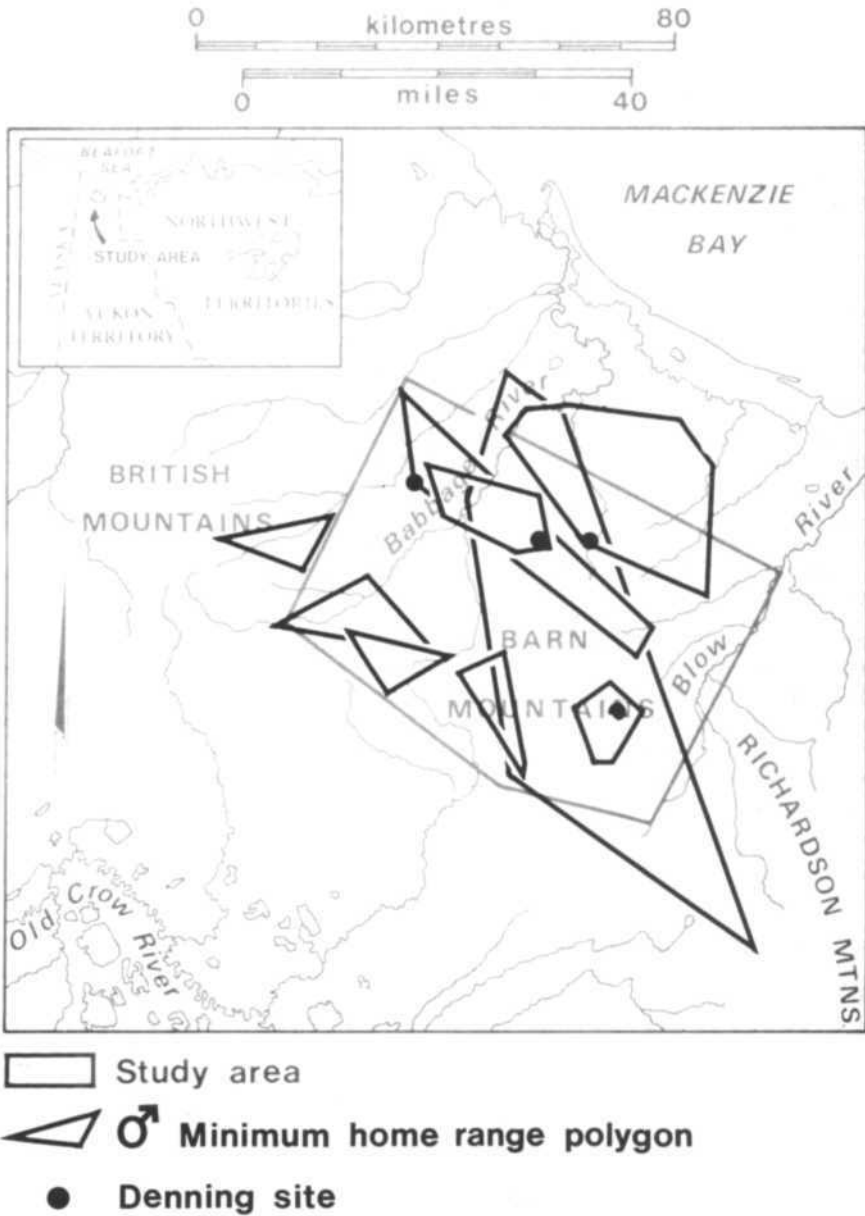


Fig. 2 Minimum home range polygons of male grizzly bear as determined by radio telemetry.

have prevented a clear analysis of the movements of the more mobile bears, movements of 106, 61 and 48km were recorded for individually marked adult animals.

The average minimum home range polygons calculated for nine adult male grizzlies (Figure 2) was 414 sq. km (160 sq. miles); similar calculations for

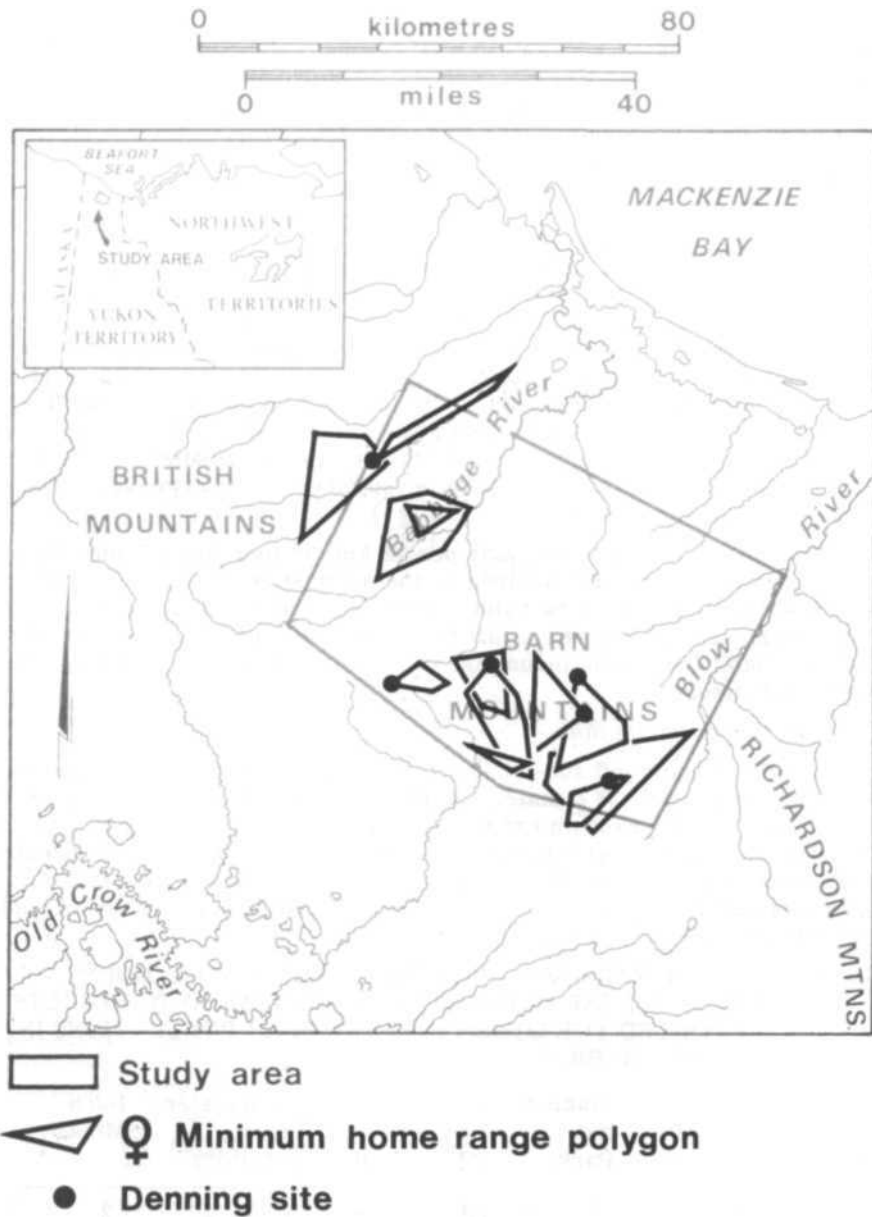


Fig. 3 Minimum home range polygons of female grizzly bear as determined by radio telemetry.

females (Figure 3) showed home ranges averaging 73 sq. km (28 sq. miles). Those areas were similar to the values of 111 square miles and 33 square miles respectively, found for the Northern Interior grizzly in south-western Yukon (Pearson 1975).

No long movements of female grizzlies were observed either during 1973 or from re-observation of animals tagged by Surrendi and Jorgenson in 1972. Additional evidence of the limited movements of female bears

was obtained from analyses of observation cards turned in by cooperating agencies. Some females, recognizable by unusual colouring or by family groups, were observed at various times throughout 1972 and 1973 and by several people working for different agencies. By carefully matching those observations an indication of restricted home range was obtained.

Population Parameters

(a) *Density*

Figure 4 shows the core home ranges for female grizzly bears captured during 1973 and the spring of 1974, or identified from analysis of observation cards. In the early summer of 1974, 27 different female grizzlies were resident on the 3367 km² study area. Assuming a 50 : 50 sex ratio there were at least 54 sub-adult and adult animals present. There were five cubs, five yearlings and six two-year-old young accompanying females on the study area. The total population was thus 70 grizzly bears or one per 48 sq. km. That figure is considered to be a minimum density estimate because of the superficial coverage of the area and the fact that the fate of seven other weaned two-year-olds on the area was not determined.

The estimated density of one grizzly per 48 km² is four times higher than the preliminary calculations for an area on the north slope of Alaska (Renewable Resources, 1973). Because the values were calculated by greatly different census techniques, it is possible that the variation is not real and that more grizzlies inhabit the Arctic mountains of Canada and Alaska than was previously estimated.

(b) *Sex and age distribution*

The sex ratio of adult and sub-adult grizzlies captured during 1973 and early 1974 was nearly equal (28 females : 27 males). The animals were captured through more or less random excursions through the area as opposed to the 1972 program, when effort was expended around areas of caribou concentrations and when the sex ratio heavily favoured males (4 females: 17 males). The 1973 results lent support for the use of a 50 : 50 sex ratio in calculations of population density on the study area.

TABLE 3. PRELIMINARY AGE DISTRIBUTION OF ARCTIC MOUNTAIN GRIZZLY BEAR POPULATION AS COMPARED TO RESULTS REPORTED FOR OTHER GRIZZLY BEAR POPULATIONS IN NORTH AMERICA.

Age Class	Kodiak Island	Glacier Nat. Park	Yellowstone Nat. Park (a)	Southwestern Yukon Territory	Barn Mtns.
Cubs	26	17	20	19	7
Yearlings	22	15	11	17	9
Total	48	32	31	24	11
Sub-Adult	27	—	26	32	20
Adult	25	—	43	44	69
Total	52	68	69	76	89

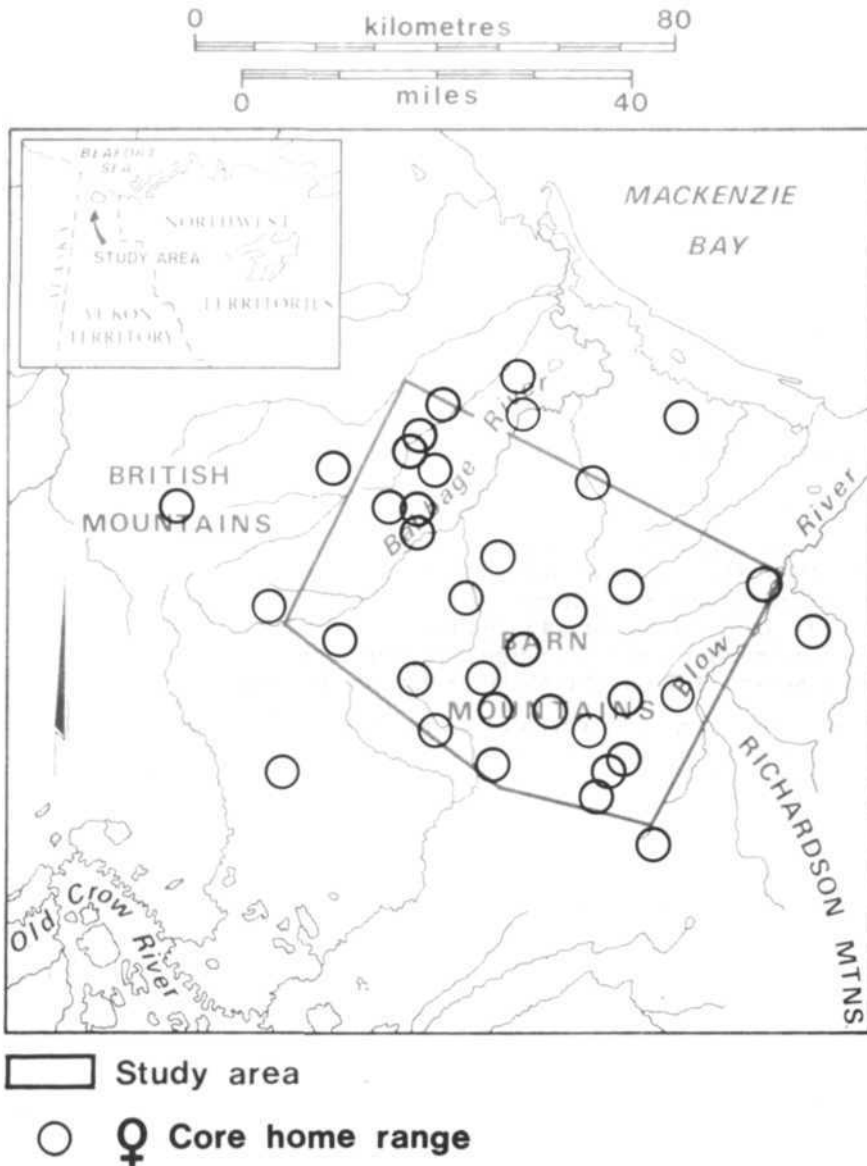


Fig. 4 Core home ranges of female grizzlies captured or positively identified on and adjacent to study area, 1973.

Surprisingly, of the nine young bears captured with sows, seven were female animals. That result was not considered representative of the population and it is postulated that a larger sample would result in a 50 : 50 sex ratio of young animals.

The ages of grizzlies handled during 1973 were determined from cementum annulations. Additionally, the age was estimated for each unweaned young animal seen on the study area, but not captured. Table 3 compared the population

composition determined from the 1973 studies with those reported from other grizzly studies. The most startling difference observed in the Arctic Mountain population was the low percentage of young and sub-adult animals in the population, a situation arising from the fact that many of the adult females seen were without young. Although the litter size was small, it was not significantly less than found in south-western Yukon (Pearson 1975).

The reason for the large number of females without young is difficult to determine. However, two captured adult female bears were lactating and showed rubbed areas around the teats, both indicating the recent presence of young. One of those sows was already in estrus as indicated by vulvar swelling and the obvious breeding display of an accompanying boar. A high mortality in the young age classes is the most obvious explanation at this time.

Preliminary results from the 1974 program suggest that the low number of young of the year recorded in 1973, was caused by a disproportionately large fraction of that age class remaining unobserved. Even so, the total percentage of young animals in the population remained below 20 percent.

(c) *Natality*

The breeding season had already begun when the first female was captured on May 25, 1973. On July 3, two instances of males accompanying females were observed and in mid-July a female in breeding condition was captured. Discontinuous observations did not permit a further delineation of those dates but they are earlier and later, respectively, than previous records for the breeding season of the Arctic Mountain grizzly (Renewable Resources, 1973).

The youngest record of successful reproduction was for a 9-year-old female who had one yearling in 1973. She must have bred in her seventh summer. Two 7-year-old females captured in late May showed vulvar swelling indicating estrus, but one 6-year-old captured during the same time period had no signs of swelling. The oldest female bear showing reproductive capability was a 21-year-old sow with a single cub, born in 1973.

The mean litter size, calculated from observations throughout the Arctic Mountain region of the Yukon throughout 1973, was 1.8 for cubs of the year (11 sows with 20 cubs) and 1.4 for yearling young (9 sows with 13 yearlings). Those figures were similar to results reported from the Arctic mountains of Alaska (Crook 1971; Renewable Resources, 1973) and similar to the low values for south-western Yukon (Pearson 1975).

The age of self-sufficiency of young Arctic Mountain grizzlies, and hence the age of weaning and frequency between litters appeared to be variable. One young bear 3.3 years of age was captured with a female in the spring of the year. They were observed separately later in the summer. One loose sow-young association was recorded in the spring when the young bear was 4.3 years of age. They also were later observed separately. Some young are weaned at 2.4 years of age, assuming a May or early June separation, as evidenced from a solitary 2-year-old captured in August. However, that animal, plus one 3-year-old captured in July, were the only solitary animals of those age classes captured. It is possible that the majority of the young stay with their mothers to at least 3.3 years of age, thus fostering a 4-year interval between litters. Females that lose their young before or during the breeding season come into estrus immediately.

(d) *Mortality*

Insufficient data exist to allow construction of population life tables showing

specific age mortality rates. However, the late percentage of adults in the population with the natality rate recorded would indicate a high mortality rate among young and sub-adult animals.

Past studies have suggested that such natality factors as disease, parasites and malnutrition, have little effect on the grizzly bears. Evidence has been presented of large grizzlies killing smaller ones (Troyer & Hensel 1962; Mundy & Flook 1973; Pearson 1975), and one confirmed case of this phenomenon was recorded in the Arctic Mountain population in 1973. A 6.5-year-old male, weighing 147 kgs, was killed by a much larger (272 kgs) 9.5-year-old male. The smaller animal wore a radio collar and was killed between September 20 and 27 along the Babbage River. The larger animal had eaten much of the carcass, cached the rest along the river bank, and remained close by in the willows. Although the larger animal was captured, no signs of physical damage were in evidence on its body.

Several other cases of suspected predation occurred but *prima facie* proof was not obtained.

Den Sites

In November, 1973, it was possible to locate the dens of 12 grizzlies because each was carrying a radio transmitter. The den opening was observed in five cases while the other seven were located only as to hillside or snowbank. One additional active den was found while searching for the telemetered animals. One den site was located in mid-summer and it was not known if it was active in the 1973-74 winter. One additional site was recorded by other CWS personnel in the area (DeBock, pers. comm., February, 1974).

The locations of the 12 dens for which the occupant had been identified are shown on Figure 5, along with the other observed sites. None was on the Arctic coastal plain even though some of the animals spent considerable time in that area immediately prior to denning. Reports of grizzlies along the Arctic coast in the early spring, particularly female-young groups, strongly suggest that some denning occurs there; however, none of the tagged animals for which dens were identified used it.

There did not appear to be any differences, either geographically or ecologically, between the denning areas chosen by male or female bears. All sites were within the home ranges already delineated for the individual bears, thus requiring no long migrations to suitable sites. The larger home ranges of the males allowed them a greater selection of sites without leaving their area of familiarity.

The average altitude of the den sites was 732 meters above sea level with a range from 427 to 1036m. It was considered that 11 of the 12 sites were sufficiently delineated to measure the aspect of the opening. Seven were within 45° of south, two within 45° of east, two within 45° of north, and one facing west. Angle of slope was not measured during the November flights. Wooden stakes marked in 1-foot intervals were placed in snow banks as close as possible to each den.

Visual inspection of the six sites where the den opening was located indicated different characteristics from dens found in south-western Yukon (Pearson 1975). There was no heavy shrub cover around the opening of four dens in the Arctic Mountains, although it did appear in two cases. Stability of the soil above the den cavity must be created by other factors. It is postulated that freezing of the active soil layer or actual permafrost may provide the cohesive-

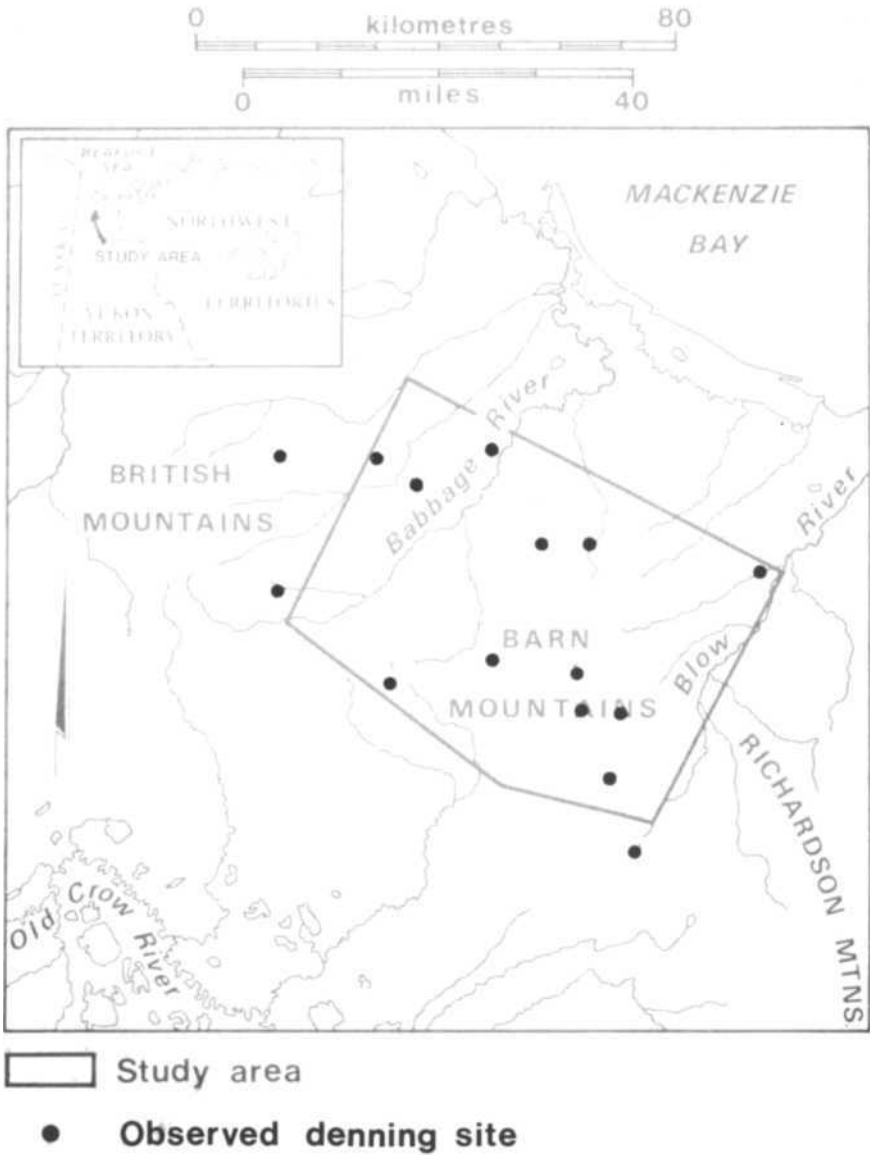


Fig. 5 Observed denning sites for grizzly bears on the study area.

ness that prevents the den from collapsing. If that is the case, it is expected that most of the dens collapse during the thaw period of the summer following excavation.

SUMMARY

The Arctic Mountain grizzly bear was studied on a 3367 square kilometer study area in the Barn Mountains of the Yukon territory during 1973 and 1974. A

seasonal change in the effect of Sernylan (*phencyclidine hydrochloride*) on the grizzlies was observed. The bears fed mainly on vegetable matter which varied with the season. Minimum home ranges of 414 km² for males and 73 km² for females were determined from radio-telemetry studies. A minimum population density of one grizzly per 48 km² was calculated. Preliminary information on the population parameters and dynamics are presented. Den sites were located and described.

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Paper 24

An Evaluation of the use of Erts-1 Satellite Imagery for Grizzly Bear Habitat Analysis

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INTRODUCTION

Considerable data on grizzly bear, *Ursus arctos*, ecology have been gathered during the course of a 13-year study in the Yellowstone ecosystem (Craighead and Craighead 1970, 1971; Craighead *et al.* 1960, 1967, 1969; Craighead *et al.* in prep; Hornocker 1962). This population constitutes one of the few sizeable populations remaining in the United States outside of Alaska.

Recent research at the Montana Cooperative Wildlife Research Unit has emphasized habitat evaluation and integration of this data with accumulated knowledge of the grizzly's food habits, home range, movements and population dynamics. The result will be a better understanding of habitat usage and requirements. It will also permit more accurate estimates of population density and distribution and allow wildlife managers to predict the effects of land use changes (logging, road construction, etc.) on existing bear populations. Habitat can be evaluated to determine if grizzlies can be reintroduced and survive where they have been eliminated.

The development of remote sensing techniques using aerial photography, multispectral scanning sidelooking radar, microwave imaging, and other methods to evaluate land uses and natural resources has been rapid in recent years. These techniques have great potential for reducing the logistical effort of surveying by conventional methods extensive wilderness areas used by grizzly bears.

This report evaluates one of these techniques, multispectral imaging from earth-orbiting satellites. Viewing equipment for analyzing ERTS-1 multispectral images was recently acquired by the University of Montana Geology Department as part of an Earth Resources Program contract with the National Aeronautics and Space Administration (Applicability of ERTS-1 to Montana Geology, NAS5-21826). This provided an opportunity to compare ERTS-1 imagery with data gathered for the U.S. Forest Service and Montana State Fish and Game Department during the summer of 1972 (Sumner and Craighead 1973). Our comparison of multispectral images with habitat data have enabled us to come to some conclusions about the usefulness of this technique and to identify some promising areas for further investigation.

The imagery analysis described in this report was supported by National Aeronautics and Space Administration grant NGR 27-002-006. Dr. Robert Weidman made available to us the multispectral viewing and cartographic

equipment and provided much assistance and helpful advice. Ground truth was obtained from a habitat survey of the Scapegoat Wilderness Area sponsored by the U.S. Forest Service and the Montana State Fish and Game Department, and conducted by the Montana Cooperative Wildlife Research Unit.

STUDY AREA

The 135 sq. km (52 sq. miles) study area is in the center of the newly-formed 970 sq. km (240, 500 acre) Lincoln-Scapegoat Wilderness which is 120 km (75 miles) west of Great Falls, Montana. It lies within the Lolo National Forest, bordered by the Bob Marshall Wilderness area on the northwest. Elevations range from 1700 to 2800 m (5600 to 9200 ft), with over half the area above 2400 m (8000 ft). Relative isolation and light use, combined with specific vegetation and topographic characteristics, make the area favorable habitat for grizzlies. Between 29 July and 15 September 1972, the area was type-mapped for food plants utilized by grizzlies. A population survey of grizzlies, black bear, *Ursus americanus*, and other mammals and birds was made over a somewhat larger area at the same time (Sumner and Craighead 1973).

A recent food habits and habitat requirement study indicated that the following criteria are important to maintain the grizzly population of the Yellowstone ecosystem (Craighead *et al.* in prep):

1. Space.

The home ranges of grizzly bears may encompass areas up to 3900 sq. km (1500 sq. miles). Large undeveloped or *de facto* wilderness areas of national parks and national forests meet this requirement.

2. Isolation

Grizzlies conflict with man and his livestock, and have been eliminated from developed areas. Areas where bears remain and potential habitat for re-introduction of grizzlies is isolated, receiving only light public use. Roads and extensive trails degrade grizzly habitat.

3. Food

An abundance of natural foods must be available from April to November, and must be sufficiently varied so that intermittent deficiencies of one or more sources do not jeopardize the population. Basic foods are carrion, ungulates, rodents, berries, pine nuts, green vegetation, bulbs and tubers and, in some situations, fish.

4. Vegetation types

A wide range of vegetational types characterize prime grizzly bear habitat. A mixture of timber and alpine meadows provide places to forage, socialize and breed. Alder thickets *Alnus* spp., lodgepole *Pinus contorta*, downfalls and other dense vegetation are preferred bedding sites. Large tracts of undisturbed timber provide protection and seclusion.

While other factors may influence a population in a particular situation, those above were given primary consideration in our investigation.

METHODS

The coverage of ERTS-1 MSS imagery develops for Montana as the satellite moves from north to south along the paths shown as dotted lines in Figure 1.

Images are taken at approximately 160 km (100 mile) intervals along each path with adjacent paths covered on successive days moving from east to west. The same orbit path is repeated at 18-day intervals.

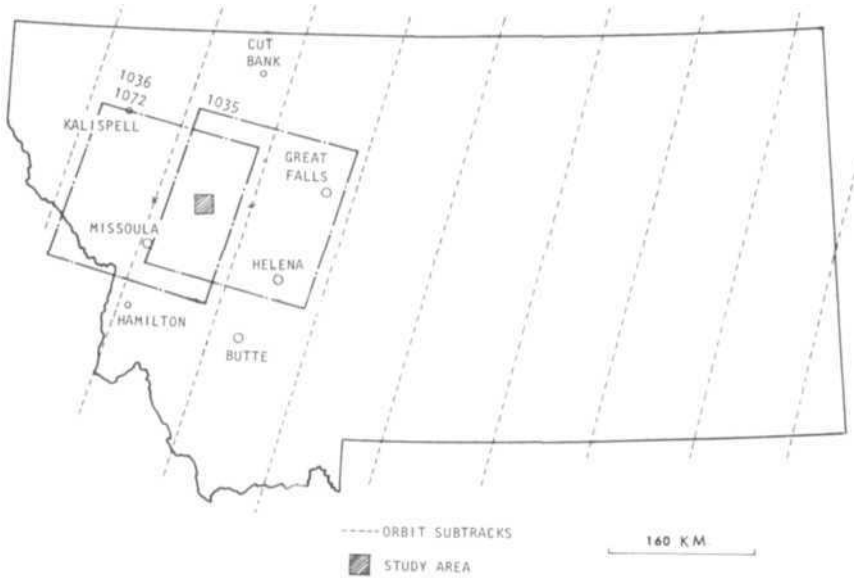


Fig. 1 ERTS-1 Coverage of Montana and study area.

TABLE 1. ERTS-1 IMAGERY OF STUDY AREA
JULY-NOVEMBER 1972.

Date	Frame	Percent Cloud Cover	Subsatellite Point		Sun Angle	
					Elev.	Az.
8-10	1018-17571	10	47.12°N	113.88°W	51.7°	137.3°
8-27*	1035-17513	0	47.28	112.43	47.1	142.7
8-28*	1036-17571	0	47.30	113.80	46.0	143.0
9-15	1054-17571	60	47-33	113.77	41.2	148.6
10-2	1071-17513	10	47.51	112.23	35.3	153.3
10-3*	1072-17571	10	47.43	113.72	35.0	153.5
10-20	1089-17515	0	47.38	112.35	29.3	156.8
10-21	1090-17574	70	47.33	113.80	29.0	156.9
11-7	1107-17521	30	47.26	112.45	23.8	158.7
11-8	1108-17575	40	47.26	113.85	23.5	158.8
11-25	1125-17522	40	47.32	112.46	19.3	159.2

*Frames selected for evaluation

Each image is roughly square and covers an area measuring 185 km (115 miles) on each side, so there is about 10% north-south overlap on successive frames taken in each orbit, and about 40% overlap on frames taken on successive days from adjacent orbits. It is thus possible to obtain side-lap stereo viewing of most areas with images taken in adjacent orbits.

The images used in our evaluation were selected by checking the NASA indexes (ERTS U.S. Standard Catalog, NAS1. 48:872) and by examining the print file maintained by the Geology Department. Coverage began after launch of the satellite in July 1972 and continues at present. The time from July to



Fig. 2 Boundaries of MSS frame, area displayed on color additive viewer (Scene I), and study area.

November 1972 was of greatest interest. This included the period when personnel were afield obtaining ground truth data. Satellite imagery obtained is listed in Table 1. Although study area coverage occurred every 18 days, many images were unusable because of cloud cover. One cloud-free set obtained in August, and another in October, were selected for evaluation. Frame 1036-17571 (28 Aug.) was used for most of the vegetation analysis. This frame and frame 1072-17571 (3 Oct.) were used together to examine time-lapse effects in appearances of vegetation and snow cover. Frame 1035-17513 (27 Aug.) and frame 1036-17571 (28 Aug.) were used together for side-lap stereo viewing.

Most image analysis was done with a color-additive viewer using positive transparency enlargements (23 x 23 cm, scale 1:1, 000, 000) of multispectral scanner scenes. Portions of these transparencies encompassing the study area, 8 x 10 cm in size, were cut out and mounted in 70 mm glass and metal slide holders. The area covered, designated Scene 1, is illustrated in Fig. 2.

The prepared slides for each of the four MSS bands were then placed in a Spectral Data Corporation Model 64 Multispectral Viewer. Red, green, blue, or white light of variable intensity was projected through each transparency to form a color composite image on a 23 x 23 cm ground glass viewing screen. The viewer optics provide a x 37.37 enlargement of the slide, giving an image scale of 1:297, 000 on the viewing screen. After adjustments to place all four images in register, various combinations of band, color and light intensities can be sent up to give maximum enhancement to features of interest in the composite image.

After obtaining the desired scene display adjustments, the image was permanently recorded by photographing the viewing screen with a 35 mm camera and Type B High Speed Ektachrome film. The resulting slides could later be examined, projected or used to make prints as required.

A 23 x 23 cm transparent overlay was prepared for the viewer screen to aid in identifying major topographic features and landmarks. A convenient and low cost method of making such overlays consisted of copying a portion of a 1:250, 000 scale USGS topographic map on a Xerox 7000 electrostatic copying machine at a #2 reduction setting (84.5%) and then making a 1:1 thermographic overhead projection transparency from this reduced-size copy. The resulting overlay matched the image scale on the viewing screen within 1% and allowed forest boundaries, drainages, mountains, and other features to be easily identified.

A composite aerial photograph map of the study area was also prepared from Forest Service 1:15, 840 black and white panchromatic photographs to aid in identifying small features not shown on the topographic map.

A Bauch & Lomb model ZT-4 Zoom Transfer Scope was used to draw vegetation maps from the 35mm slides of color composite images and to superimpose topographic maps on images for identification of major features and determination of snow cover elevation.

RESULTS

Image color effects

Conclusions similar to those of other investigators (Heller *et al.* 1973, Barnes & Bowley 1973, Tueller 1973) were reached after evaluating the comparative utility of the four MSS images, both individually and in combinations.

The two infrared bands (band 6, 0.7 to 0.8 μm ; band 7, 0.8 to 1.1 μm) were very similar in appearance, with rivers and lakes showing black and growing plants in light tones. They reduced the dark tones of forested areas normally apparent in visible light so that scene topography was very clear. Band 5 images (0.6 to 0.7 μm , red) closely approached the appearance of normal aerial photographs; forests and growing vegetation appeared in dark tones and dry vegetation in light tones. Band 4 images (0.5 to 0.6 μm , green) were the least useful for vegetative mapping and had a slightly hazy appearance due to atmospheric scattering, but were the best for identifying snow cover.

A combination of bands 5 and 7 gave the finest detail for vegetative mapping. Adding band 4 to these two gave greater subtlety of color but resulted in a slight reduction in detail, because of both haze effect and the additional difficulty of adjusting three images for perfect registration instead of two.

Simulated false-color infrared images were obtained by illuminating band 4 with blue light, band 5 with green, and band 7 with red. Usually band 6 was not used because of its similarity to band 7. In these images growing vegetation appears in various shades of red. A simulated normal-color image could be obtained by projecting band 4 in blue, band 5 in red, and band 7 in green. The resulting image shows growing vegetation in exaggerated shades of green and was easier for inexperienced observers to classify accurately.

Scene illumination effects

The transparencies supplied by the EROS data center are photometrically accurate, having densities which correspond to absolute scene brightness. As a result, scenes obtained during winter months at high latitudes are often very dark. Two effects are responsible for this darkening: one is the lower average illumination level due to oblique lighting; the other is the presence of many more shadows in areas of uneven topography. Sun angles above the horizon for imagery of the study area (summarized in Table 1) vary from 52° on 10 August to 19° on 25 November.

We found that vegetation mapping was more difficult in mountainous areas with November imagery than with August imagery. North- and northwest-facing slopes received much less light at low sun angles than south-facing ones, resulting in tone variations larger than those used to discriminate between vegetation types in bright evenly-illuminated areas. Discrimination within large sloping areas illuminated at very low angles was poor because of the general dark tone, and no details could be distinguished in full shadow.

Determination of general vegetation character

High alpine meadows appear in light red or pink in the simulated false-color infrared images and can be easily identified and distinguished from the darker red or grayish-red timbered areas. Large areas can be quickly examined on the images and those portions with combinations of forest and meadow (favorable grizzly bear habitat) can be noted for further examination.

Classification of habitat quality by type and intensity of land use

Areas identified as potential bear habitat based on vegetation character can be classified by eliminating portions heavily used by man and grading the remaining area by a measure of land use intensity.

An overlay can be prepared to show all settlements, agricultural land, grazing

land, logging or mining activity, roads and trails in the area. Land in use for agricultural or livestock production, areas within a certain radius of settlements and residences, and a strip (with width proportional to traffic volume) adjacent to roads and trails, are excluded. Grizzlies avoid such areas or are eliminated as a result of eventual bear-man conflicts. A simple example of an overlay is shown in Fig. 3. Urban, agricultural and grazing areas are identifiable on satellite imagery by color characteristic and can be directly mapped. Roads and trails are generally not visible: their locations must be obtained from maps. The width of adjacent strips can be determined from traffic counts, visitor statistics and other sources.

Before this method can be used it will be necessary to approximate a scale factor to exclude high-use areas; on trails, for example, the width of the exclusion would be a certain number of meters per visitor man-day. Such scales would be rather arbitrary. An analysis of Yellowstone Park visitation may provide a starting point since better distribution records, both bear and human, exist there than any other area. The scales would need to be modified for habitat evaluation outside national parks. This could not be expected to be accurate in any absolute sense, but would permit use intensities to be compared with one another and the ranking of habitat by quality.

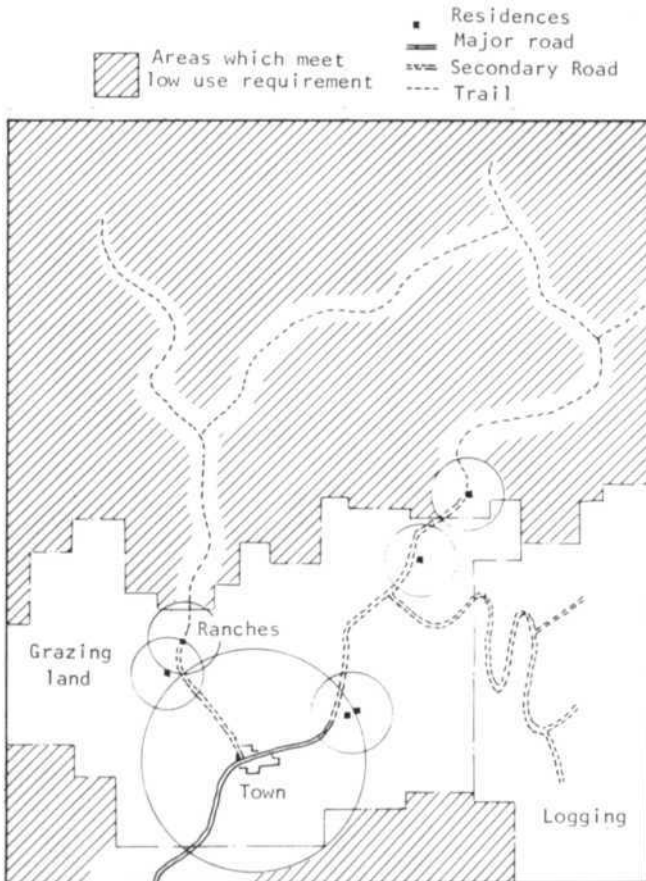


Fig. 3 Example of a use-intensity overlay.



Fig. 4 Simulated false-color infrared image of Scene 1 as displayed on color additive viewer. Growing vegetation appears in shades of red in viewer and shades of grey in this photo.



Fig. 5 Scene 1 with high-altitude overlay superimposed in white light. Only the areas above 2100 m remain visible.

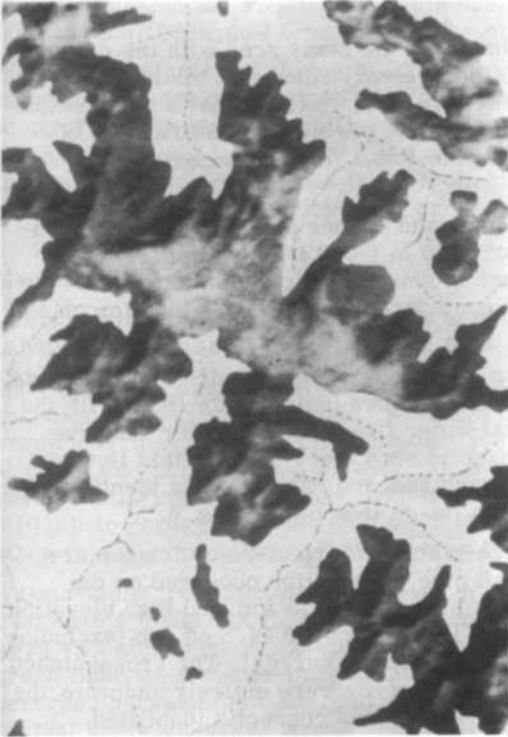


Fig. 6 Enlarged view of study area with altitude overlay. Darker areas are vegetation.

Fig. 7 Distribution of Whitebark pine observed on the ground compared with high-altitude timbered areas mapped from satellite imagery.



Identification of Whitebark pine

Examination of the color composite image of the study area with the color-additive viewer did not reveal any distinctive variations that would permit differentiation of various tree species. However, we found that a combination of tree cover imagery and altitude information permitted identification of Whitebark *Pinus albicaulis* and limber pine *Pinus flexilis*, important food species of grizzly bears.

The ground survey showed that Whitebark and limber pine occurred predominantly on higher ridges, usually above 2100 m (7000 ft) elevation. The approximate distribution of these pines is shown in Fig. 3 of Sumner and Craighead (1973). Both species were considered as Whitebark pine for classification purposes.

A projection mask was prepared from a topographic map which showed areas above 2100 m in black. This image was combined (using white light) with the false-color infrared (Fig. 4) or normal-color images in the color-additive viewer. The resulting false-color image is shown in Fig. 5. In this image timbered areas above 2100 m appear dark red, and can be easily identified and mapped. A simulated normal-color image is shown in Fig. 6.

Timbered areas mapped from the false-color or normal-color images are shown in Fig. 7 in relation to Whitebark pine distribution observed on the ground. The area covered by Whitebark pine is 30.6 sq km, and high elevation timbered areas identified from satellite imagery cover 44.3 sq.km (excluding two southernmost areas, not checked in the ground survey). The crosshatched common area is 25.4 sq km. If the ground survey were entirely accurate, the results indicate that 83% of the Whitebark pine was correctly identified.

Additional area amounting to 45% of that classified as Whitebark pine was actually other species. This is a good result especially considering the simplicity of the method and limited accuracy of the ground survey.

Other factors influencing Whitebark pine distribution include aspect, exposure, soil type and available moisture. On north-facing slopes it was often found at lower elevations than on south-facing slopes. More accurate estimates could be made from satellite imagery by incorporating such factors into the discrimination process.

Identification of shrubs, grasses, and herbs

Other important plant food items in the study area utilized by the grizzly include huckleberry and grouseberry, *Vaccinium* spp., tubers of *Claytonia* spp. and *Lomatium* spp., and several other herbs and grasses. These occur as a low shrub understory among larger trees or small plants in open areas.

It was not possible to identify these species from the satellite imagery alone. Open alpine meadows could be easily distinguished from timber stands, but particular species could not be separated. Mapping meadows may provide data to estimate the amount of tuberous and other foods since composition of alpine meadow vegetation is stable. It can be assumed, for example, that the amount and distribution of *Claytonia* spp. and *Lomatium* spp. determined by sampling in one location would represent other alpine areas within the ecosystem.

Understory species, *Vaccinium* spp., were not visible, and their typing would probably be limited to identifying likely areas for ground sampling.

Some discrimination between visible vegetation types should be possible based

on their association with identifiable species (Whitebark pine), or other factors as altitude, soil type, topography or a combination of these.

Since green plants are distinguished from dry or dead ones by higher reflectance in the infrared bands, a series of scenes at 18-day intervals can be used to determine phenological differences during spring late summer and fall. To the extent that this is species-specific, it provides a promising technique for distinguishing coniferous trees from hardwoods, and for identifying some hardwood species and agricultural crops (Dethier 1973).

Mapping snow cover

Information about snow conditions is helpful in grizzly studies since it affects behavior and seasonal availability of food.

Snow appeared distinctively in bands 4 & 5, where it has highest contrast with surrounding snow-free terrain. Although clouds and snow had about the same brightness, they could be distinguished because of differences in shape and the shadows that accompanied clouds. Boundaries of snowcovered areas are easily distinguished on bare or lightly-vegetated terrain, but become more difficult to recognize in heavy timber. These findings agree with those of other investigators (Barnes and Bowley 1973; Meier 1973; Weller 1973).

A time-lapse technique proved useful in determining changes in snow cover. Two band 4 images of the same area, one taken in August and one in October, were superimposed on the viewer. The August image was illuminated with green light, the October image with red. In areas where no changes in tone had occurred between the time images were taken, the resulting composite was a neutral greenish-gray. Areas that were lighter in the October image appeared red, and areas that were darker appeared green.

Areas covered with snow in October and not in August were bright red and easily distinguishable. Examination of this image with a topographic map overlay showed that the snow level on 3 October was at 3400 m (2300 m on north-facing slopes) in the study area.

Additional data for vegetation type mapping can be obtained from snow cover information, since it is closely related to moisture conditions. Differential melting rates and changes in snow field boundaries provide exposure and average temperature data that helps discriminate between some vegetation types indistinguishable by appearance alone. Appearance and flowering of certain plant species is closely related to snow field boundaries, so the location of these boundaries indicate vegetation type and general phenology.

DISCUSSION

The results of this preliminary investigation show that ERTS-1 multispectral scanner imagery can be of value in habitat analysis. Useful information about grizzly habitat can be obtained with minimal cost and effort. The authors have not had prior photointerpretation experience, so information may have been overlooked that could be obtained from the imagery. We plan to continue evaluating this technique in ongoing programs where habitat data are needed.

We feel that satellite imagery is most valuable at present as a supplement to, not a replacement for, field observations by personnel on the ground. Limitations in image resolution and kinds of information that can be obtained from multispectral scanning allow errors if used alone. The imagery can be used,

however, to perform initial screening and to select these areas where field effort can be productively concentrated. In surveying wilderness areas to locate suitable reintroduction habitat, large portions could, for example, be eliminated on the basis of the imagery alone. Field work can then be focused on remaining locations which appear to meet minimum requirements. Examination of satellite imagery early in a study should thus allow an effective sampling strategy to be developed to minimize field effort and overall program cost.

Computer-assisted analysis of multispectral scanner images offers several advantages over the visual methods described in this paper, and we are investigating this technique to minimize subjective factors and reduce time required to classify larger areas. The general approach involves displaying a 3-band color composite image of the area under investigation on a CRT screen. The image is derived by transferring picture-element data from ERTS computer-compatible digital magnetic tapes to a buffer-storage system, which is in turn scanned to produce a periodically-refreshed color image on the CRT. The digital form of the image data permits a computer to be used to perform decision functions or computational algorithms upon each image element before it is displayed. This allows a variety of operations to be performed on the image such as density slicing, color enhancement, selective color display, and false-color display. It also permits 'learning' techniques to be applied in which a small portion of the image, for which ground truth is available, can be analyzed by the computer; similar areas in the remaining scene are then identified and displayed as one color on the CRT. This is a powerful method for developing land classification maps. The computer-enhanced images and type maps can then be compared with vegetation type maps obtained by selective ground sampling to validate the classifications.

Using techniques described, we could rapidly survey the three largest ecosystems in the western United States (Yellowstone, Selway-Bitterroot and Bob Marshall) to classify favorable grizzly habitat, to assist in making more accurate estimates of the present grizzly population and to locate the most promising sites for reintroduction. Such information is badly needed and could be obtained with comparatively modest funding. Together with extensive data on grizzly food habits, movements, ranges and bear ecology that has already been gathered, such a survey could provide several western states the means to evaluate hunting regulations and harvest, and better data than is now available for making management and land use decisions.

Satellite remote sensing methods are a valuable addition to the tools of the wildlife researcher and manager. The usefulness of ERTS-1 imagery will expand in the near future as other researchers develop analysis methods to increase types and quality of data obtained from the images. This should result in additional techniques useful in habitat analysis. Remote sensing will become increasingly valuable as equipment with improved resolution and additional spectral bands becomes available on future satellites.

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The Use of the Skull in Age Determination of the Brown Bear

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To understand many aspects of the biology of bears, it is necessary to establish age of animals. Without this ability, it is impossible to determine the age structure of the population, rate of growth, onset of sexual maturity, lifespan, etc. Accurate age of bears after one year may be determined by the number of layers in dental root cement. The first work on this technique was reported by Smimov (1960) ... 'in the bear, the layer of cement is most exact and one can consider that each layer signifies one year of life.' Rausch (1961) studied American bears of known age and established that there is an annual layer of dentine and cement and also a yearly outgrowth on the root of the tooth; according to the number of annual layers in the length of the tooth, one can distinguish ten age classes. Mundy and Fuller (1964) determined the age of grizzlies (*Ursus arctos*) by the cement layers of the third molar. Because the third molar of the lower jaw cuts through in the bear in the second year of life, its age can be determined by the number of cement layers plus one year. Manning (1964) took as significant the degree of concretion of skull sutures, the thickness of enamel on teeth, and the form of the skull outgrowths as a technique in the determination of the age of the polar bear. By these criteria he identified four age classes and determined the ages of the bears to the sixth year. Sauer, Fry and Brown (1966) determined the ages of black bears (*Ursus americanus*) according to the lengths of the incisors to a thickness of 250 microns in sequential sections of 25 microns. They discovered that wild bears did not differ from bears living in captivity. They showed that sequential layers of cement did not always correlate with age or were sometimes completely absent, and in wild bears of known age each cement layer corresponded to one year in the life of the bear. Ushivtsev (1972) used the same criteria for determining the age of the brown bear (*Ursus arctos*) of Sakhalin Oblast and came to the same conclusion. Inukai Masaaki (1972) discovered that the age of the brown bears of Hokkaido, according to sections of the incisors, up to a year old cannot be determined by this method because there were no definite layers of dental cement, but in older bears they are in annual layers.

Thus all researchers attempting to determine the ages of bears came to the same conclusion: that the number of layers of tooth cement corresponds to a year in the life of the bear.

This position was taken for the basis of our studies and thus accurate growth of bears of the Turykhan population was determined according to the number of cement layers at the root of the tooth. As the basis of our research on the skulls of brown bears in the Borogov State Agricultural Enterprise, located in the middle Yenesei region (33,040 sq. km.), forty-three skulls were collected between 1967 and 1973 from bears in a comparatively small region. Therefore, errors connected with geographical variability of the species can be excluded.

The analysis of the collected material was conducted according to the method of Klevezal and Kleynenberg (1967) on microtome sections of roots of bear teeth. To select the most suitable tooth from several skulls of the collection,

we sliced all teeth, sections of jaws, and different parts of each tooth. It was shown that the number of layers in the cement were the same whatever portion of the tooth was studied aside from the third molar of the lower jaw, where the number of layers on one side was less than in the remaining teeth. Therefore, in the majority of samples collected, age was determined according to the first section of the lower jaw, as being the easiest for treatment and the least expensive for collection.

The teeth were decalcified in a 7% solution of nitric acid to the point that the tooth could be pierced with a needle. Sections were made at 3, 4, 5 and 6 days. After decalcification, the tooth was fixed in a 5% solution of potash alum for 20 to 24 hours and rinsed in distilled water; then the root of the tooth was sectioned on a freezing microtome. The most defined cement layer was visible in the upper third of the root. From one tooth, we made about 100 sections varying in thickness from 30 to 60 to 90 microns. The cement layer was clearly visible under the microscope even in unstained sections. After staining the sections with hematoxylin for one hour, we studied the most successful slides under the microscope. The selected samples were differentiated in 96% alcohol to a reddish color, then mixed in slightly alkaline water until slightly bluish. Samples were then transferred to glycerine (25, 50 and 75% for 1, 1.5 and 2 hours respectively), prepared in gelatine or Canada balsam, and photographed. Such a method was used to determine the age of all the specimens in the collection.

This method determined age with sufficient accuracy; however, it requires laboratory conditions, specialized equipment, chemicals, and a lot of time. In field conditions, when it is not always convenient to transport skulls, or there is no suitable laboratory, we worked out a more simple and rapid method of determining the age of bears according to a complex of craniological and morphometric indicators.

The skull of the brown bear grows and changes structure in the course of the entire life of the animal. In the bear cub the skull is nearly circular in form, predominant according to the size above the facial portion of the skull with weak development of the mandibular arch. During growth, the skull lengthens and, with the attainment of sexual maturity of the individual (females, 3 to 4 years; males, 4 to 5 years), the skull has the characteristic form for the species. A mix of juvenile and adult teeth begins at age 5 to 6 months, depending on conditions of development for the cub, and ends at 1.5 years. Towards the first autumn, in sequence, there are changes in the incisors, the first upper molars, the first and second upper molars. Incisors and molars grow quickly and toward the fourth year reach their maximum size.

Canines grow more slowly. In the first year of life, they are about 5 to 8 mm long; in the second they grow to 20 mm, and finish their growth by the 8th to 10th year. The wearing down of the teeth begins with the incisors from the internal side, then the molar teeth of the upper jaw and the lower molars and finally the canines.

The growth of skull sutures begins in females at the age of 3 or 4 years, in males at 4 or 5 years. The growth of the basic skull sutures ends in females at 8 or 9 years, but the sites of suture growth at that age are still well marked; later it smoothes down and in old animals is completely unnoticeable. Latest of all, by the 15th to 18th year, the bones of the lower jaw and skull knit. The character of the knitting of skull sutures of bears is complex and requires further study.

On the basis of analysis of age changes in the form of the skull, the characteris-

tic changes and wearing of the teeth and sequence of knitting of skull sutures, other indicators include the measurement and weight indicators of the animal. All skull collections, independent of determination of growth by cement layers, were distributed in 11 age classes.

1. Cubs to 5 months of age

Live weight (LW) to 8 kg. Condyle-basal length (CBL) of the skull to 150 mm. Weight of skull without lower jaw (WS) to 80 g. These three changes will lead to a shortening of the corresponding LW, CBL and WS. The teeth of the young bear: canines to 15 mm in length. In the lower and upper jaw the first molar tooth is visible; the others are still beneath the jawline.

2. Cubs from 5 months to one year

LW: 23 - 25 kg; CBL: 190 - 200 mm; WS: 315 - 328. In the lower jaw the second molars have appeared, the third are still in the bone; in the upper jaw, the opening beneath the second molar has opened. The milk teeth have fallen out: the canines have changed to permanent or they both appear together.

3. Yearlings (from 1 to 1.5 years)

LW: 30 - 49; CBL: 224 - 240; WS: 300 - 430. Molars of the upper jaw appear full, but the rear part of the second molar is still level with the jaw bone. The first part of the third molar appears in the lower jaw, the rear part is still beneath the jaw surface. The tooth surface is very irregular and rugose. The tooth capsule of the second upper molar is separated and protrudes from its socket by 2.5 to 3 cm.

4. Immature Bears (from 1.5 to 2.5 years)

LW: 50 - 70; CBL: 234 - 260; WS: 300 - 530. The process of closure of the skull sutures has not begun. The last molars of both jaws are almost emerged, and the capsule of the second upper has diminished to 1-1.5 cm; its rear end from the circular form gradually takes on the form of a point. The semi-circular lines are almost parallel.

5. Immature Bears (from 2.5 to 3 years)

LW: 62; CBL: 254 - 285; WS: 530 - 610. The semicircular lines go out to 3 - 4 cm from the occipital bone where growth of the sagittal crest begins and where closure begins in an almost lamellar suture. Closure begins from the lower part of the coronal suture.

6. Females from 4 to 6 years

LW: 103 - 105; CBL: 283 - 304; WS: 560 - 870. The suture between the upper jaw and the cheek bones begins to close. The rear edge of the upper incisor starts to wear off. The length of the sagittal crest is up to 3 cm and its height is 1.5 cm.

7. Females from 6 to 10 years

LW: to 125. Coronal and basal sutures closed. Internal and external surfaces of the upper median tooth worn evenly, the outermost only on the internal side. External parts of some of the molar teeth higher than internal by 2 - 5 cm.

8. Males from 6 to 9 years

LW: 130 - 184; CBL: 313 - 323; WS: 950 - 1100. Frontal suture closing or closed. Length of sagittal crest 9-11 cm, height 1.5 - 2 cm. Boundaries of the teeth of the upper jaw 5-6 mm higher than the middle. Rugosity of the molar series still well marked. All edges of canines sharp.

9. Males from 12 to 14 years

LW: 170 - 230; CBL: 223 - 247; WS: 1100 - 1340. Height of sagittal crest 2.5 - 2.7 cm. Internal crown of upper canine is worn. Intermediate molars appear grooved, outer edges worn almost to the level of the middle. Upper fissures nearly closed, including those between the frontal bones and the upper jaw.

10. Males 15 to 18 years

LW: 165 - 264; CBL: 333 - 349; WS: 1130 - 1500. The external surface of the upper canines is worn—little pits are formed. There are grooved depressions in a series of upper molars. The outside edges of both jaws are worn down to the level of the centers. The zygomatic suture is closed.

11. Both sexes—older than 18 years

The zygomatic arch and bones of the lower jaw are joined. On the skull there is no evidence of former sutures visible. The molars in the majority of cases are cariose; the upper molars are almost all filled with cavities. The upper row of molars is worn evenly. The outpart of the molar is about 8-10 mm higher than the internal and is sharp in form. Some teeth are absent and canines often broken.

Thus, according to external signs, the sequence of joining of the skull sutures, the type of wearing of the teeth, weight, and linear indicators can determine the approximate age of the brown bear under field conditions with the aid of measurements of length and weight. No recourse to complex laboratory techniques is needed. With this method, accuracy of age determination to the 4th year is within 1-2 months, and from the 4th to the 18th year, to within 2-3 years. According to the accumulation of collected materials, the given method will be made more accurate and the number of age classes will increase.

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PART IV. STATUS OF BEARS

Paper 26

A Remnant Brown Bear Population in Southern Norway and Problems of its Conservation

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INTRODUCTION

About the year 1850 the brown bear *Ursus arctos arctos* L. was common in forested areas over most of Norway, with a population estimated at several thousand individuals (Helland 1913). The development of better firearms, in certain places combined with changes in the environment, radically changed this situation within a hundred years. By 1969, it was estimated that only 25-50 brown bears were left (Myrberget 1969). The majority of these individuals are connected with larger populations in neighbouring countries (Fig. 1).

Only one small isolated population still exists, situated less than 100 km to the north-west of Oslo in the so-called Vassfaret Area, named from one of the main forested valleys.* The population has been under study during the past 25 years. The aim of this study has been to follow the destiny of this small population, isolated in a restricted area exposed to increasing human invasion and influence. Some major results on distribution and population development in the period 1949-73 will be presented here. Previous results are given in Elgmork (1954, 1962, 1966a, 1966b, 1969). A more comprehensive account will be published elsewhere (Elgmork in press), as well as results on other topics such as seasonal occurrence, food and feeding behaviour etc. (Elgmork in prep.).

In the period 1969-73, the Vassfaret Valley was studied by a team of biologists under the International Biological Programme, Section CT (Conservation of Terrestrial Communities). The results of the bear studies undertaken in this project will be published elsewhere and are not included in the present material. When these investigations are referred to in the text, the symbol (IBP-CT in prep.) is used.

STUDY AREA

The general situation of the study area is illustrated in Fig. 1. The bear area given on the map in Fig. 2 is defined as the Main Area, covering about 1400 km² of which 1200 km² are forested. The Main Area has been divided into 5 zones.

Bears are also occasionally reported from adjacent districts and reports from an area covered by a circle within a radius of 90 km are included in the material. This is referred to as the Surrounding Area, covering approximately 25 000 km².

* Since this paper was sent to the Editor, evidence has been accumulating which indicates the existence of another isolated, small population in Hordaland county, about 60 km east of Bergen.

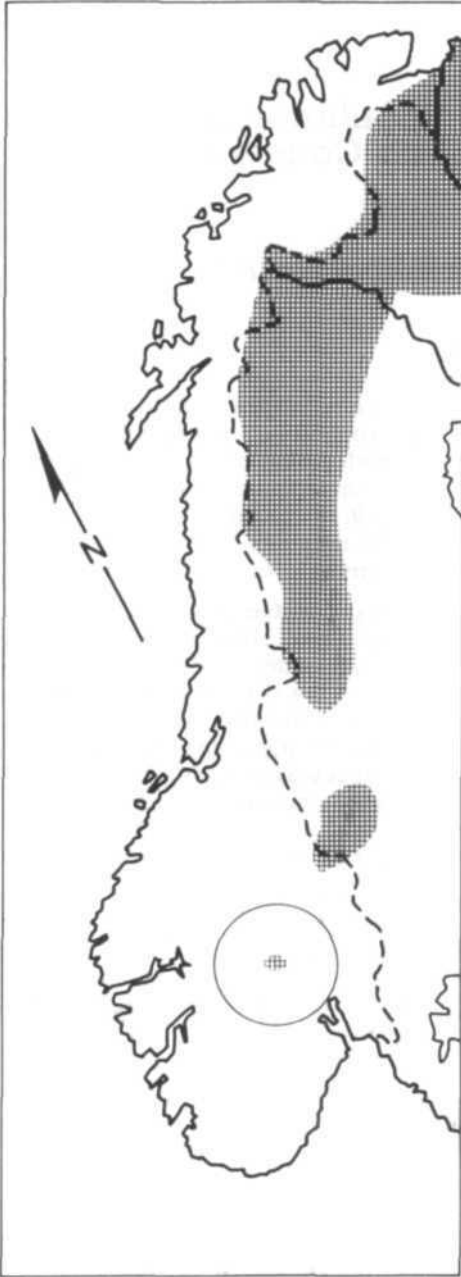


Fig. 1. Approximate distribution of the brown bear in Scandinavia about 1970. Occasional observations have also been made outside the hatched areas.

The circle gives a general idea of the limits of the Surrounding Area.

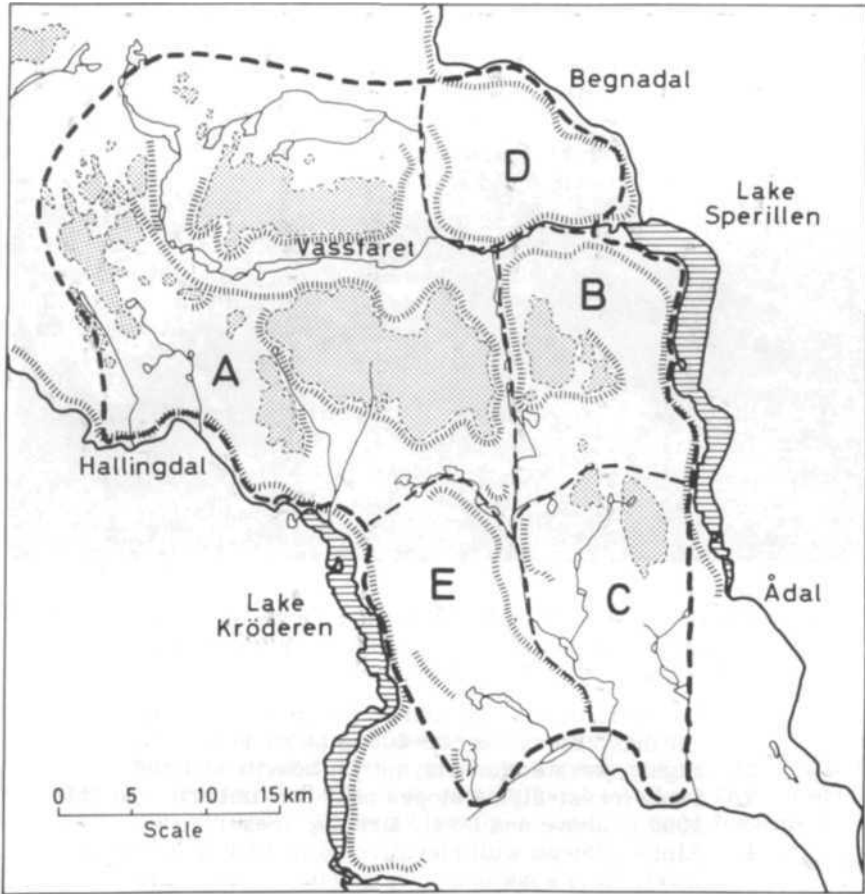


Fig. 2. Study Area: the five Zones A to E of the Main Area are indicated and the more heavily marked outer boundary is that of the Surrounding Area. The finer dashes, enclosing the stippled areas, mark the 900 m contour, which also approximates to the timberline (cf. Fig. 4).

The Main Area is composed of forests intermingled with alpine plateaus with the timberline situated about 900-1000 m above sea level (Fig. 3). The dominating and climax forming forest tree is the spruce *Picea abies* (L.).

Along the forested valleys, especially in Zone A, steep and rugged Subalpine slopes with snowslides are found near the timberline. Parts of these areas have a lush vegetation suitable for the bears, especially in the spring. These areas are difficult for man to traverse, and the bears have found here a niche relatively undisturbed by man. Most of the known dens are situated in this type of habitat (IBP-CT in prep.). The presence of this type of landscape is probably important in explaining why this became the last resort of an isolated brown bear population (Elgmork 1966a & b).



Fig. 3. Main ecological zonation in the core area of the bear habitat. Aerial photograph from the eastern part of the Vassfaret Valley looking south-east, 15 May 1970. From the bottom:

1. Lower forests traversed by forestry roads and clear-cuttings. Elevation 500-600 m above sea level.
 2. Highly elevated forests, not yet heavily utilized.
 3. Steep forest-alpine slopes near the timberline at 900-1000 m above sea level. Denning areas.
 4. Alpine plateau with elevation up to 1200 m above sea level. This zone is not frequented by the bears.
- (Photo. K.Elgmork)

The Main Area and its immediate surroundings are sparsely inhabited by man, with a mean density of about 2-3 permanent residents per km². Human habitation is concentrated in the valleys and in some small forest communities as shown in Figs. 4 and 5 (right: pp. 287, 299).

At the beginning of the study period the Main Area was one of the least disturbed wilderness areas in southern Norway, which also helps to explain the preservation of a remnant brown bear population in this area.

The picture has changed radically during the study period and most of the forested area has gradually been invaded by mechanized forestry, including the building of a large number of forestry roads and the use of large clear-cuttings. After the forests were opened up by the roads, an extensive building of private holiday cabins followed, as well as other forms of tourism (Figs. 4 & 5, right).

An attempt has been made to quantify some of the human factors in Fig. 6 B and C. Fig. 6 B gives a survey of the development of forestry based on statistical material from the Main Area and adjacent districts. Altogether, the diagrams indicate a rather extensive utilization of the forests, with a steady in-

crease in the lengths of forestry roads and in clear-cut areas. The length of forestry roads and summer tractor roads increased by 13 per cent over all or from about 50 to 400 m per km² of forest in Zone A, and from about 250 m to nearly 900 m in Zone C. Cutting class I (clear-cutting) and II (early successional stage) as the mean for the two counties constituting the bear area, increased from 7 per cent around 1950 to about 24 per cent in 1963. In the southern part of the Main Area the percentage in 1950 was considerably higher than the mean. Other areas, especially in Zone A, lag behind the mean values.

Tourism can be divided into hiking tourism and the building of private holiday cabins. Fig. 6 C gives an estimated curve for the increase in the number of houses, predominantly private cabins, in the Main Area. The density of cabins is highest in Zone B with about 2 per km² of forest. The relatively few houses present at the beginning of the study period were mostly associated with summer pastures and dairy farms, the majority of which were no longer in use at that time.

MATERIAL AND METHODS

In spite of a large number of sampling trips to the bear area, only a very few random bear observations were made. Consequently, the study had to rely mainly on second and third hand observations which were gathered from many sources. These are personal communications, interviews, both direct and through questionnaires, and newspaper clippings. A total of 430 reports are now available. The collecting of interviews is being continued.

A problem with information of the above type is the authenticity of the reports. About 3 per cent of the material was discarded as false, while about 27 per cent of the material was characterized as doubtful and treated separately. About 6 per cent was confirmed by the author or some other biologist. The material was re-evaluated at the end of the study period to ensure equal treatment.

Of special concern were the newspaper clippings (43 per cent). These proved, however, to be more reliable than expected. Of 247 newspaper clippings available 60 have so far been checked by field studies, personal communications or interviews. In all cases the basic information in the newspaper clippings corresponded with the personal reports. There were only some exaggerations and minor inconsistencies in details.

The authenticity of the material is supported in different ways. Most reports came from local newspapers and from the local population. The majority of accepted reports are claimed to be visual observations, while the large majority of doubtful reports are of tracks and signs.

Assuming a similar proportion of error throughout the study period and for different population categories, the relative parameters should be uninfluenced by the error.

Final support for the reliability of the material is the arrangement and logical pattern of the emerging results, as e.g. systematic trends and statistically significant similarities and differences in the material. Such results cannot be explained on the basis of material dominated by false reports. Nor are the results in agreement with known variations of other mammals that might be suspected to lead to false bear reports.

The material is consequently interpreted on the basic assumption that variations in the number of reports reflect parallel variations in the population.

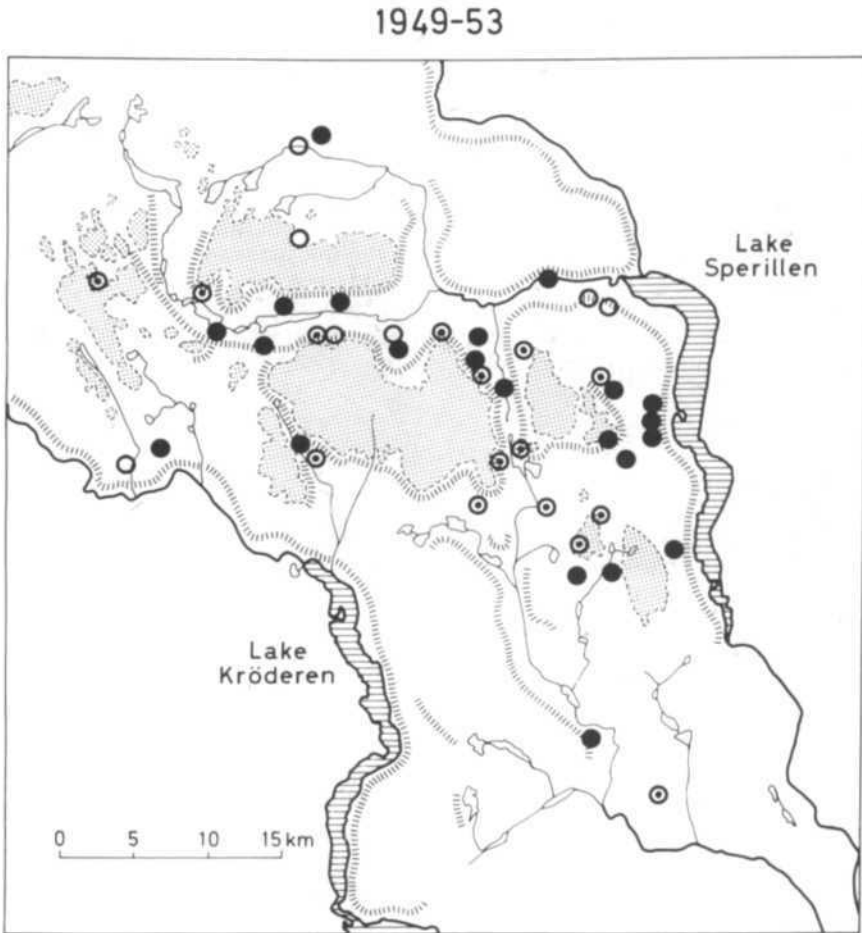


Fig. 4 (left). Accepted bear observations. Two or more independent reports of the same occurrence and reports of different observations made within the same month and less than 5 km apart are condensed into one symbol as follows:

- Newspaper reports.
- ⊙ Personal reports and interviews.
- Doubtful, observation not fully acceptable.
- ▨ Above the timberline.

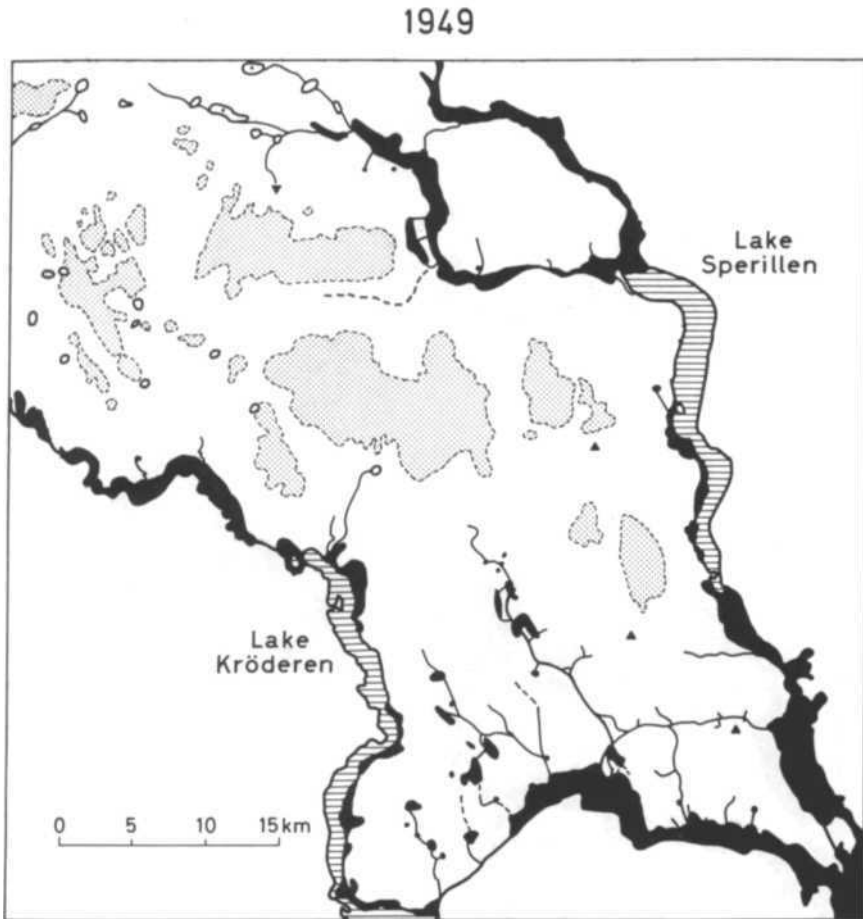


Fig. 4 (right). Indicators of human activities.

Black areas: permanent habitation with agriculture, variably interspaced with forest.

Circumscribed areas with or without dots: not permanently inhabited but with 5 or more cabins or houses less than 500 m apart. Each dot represents 10 cabins or houses. Absence of dots indicates 5-9 cabins or houses.

Triangles: lodging open to the public

Apex up: Norwegian Tourist Association cabins

Apex down: Mountain hostel

Thicker lines: public roads open throughout the year

Thinner lines: forestry roads, varying in quality but passable for cars, though many are closed in winter and some are open to special permit holders only.

Broken lines: tractor roads not usable by cars.

Stippled areas: above the timberline.

1969-73

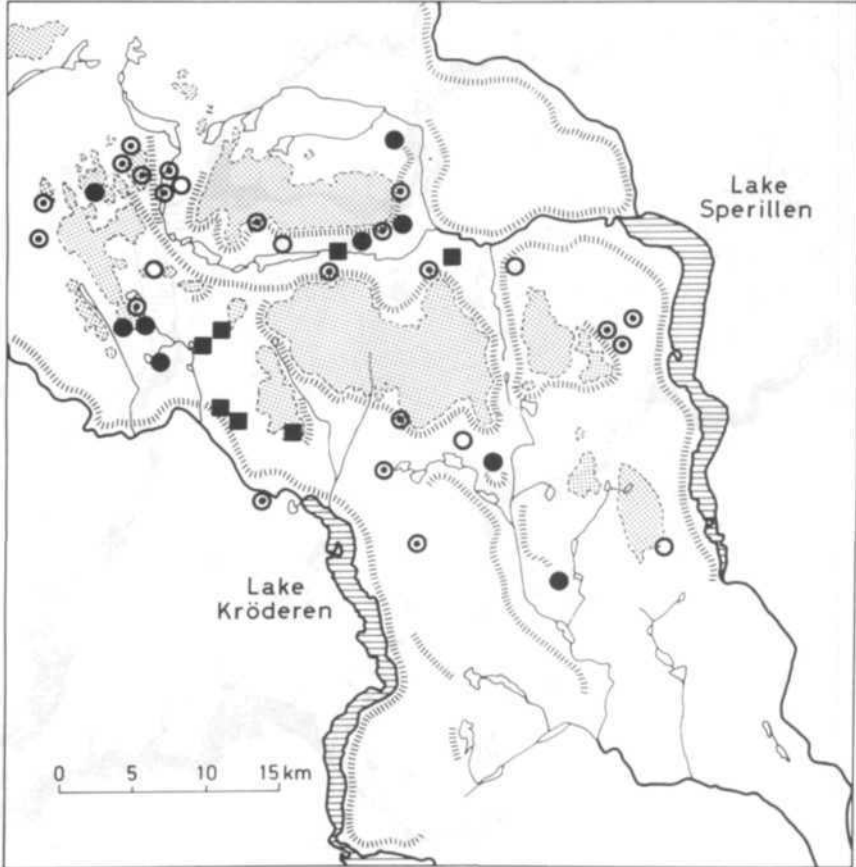


Fig. 5 (left). Accepted bear observations. Two or more independent reports of the same occurrence and reports of different observations made within the same month and less than 5 km apart are condensed into one symbol.

- Reports controlled by the author and found to be authentic.
- Newspaper reports.
- ⊙ Personal reports and interviews.
- Doubtful, observation not fully acceptable.
- ▨ Above the timberline.

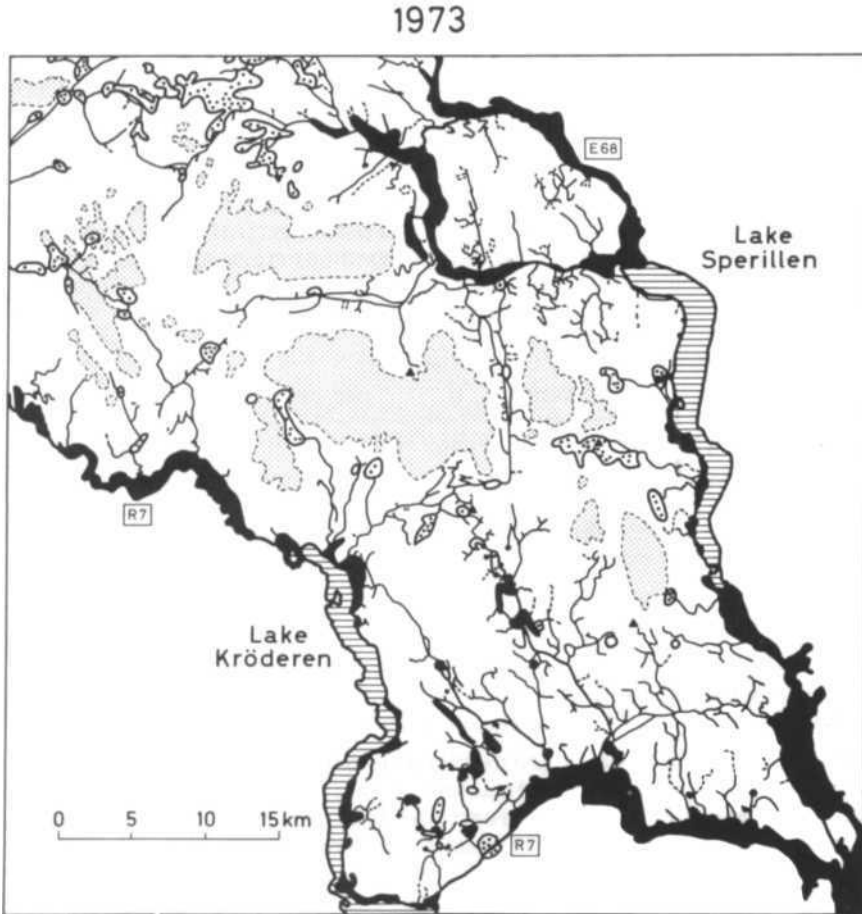


Fig. 5 (right). Indicators of human activities.

- Black areas: permanent habitation with agriculture, variably inter-spaced with forest.
- Circumscribed areas with or without dots: not permanently inhabited but with 5 or more cabins or houses less than 500 m apart. Each dot represents 10 cabins or houses. Absence of dots indicates 5-9 cabins or houses
- Triangles: lodging open to the public
 - ▲ Apex up: Norwegian Tourist Association cabins
 - ▼ Apex down: Mountain hostel
- Thicker lines: public roads open throughout the year
- Thinner lines: forestry roads, varying in quality but passable for cars, though many are closed in winter and some are open to special permit holders only.
- Broken lines: tractor roads not usable by cars.
- Stippled areas: above the timberline.

DISTRIBUTION

During the period of study the bear population occurred chiefly within the boundaries of the rather restricted Main Area. The bears apparently have kept to traditional home ranges for a long time. During the study period, however, changes in distribution occurred within the area correlated with changes in the environment.

The distribution of accepted bear reports in the Main Area for the periods 1949-53 and 1969-73 is shown in Figs. 4 and 5 respectively. By comparing the two maps, a shift to a concentration in the north-western parts and a withdrawal from the southern and eastern parts are clearly visible. This change can be specified for 3 zones as follows:

	1949-53		1969-73	
	n	per cent	n	per cent
Zone A	19	50	29	88
Zone B	12	32	3	9
Zone C	7	18	1	3
Sum	38	100	33	100

There is a clear relative increase in Zone A and a corresponding decrease in Zones B and C, the eastern and south-eastern areas. (Only one report is available from Zones D and E during these periods.)

There are no indications of a greater hunting pressure that might have chased the bears out of the southern and eastern areas. The most conspicuous difference is the general increase in forestry activity and, for the last 10 years, also in tourism. Both these factors are especially prevalent in these zones, as can be seen from the maps in Figs. 4 and 5 (right). In Zone B forestry is very marked to the north and cabin concentrations to the south. In the south-eastern zone forestry is specially prevalent, visualized by a relatively dense network of forestry roads.

There is thus a close correlation between human activities and changed occurrence of the bears, indicating a negative influence.

POPULATION DEVELOPMENT

The least biased parameter reflecting variations in the population are newspaper reports derived from 7 local newspapers. In the first 20 years of the study, the chances of obtaining reports from newspapers should be fairly evenly distributed.

The variation in the number of newspaper reports in the Main and Surrounding Areas is given in Fig. 6 A. The most significant result is the marked decrease in the total number of reports. In the Main Area the decrease starts in the second half of the 1950s. In the Surrounding Area the number of reports is fairly constant up to the middle of the 1960s where there is an increase and in

5 years reports from the Surrounding Area exceed those from the Main Area. At the end of the study period, however, there is a marked decrease in the Surrounding Area. The increase in the Main Area in the last 5-year period may or may not be real as the mechanism behind this increase is not yet understood. The chances of getting reports may have been greater due to an increased human traffic (Fig. 6 C), the IBP activity and a greater public engagement in conservation problems.

The most reasonable interpretation of the data is that since the end of the 1950s there has been a gradual decrease in the total population, brought about mainly by emigration from the Main Area to more peripheral areas.

A relatively large number of females with young are reported both personally and in newspapers from the Main Area. From the Surrounding Area only 8 reports of females with young are available. Up to now 61 reports of young (14 per cent) have been received. After excluding as doubtful about 34 per cent, one is still left with 40 reports of young, of which 18 are sight records, some giving many details. A certain reproduction must therefore have taken place.

The variation in the percentage of young in the population in the Main and Surrounding Areas is shown in Fig. 6 B. Mean value is about 16 per cent. If only the accepted reports in the Main Area are considered, the percentage of young is only 2-4 per cent in the last 5-year period.

The litter size is reported as either one or two in both the Main and Surrounding Areas. The mean value for both areas together is 1.3.

Most reproduction parameters are of a size order that could be expected to occur in a very small and decreasing population in which reproduction is about to come to a halt. The last visual observations of a female with young regarded as authentic are from 1969 in the Main Area and from 1972 in the Surrounding Area.

The known mortality in the study period is very small. Up to 1971, when the bear in this area was fully protected, there was an open hunting season from 15 May to 30 October. In the eastern part of the Main Area a private protection was introduced in 1933. In the study period only one bear was shot legally in the Main Area (1956). In addition, one bear was shot in 1949 just outside the north-western border of the Surrounding Area. There is every reason to believe that no more bears were shot, because 5 municipalities had a relatively high bounty on the bear which has not been claimed.

What remains is the problem of poaching, which in the isolated Alp population in Northern Italy is regarded as an important mortality factor (Roth 1973). Enquiries made about possible illegal killing of bears have on the whole proved negative.

POPULATION SIZE

Based on the number of reports of young, a method of calculating the population number will be attempted. The calculation is based on the assumption that the relation between the number of young and the total number of bears in the population is reflected in the relation between the reports of the same two categories. One also has to assume that the chance of observing a female with young is about the same as for single bears.

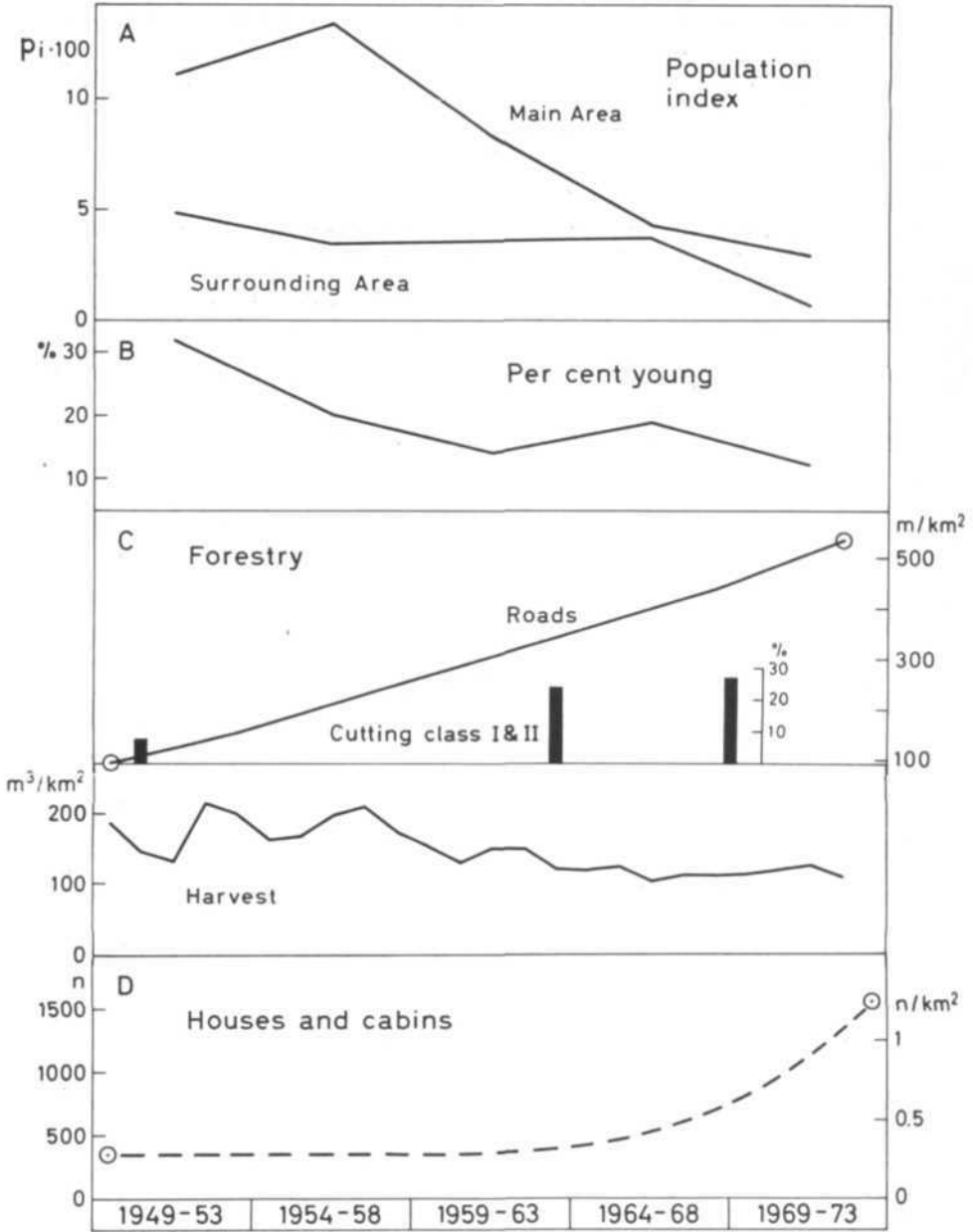


Fig. 6. Population dynamics and some parameters of forestry and tourism.

- A. Number of newspaper reports per 5-year period, Main Area and Surrounding Area.
- B. Per cent of young in the population in the Main and Surrounding Areas together, based on the total number of reports.
- C. *Roads*: Mean length of forestry roads and summer tractor roads. Gradient of the curve mainly from data for the municipalities Nes, Flå and Sør-Audal. End values of the curve refer to the Main Area, derived from official and unpublished maps.
Black Bars: Percentage of cutting classes I and II; mean for the counties Buskerud and Oppland.
Harvest: Yearly lumbering harvest represented by the mean for the same three municipalities mentioned above.
 (Data from Central Bureau of Statistics, Geographical Survey of Norway, and the National Forest Survey of Norway).
- D. *Tourism*: Estimated variation in the number of houses and cabins in the Main Area, exclusive of areas with permanent habitation. End points of the curve from official maps.

On these assumptions the following equation can be set up for the 25-year period:

$$\frac{25n}{y} = \frac{S_r}{y_r}$$

n : population number

S_r : total number of reported bears

y : number of young claimed observed under the supposition of either 1 or 2 young per year

y_r : reported number of young

This equation gives for the 25-year period a mean number of about 7 in the Main Area and about 4 in the Surrounding Area. From these means maximal and minimal numbers can be calculated by use of the variations in the reports. These calculations give for the Main Area a maximum number of about 9 in the beginning of the study period and a minimum of about 5 at the end. As more than one litter is possible in some years with many reports of young, the figures given should be regarded as minimum estimates.

If the Main and Surrounding Areas are added together, the maximum and minimum values will be about 14 and 8 respectively, with the minimum in the last 5-year period. The present number of individuals in the total population may thus be estimated to be somewhere around 5 to 8 individuals. These calculations are, of course, only approximate, but the results correspond reasonably well with previous estimates (Elgmork 1954, 1966b) and the results of other censuses (Elgmork in press, IBP-CT in prep.).

BEAR-MAN RELATIONS

The usual way of explaining relatively rapid decreases in populations of the large carnivores is excessive hunting. The bare figures for bears shot in the area and adjacent districts in the last 50 years are about 14 in the period 1923-35, about 7 in the period 1936-48, and only two in the last 25 years (Myrberget 1969, Central Bureau of Statistics, newspaper clippings, and pers. comm.). This hunting sequence may cursorily be interpreted as a reduction of a population to a critical level.

A possible reduced reproductive potential caused by too low numbers, a skewed sex distribution etc., is not, however, supported by the relatively large number of reports of young with their systematic trends. Studies of the Alp population also show that small brown bear populations with numbers down to 8-10 individuals are capable of reproducing (Roth 1970, 1973, Daldoss 1973).

The most reasonable explanation for the relatively rapid decline starting in the second half of the 1950s is therefore not hunting and insufficient reproduction, but the deterioration of the habitat caused by increasing human activity.

This explanation is favoured by the changes in distribution mentioned above, showing that areas most severely influenced by man were abandoned by the bears. Also population fluctuations further back in time support this theory (Elgmork in prep.). About 1930 the bear population in this area was isolated and very small. After a private ban on hunting, mainly in the eastern areas, the population regained its number very quickly, however, and even after the shooting of about 7 bears the population at the beginning of the study period was considerably larger than in the 1930s. But after about 10 years it started to decrease, despite a lower hunting pressure than in the 1930s. The difference in population dynamics about 25 years apart is explained by the alterations which had taken place in the meantime in the habitat.

The first human factor which severely influenced the habitat in the study period was mechanized forestry. Throughout the period there is a clear negative correlation between length of forestry roads and number of bear reports in the different zones of the study area, with a correlation coefficient of about -0.8 (Elgmork in press). This close relation indicates a negative influence from activities connected with forestry roads, which are taken as an index of human disturbance and influence on the habitat. It is interesting to note that the decrease in bear reports had already started when the impact of all the private cabins set in.

A similar influence on a bear population caused by extensive forestry is indicated from Swedish forests (Burmam 1974). Pulliainen (1972) also regards roads and forestry activities as negative factors for the bear in Finland. In the Abruzzo population in Italy, Zunino & Herrero (1972) indicate that logged areas may be abandoned as denning areas for many years.

The small remnant brown bear population in the Italian Alps of about 8-10 individuals, and with comparable areas, seems to be stabilized and is reproducing (Roth 1970, 1973, 1974, Daldoss 1973). As far as could be ascertained during a visit to Trentino in the summer 1974, the bear habitat in the Alps is considerably less influenced by human activities than its Norwegian counterpart. The lumbering practice is nearly exclusively a lenient selective cutting. In spite of a considerable assumed hunting pressure, the Alp bear habitat thus seems capable of sustaining a very small reproductive population.

The influence of forestry is complex, representing both an immediate direct disturbance and short and long term alterations of the habitat caused by the

large clear-cuttings. In the early phases these lead to a reduction of the forested area and of shelter possibilities. Of importance may be the reduction of old spruce stands, which are shown to be preferred habitats in the Leningrad area by Novikov *et al.* (1969). A serious effect of the forestry roads is the subsequent use of the habitat for other activities.

The hiking tourists may roam over most of the area, but the great majority are presumed to follow trails. The most serious aspect of tourism in the bear area is the presence of all the private cabins. The traffic from these must represent a significant disturbance for the bears during certain times of the year.

The direct reaction of the bears to the various types of disturbance and environmental change is difficult to evaluate in detail. The bear is capable of adjusting to a certain degree of disturbance in its area, and may also occasionally accept the presence of people in the neighbourhood. Bears have e.g. been reported several times from forestry roads and clear-cut areas. On the other hand, there are reports of bears chased out by the starting of motor saws, being scared by motor vehicles, and startled by cabin owners close to the cabins. Excrement trails are occasionally reported from such incidents, indicating nervous excitement.

One aspect of such disturbances is that the animals always have to be on the alert. Radio tracking in the USA has shown that the brown bear follows the movements of the human intruder (Craighead & Craighead 1965). However, if the human traffic becomes too complicated to follow, the bear may abandon the area. The gradual reduction in the eastern and southern parts of the Main Area, as well as the increase in the Surrounding Area in the middle of the 1960s may be interpreted along these lines.

All the new roads, clear-cuttings and cabin concentrations may also cut off traditional migration routes and break up traditional behaviour patterns. The disturbance may also interfere negatively with food uptake and reproduction.

The shyness and the reactions to human disturbance probably change in the course of the year. The most critical period is late autumn when the bear prepares for denning. At this time, the bear is extremely shy and tries to withdraw to undisturbed areas. This may be regarded as an adaptation to a long period of co-existence with *Homo sapiens* L. (Craighead & Craighead 1972). The increasing infiltration by humans and alteration of the habitat also in the denning areas is one of the most serious aspects of the impact of man in the study area.

CONSERVATION MEASURES

The first attempt to conserve the bears in this area was apparently the private initiative to reduce hunting in 1933. Of importance has been the fact that the landowners have been very restrictive in selling and leasing sites for cabins in the Vassfaret Valley. In 1973, the Vassfaret Valley and surroundings were protected against impoundment of the lakes for hydro-electrical power. In 1971, a general ban on bear hunting was introduced; and in May 1974, the building of private cabins was generally prohibited in an area of about 300 km² in Zone A. These are, so far, the more important steps taken to preserve the bear population and its habitat.

However, much work and energy has been put into planning and discussions.

Zoologists at the University of Oslo have been engaged in this effort by working out a conservation plan based on the present study (Elgmork 1966a & b).

The greatest concern at present is the extension of the net of forestry roads leading to lumbering and clear-cutting in the highly elevated forests close to the known denning areas, and to an increased secondary traffic generally in the few remaining relatively undisturbed areas.

The overall problem is whether the manipulation of the ecosystem has led to such radical changes in the bear habitat that the bears are no longer capable of surviving. The limit may or may not have been reached. Very little is known of the viability of such small populations, and only further studies may give the answer.

SUMMARY

Except for one small isolated population the brown bears in Norway, *Ursus arctos arctos* L., consisting of probably less than 25-50 individuals, are connected with populations in neighbouring countries. The isolated population is situated in a restricted area less than 100 km to the north-west of Oslo in a rugged forest-alpine area which has been under increasing pressure from human activities, mainly forestry and tourism.

The population and its habitat have been under observation since 1949. There is a clear tendency towards a gradual decrease in numbers and a shift in distribution. Reproduction has taken place, but was evidently reduced to a very low frequency, if any, in the 1970s.

Direct depletion by hunting has been insignificant. The deterioration of the habitat caused by human activities is most likely the main reason for the reduction.

A plan for the conservation of this bear population was proposed in 1966, but so far few steps have been taken to preserve the bear and its habitat.

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Distribution and Quantity of Brown Bears in Kazakhstan

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The brown bear (*Ursus arctos*) is found throughout the territory of Kazakhstan to the Tien Shan border along the ridges of the Ugam, Pskem, Kirgiz, Talaz Alatau, Zailiy Alatau, Kungey Alatau, Ter Alatau, Ketmen, Dzhungar Alatau, Saure, Tarbagataye and Southern Latay regions. At the end of the 19th century and the beginning of the 20th, the bear was established in pine forests of the Kazakh foothills and piney ravines of Northern Kazakhstan where they are now absent (Sludskiy *et al.* 1953)

The basic habitat of the brown bear in the Altay is in mixed fir-cedar-deciduous forest; in the Saure, purely deciduous stands; Tarbagatay, nominal aspen-birch timber; in the Dzhungar Alatau and Northern Tien Shan, spruce; Western Tien Shan, juniper, apple, apricot and walnut forest. In the underbrush everywhere is encountered a multitude of berry bushes—dogrose, honeysuckle, raspberry, current, barberry and others. However, the animals do not always keep to the forest and, depending on the availability of food (basically juicy greens and berries), engage in significant altitudinal migration. In spring, immediately after leaving the den, they often spread out along the mountain ridges and migrate to the bordering lower forests to mid-slope where they soon approach where the snow slides have exposed the slopes; here they quickly uncover green shoots which they eat. In summer, depending on the type and timing of emerging herbaceous plants, the bears migrate up to the edge of the forest and then into the Subalpine and alpine zones. At the end of the summer and in autumn, when the berries, apples and other fruits ripen, they concentrate in the region of ripe fruit distribution on the lower slopes. In autumn, after the snow falls, the majority of bears again migrate upward to their den sites. Thus, the vertical distribution of bears is from 700 - 800 to 3500 - 4000 m or to the snowline.

We counted the bears from 1971 - 1973. The counting method was based on visual observations (binoculars) in the early morning and in the hours just before sunset—the times at which they are most active during the daylight hours. The forest mass in the mountains is rarely uniform; it exists as islands, bands, or very much more thinly on the slopes of ravines which can be sufficiently well observed from an opposite side. In thick areas, where observation is difficult, we recorded signs of bear activity—remains of meals, excrement, etc. The bears were counted in well-defined territories during the course of several days. Data on their population density was extrapolated afterwards for mixed forest and mountain territories.

According to data for the southern Altay, in a forest area of 1,780,000 ha we counted about 440 bears (an average of 0.25/1000 ha); in the Western Tarbagatay (480,000 ha)—105 bears (0.22/1000 ha); in the Dzhungar Alatau (833,600 ha)—314 bears (0.37/1000 ha); and in the Kungey Alatau (100,800 ha)—5 bears (0.04/1000 ha). In the Zailiysk Alatau territory bears were rarities—largely confined to Alma-Ata forest reserve (valleys of the rivers Talgar and Issyk). In the western part of this range and the Kirgiz Alatau bears were also few in number. Bears are common in the territory of the Aksu-Dzhubaglin forest

reserve and also along the Ugama, Pskem and Chatkal'sk ridges. In all, the mountains of Kazakhstan contain about 900 -1000 bears. In general, numbers are highest in regions remote from human settlement. In comparison with mixed regions, the number of bears is markedly higher in the Southern Altay and Dzhungar Alatau. In the Southern Altay this bear is plentiful in regions lying east of Lake Markakol', the valleys of the rivers Chernaya and Belaya Bepel', Yzaovaya, Kurtynskaya, and in the Dzhungara Alatau—on the northern forested slopes of the ridges and basins of the rivers Tentek, Baskanov and Aganakta. Here we often observed 4 - 6 bears per day, and on some days up to 10 solitary bears and females with cubs.

According to data from the literature, at the end of the 19th century and the beginning of the 20th, there were markedly greater numbers of bears in the mountains of Kazakhstan. In the Semirechenskaya territory alone (i.e. the Dzhungar Alatau and Tien Shan) 100 - 200 per day could be counted, and in some years, up to 300 or more (Smirnov 1965).

At present, bears are encountered rarely in the Ketmen, Kungey Alatau, or Terskaya Alatau, the fields of which have been used intensively to graze cattle for the last 20 years. Lumbering and construction activity has also driven the bears away. The land area is controlled and poaching is common.

Currently hunting licences for bears can be obtained in some regions of the Altay and Dzhungar Alatau; in the rest of the territory of Kazakhstan bears are still protected.

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The Popular Bears of Cape Churchill

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ABSTRACT ONLY

Polar bears (*Ursus maritimus*) have been abundant along the Manitoba coast of Hudson Bay throughout historic times, and apparently this species contributed considerably to the economy of coastal native peoples within and north of the treeline. The closure of the York Factory settlement at the mouth of the Nelson River in 1957, the organization of Registered Traplines in Manitoba during the early 1950s, and the concurrent cessation of military manoeuvres at Ft. Churchill, all provided increased protection and decreased killing of the bears.

Apparently in response to this, as well as to a decrease in the hunting of ringed seals (*Phoca hispida*)—the main food of polar bears—, the number of bears on Cape Churchill rose rapidly during the 1960s. Little was known of their biology and abundance when each autumn they began to appear in large numbers within the four settlements near the mouth of the Churchill River. A situation rapidly developed wherein law enforcement officers and residents were required to kill 10 to 15 bears annually to protect themselves.

During 1966 to 1968 one or two persons were attacked or killed each year, workers required guards and transportation from door to door when ending night shifts during October to December, and a strong dislike for the bears precipitated the tormenting or shooting of bears with small calibre rifles. R. C. M. Police officers were frequently replaced on the force, and therefore had little experience in controlling the bears.

In 1966, a study of the problem and of the Cape Churchill bears was begun by the Canadian Wildlife Service. In 1966 and in 1969, two of the garbage dumps where the bears concentrated were closed down on the basis of this research and on experience with other species of bears elsewhere. A public education project was begun to inform people about ways to avoid conflict with the bears, and various attempts at fencing, burning of garbage and improving the garbage pickups were made.

In 1969, the provincial government assigned Game Management Officers to the area to provide a 24 hour patrol, culvert traps were sent to Churchill for catching and shipping problem bears, and the Federal Department of Public Works began burying the garbage with sand. Funds were allocated for the construction of an incinerator, but work on it did not begin.

During 1970 through 1973, the patrols by game officers kept an uneasy control over the bears, and research confirmed emphatically that the existence of the garbage dumps contributed substantially to the problem of the polar bears

staying in or near the settlements. The Game Officers determined in 1971 that they had little recourse but to kill a large number of problem bears addicted from year to year to the garbage dumps. However, a temporarily arranged air lift of 24 problem bears to 250 km southeast of Churchill in that year by a private organization, and an early freeze up of Hudson Bay in 1972 and 1973, helped the officers to control the bears.

Completion of an incinerator late in 1973, promised to control the problem in the future, but adjustment problems, associated with bears accustomed to returning to Churchill each autumn, the storage of bait by resident trappers, and garbage pickups, are expected. A complete biological report on the Cape Churchill bears is now in preparation, and this history of the bears and the bear problems will form the introduction to it.

Ecology, Protection and Prospect of Utilization of the Brown Bear in the Estonian S.S.R.

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The brown bear (*Ursus arctos*) is indigenous to Estonian forests. According to the paleo-zoological studies of K. Paaver (1965), this animal inhabited the present area of the Estonian Soviet Republic as far back as the beginning of the Holocene Epoch. Until the end of the 18th century bears could be found in large numbers over much of the natural landscape (Fig. 1) even reaching the West Estonian islands. Since that period, the number and range of bears has dwindled due to the intensification of hunting (Fig. 2).

On the eve of the First World War approximately ten bears were known to exist in Estonia, living in the forests and swamps of Alutaguse in the north-eastern part of the country. As there was very little interference from people (also thanks to migration from the east), the number of bears doubled by the end of the war, remaining at approximately the same level up to 1934; at this time new hunting regulations were established in Estonia. The new law gave more-or-less full protection to the bears and they spread rapidly and increased in numbers immediately. After the reestablishment of Soviet power in 1940, the hunting law remained in force. The bears continued to increase and reached their peak in the mid 1960s when a decline was noted; however, in the 1970s their numbers have again increased.

Approximately 150 bears now exist in Estonia and make up two separate populations, essentially the north-eastern and south-western populations. Apart from these there are a few scattered individuals (Fig. 3).

The north-eastern population constitutes about 90 percent of the total number of bears. They are in contact with the bear population of the Leningrad region, where, according to Novikov *et al.* (1970), there are about 500 to 600 bears.

The center of the brown bears' habitat is steadily moving westward and south-westward because of extensive industrial development in the northeast of the republic. The further growth of the oil-shale industry may eventually separate the Estonian population from the bear population of the Leningrad region, a result of which may be the danger of inbreeding.

The south-western population lives in the southern part of the midland strip of forests and swamps and is considerably more unstable. The bears of this region are unusually prone to vagrancy, with a low rate of reproduction. It seems clear that this population is doomed to extinction since the whole district is already too densely settled to afford the bears a natural habitat.

The brown bear in Estonia feeds mainly on plants, which vary according to the season. Accordingly, bears can be found in different types of forest at different times of the year. In autumn and early spring the carcasses of dead animals form a substantial part of the bears' diet; at this time the killing of large ungulates occurs, but the damage to the game economy is negligible. The supply of plant food when compared with the number of bears living in the forest areas and the settlements in the vicinity could support a much larger number of



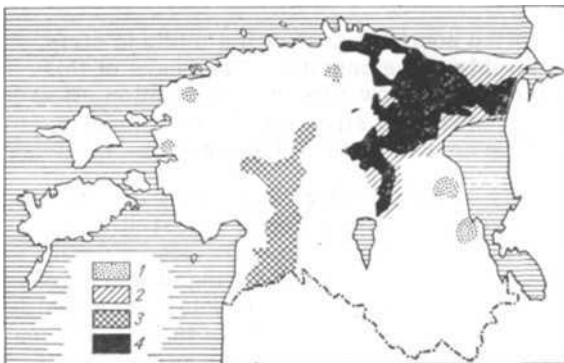
Fig. 1. Natural Landscape of Estonia, S.S.R.

- I - The midland belt of forests and swamps
- II - Jõetaguse forest and swamp area
- III - Alutaguse forest and swamp area
- 1-8- Other forest areas



Fig. 2. Changes in distribution of bears in Estonia, 1860-1900

- Fig. 3. (1) Areas inhabited by single bears
 (2) Areas where bears have only been sighted in spring.
 (3) Habitat of the south-western population
 (4) Habitat of the north-eastern population



bears. It is evident that the spread and reproduction of bears are restricted by such negative environmental factors as the increasing activities of people in the forests.

During the past few years there has been a marked increase in the number of ungulates in Estonia. In our small republic we have at present about 12, 000 elk, of which the annual harvest quota is 5, 000. With this comparatively large quota and under the existing conditions of game management, it is inevitable that a number of wounded animals are not retrieved. This explains the above-mentioned rise in the bear population at the present time, for the bears can feed unmolested. On the whole, the hunting season coincides with the time when people from towns and villages go *en masse* to pick berries and gather mushrooms in the forests and swamps. Consequently, bears have been sighted in places which they formerly never inhabited. For example, a relatively stable, small population of bears has now become established in the forests on the western shores of Lake Peipsi; in former times only a few migrant bears ever roamed in this area.

The large number of ungulates exceeds the carrying capacity of this area of our republic and the welfare of our forests suffers. The permissible number of elk should be limited to 6, 000 to 6, 600 individuals. Eventually this lower level will be reached, which means that the present food supply for the bear population is only temporary. Thus it is time to consider seriously, the welfare of the bears. At the present time bears enjoy full protection by the law and poachers are fined 1,000 roubles per head.

The Tudu State Hunting Base harboring approximately 30 bears is situated in the center of the area inhabited by the main bear population of the Estonian S.S.R. This Base was made into a sanctuary for the brown bear in 1973. The



Fig. 4. Den Site of a European Brown Bear in Estonian S.S.R.

felling of timber and the presence of people in this area is strictly controlled; this appears to be especially important during the period of hibernation.

The bears of Estonia hibernate from November till March or April; however, this may vary from year to year according to meteorological conditions. The structure of a bear's winter den is extremely variable; these may vary from a simple bed in the open to a carefully prepared cave which sometimes contains two beds (Fig. 4). In most cases the bears hibernate in a clump of young fir trees, in the debris of wind-thrown trees, or under stumps in water-logged districts.

At the Tudu Hunting Base certain management practices are being undertaken; for example, carcasses of animals are left in the forest, oats are sown especially for the bears, etc. In the future if our bears should be cut off from the bear population of the Leningrad region, bears from there can be brought to the Reservation.

The management program on the Reservation is not yet complete and will most likely change considerably as time goes on. With the help of all these measures it is hoped that we shall be able to preserve the bear as a worthy representative of our ancient native fauna; at the same time the bear may in the future also become a game animal. The present rate of reproduction prohibits this, but by employing various management practices, we hope to raise the number of our bear population to the level that has been achieved in Czechoslovakia, where it is reported (Randik 1971) that 5 percent of their bear population is made legitimate quarry for hunters, the more aggressive animals being chosen for this purpose. The fees for hunting licences would be used as funds for projects to help conserve the bears.

The habitat of the Estonian brown bear lies on the western border of the basic area inhabited by the brown bear. Therefore, the preservation of our small population is not only important for the republic alone but is all-important for the preservation of this diminishing species over the rest of the world.

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Status of the Last Brown Bears of the Alps in the Trentino, Italy

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ABSTRACT ONLY

Less than 1,000 years ago, brown bears, *Ursus arctos* L., were found throughout most of continental Europe, but today only remnant populations occur in small and isolated areas. Although mountainous regions typically form a last stronghold for the bears, they were exterminated from the greater part of the Alps during the 1800s. Only two small populations survived by 1900, one in the French Alps and one in the Italian Alps. Those of the French Alps disappeared before World War II, whereas, in Italy, one small group still remains in the Alpine province of Trentino. These bears are extremely shy and nocturnal, so to obtain information on their status and biology we used indirect methods such as measuring tracks, counting scats and interviewing local people.

In order to obtain an adequate coverage of the 1640 km² study area which includes the entire bear range, interviews for mapping purposes were based on a stratified sampling plan using the Communities—which also conform to hunting management units in the Trentino—as spatial strata. A frequency was used of one interview per 10 km² community area.

All personal observations of bears or their signs (tracks, scats) were located on a map by persons interviewed, mostly hunters. We tried to use objective mathematical-geometrical procedures to convert the resulting 'point-maps' into 'area-maps' showing areas of different bear-use intensities. Two maps for the periods of 1913-1966 and 1967-1970 were prepared on the basis of 654 observations.

These maps suggest total bear range (outermost observations connected) had decreased a relatively unimportant 20 percent, but that heavily used bear-range had decreased a substantial 75 to 90 percent. These maps and other data (calculated population indices based on sighting frequencies for sub-areas) suggest that bears actively concentrated in the northeastern corner of the Trentino bear area (Val di Non) during the 1960s.

Tracks and direct observations provided a minimum population estimate of eight bears for 1969, including a female with two yearlings (or two-year-olds), a female with a single yearling, a female with at least one cub, and a minimum of one single bear. A figure of about two additional single bears, which makes a total of ten animals, is probably a more realistic estimate. Additional data from Daldoss (1973 and pers. comm., Sept. 1974) suggest a stable population since 1969.

These bears have adapted remarkably well to this densely populated region. They make extensive use of the partly abandoned orchards along the lower edge of the mountain forests during fall. I have found tracks and scats as close as 50 m to an occupied farmhouse, but only very rarely are they discovered further than 25 m from the forest edge. The local people are often unaware of these night visitors.

Our information indicates that poaching is the primary factor causing a decline in the bear population of the Trentino. Using the Petersen-Lincoln index as a procedure, and a list of illegal bear killings compiled independently by Marti (1969), we estimated an average of 2.2 bears killed annually from 1939, when the species was fully protected, to 1970.

In the Cantabrian Mountains of Spain a similar situation prevailed after World War II. Poaching was slowly exterminating a small brown bear population. After the establishment of a special bear reservation of 879 km² and extensive patrols by 12 game wardens, the bears increased to about 70 (Notario 1964). It seems that similar action is necessary to save the bears of the Italian Alps.

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On the Ecology of the Brown Bear in the Southern Urals

by I. YU. SHARAFUTDINOV and A. M. KOROTKOV

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This paper relates the investigational data of more than three years of observations on the ecology of the brown bear (*Ursus arctos*) in the region of the Bashkir State Forest Preserve, U.S.S.R. The Preserve is situated in the southern spur of the Ural-tau and Southern Krak ridges.

The sharply delineated relief, distance from the sea, and the high elevation above sea level have a dramatic effect on the local climate. The area has the rather harsh winters (temperatures down to -50°C) and hot summers (maximum $+40^{\circ}\text{C}$) characteristic of a continental climate. Aerial convection currents and significant heating of the southern unforested parts of the mountains cause an irrotational mosaic microclimate. The forests of the Preserve are not confined to these particular climatic zones. The mountain ridges stretching far to the south preserve forest lands in a steppe zone.

The trees in this Preserve are principally conifers. On the southern and south-eastern slopes are mixed steppe pines and unforested areas. In the north and north-west the cover is pine forest and scrub with bilberry predominating. In the ravines pines grow mixed with a great number of larger herbs and grasses. Bird cherry, raspberry and currant are located along the rivers.

The distance of the Preserve from populated centers (hamlets, villages, towns), the presence of a rich assortment of plant cover and high relief, the general inaccessibility combined with abundant rivers and streams constitute excellent conditions for animal habitats in general and for bears in particular.

We found the most practical censusing method under the conditions of the Bashkir Forest Preserve to be simultaneous tracking and recording of bears according to age, usual territory and body size (e.g. fatness).

The determination of the habitat of the brown bear and the determination of their distribution on the area are favored by methods of calculation during the morning hours when the dew is on the plants. Counts were undertaken simultaneously throughout the Preserve wherever feeding locations of the bears had been determined; that is, a 'dew count' was undertaken. It has been established that in the summer the bears gather near the rivers and streams in places with copious green cover consisting of angelica, cow parsnip, etc. The daily lair of the bears, as a rule, is located in these places. The trail through their usual range is 12 to 16 km long, is traversed from day to day, and is particularly defined in the morning hours. Therefore, in consequence of the above, a method of making morning bear counts was established.

Additional signs included logs which had been turned over and trees which have been used for scratching, which also often involves bark stripping.

As a result of extensive mapping and analysis of data on the distribution of individuals, it was established that there is similarity in the composition of diets of individuals.

Under the mountainous conditions of the Ural-tau and the Southern Krak, the

bears live in the vicinity of each other, in small groups, forming a defined location in which they spread over an area about 5 to 7 km from each other. The few really solitary bears encountered consisted of young animals.

As a result of many years of study, it was noted that the number of bears in the Preserve is increasing. The average dimension of the feeding area in 1971 was about 2000 ha. In that period, approximately 35 bears lived on the Preserve.

Favorable living conditions and the presence of a rich food base resulted in a decrease in the home range to approximately 1700 ha, thus an increase in the population density of bears. In 1972, 38 animals were recorded. In 1973, 45 bears lived in the Uzyansk part of the Preserve; the average home range decreased to 1500 ha. In 1974, no significant increase in the population was noted; only one additional animal was added.

Recently there has been a decrease in the number of bears at the periphery of their range. In our view, a deciding factor is one of safety. The territory of the Southern Urals is subject to intensive agricultural activities, lumber operations and land clearing near the forests; this causes bears to move to more secluded places. Presently the territory of the Preserve has a bear population consisting of a majority of females with cubs.

The division of the total feeding grounds among the bears is also of practical and theoretical interest. As a rule, females with cubs choose the part with the richest food supply. The dimensions of each female's feeding area are not great and do not exceed 500 to 1000 ha. In comparison with the range of solitary bears, that of females and their cubs is 2 to 2.3 times smaller. In the above connection one can guess that this is the area of the Preserve quietest and least disturbed by man; it contains the richest food supply and becomes, by its nature, a natural 'nursery' for bears. In the above situation, the bears change their form of behavior with respect to humans. Therefore one can see that the natural ecology is transformed into an anthropogenic ecology.

An important aspect of the life of the bear on the area is hibernation. The most important determinant of den location is its angle of southern exposure. The den is constructed, as a rule, close to a ridge crest. In autumn when settling in for their winter sleep, bears break off branches and boughs to line their dens. In spring the process of breaking off and stripping branches is repeated. The nature of the spring 'stripping' is unclear. Perhaps it is a form of muscle conditioning.

Under the conditions of the Southern Urals in autumn, the bears concentrate in their preferred denning places. In these places there may be ten dens in 1 to 2 km.

There are differences in the construction of the dens. It is notable that 'earthen' dens are built in dry years when the soil under the surface is well dried. In wet years the bears build dens in rock crevices or in small rocky grottoes and caves where the soil stays relatively dry. Such dens, as a rule, are hard for humans to find. The bears spend an average of 5 to 6 months in their dens. The length of the denning period depends on the food supply. In mountain pine stands, hibernation begins with the first snowfall, in oak-linden stands after snowfall. In oak forests when there is a rich harvest of acorns, bears do not spend long periods in their dens. Bears leave their dens simultaneously in all types of forests in April.

In the initial period after leaving the den, bears remain on small, thawed patches on the well-heated sunny slopes. At this time we can count the bears on the ridges and crests.

Stopping on a thawed patch in the spring period, the bears seek out their usual food. An analysis of bear droppings (228 samples) collected in the Preserve in 1973, showed that in the spring plant matter is the primary constituent of the bears' diet (46.5%); of this, leaves and stems made up 11.6%, fruit and berries—18.6%, young leaves of birch and aspen—2.4%, roots—4.6%, and other plant residues—9.3%. The insect component at this period was 37.2%; flies—32.6% and beetles—4.6%. Mammals made up 16.3% of the diet, and of this carrion accounted for 13.9% and rodents for 2.4%. As shown in our study, in the spring period bears feed primarily on plants and ants. The amount of animal food, including carrion, is negligible.

In summer, the bears' diet is more varied. However, plants are still the most prevalent type of food, making up 73.2% of the total; fruits and berries—17.3%, leaves and stems of high-growing cover vegetation—29.9%, birch and aspen leaves—4.7%, roots—0.8%, and other plant residues—20.5%. Insects, especially ants and larvae, made up 22.9% of the diet and mammals—3.9%.

In autumn, the fattening bears consume 74.1% vegetable matter, primarily fruit and berries (48.3%). Stems and leaves of herbaceous plants—6.9%, birch and aspen leaves—3.4%, other plant residues—12.1% make up the other vegetable components. The insect component decreases to 10.9%. The use of mammals as food in autumn increases to 15.5%.

In the annual diet of bears, plants predominate (68.3%), with berries making up 25.4%. Insects account for 22.4% and mammals, including carrion, make up 9.3%.

Climate exerts a great influence on the bears' feeding habits. In the very dry, hot summer of 1972 there occurred in the Preserve a massive proliferation of ground wasps which became a basic article of food in the bears' diet. In 1973, conditions favored growth of rich herbage; in this year the bears were basically 'vegetarians'.

Because of the above results, one can conclude that feeding on the natural food of the biocenosis, especially berries, insects and a variety of plant food, accomplishes the deposition of fat reserves necessary for winter.

The role of the bear as a predator in the Preserve is insignificant. Despite the prevalence of bears, incidents of their attacks on foxes, Siberian stags and domestic cattle are unusual. More significant is the sanitary role bears play in the removal of carcasses of animals killed for various reasons.

It is notable that in the regions surrounding the Preserve, intensive predation of bears on stragglers from animal herds has been noticed. According to our data in 1972, 159 head of cattle, 58 head of other livestock and 13 horses were so attacked. In 1973, the figures were 234, 44 and 13 respectively. Both males and females with cubs were involved in the attacks.

Predation by bears inside and outside the Preserve lands increases in years of unfavorable conditions for the food base. Thus, higher exposition gives a basis for consideration that, in good agricultural management, predation by bears can be kept at a minimum and thus protect this superb animal in our forests for future generations.

The European Brown Bear in the Carpathians

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Data on the ecology of the European brown bear (*Ursus arctos*) were collected on the territory of the state hunting preserve 'Osmoloda', in the central part of the Eastern Carpathians. At the present time, there are an estimated 64 bears occupying this area of 84,000 ha. Seventy percent of the population consists of young animals and the total number is increasing.

The density of European brown bears on the area in the last century was high. As a result of intensive lumbering operations their numbers decreased; in the first third of the twentieth century they were placed under protection. From that time, exclusive of the war years, the number of bears in the Carpathians has increased markedly. If Nezavitovskiy (1933) assumed that 100 individuals had been counted, then in the middle of the twentieth century, according to Tatarinov (1956) there were almost 200 bears in the Transcarpathian, L'vov and Ivano-Frankov oblasts alone. In 1970, there were 1300 in the Ukrainian Carpathians or 0.5 to 0.6 specimens/1000 ha of mountain forests.

To determine the diet of the European brown bear, we analyzed 85 droppings, studied 62 meals at their place of consumption and the contents of two stomachs. The results of the food habits study are presented in Table 1 and characterize the composition of diet of the bears, namely incidence of occurrence and the relative percent composition of various types of food according to the season of the year. The diet of brown bears consists primarily of plant material (61.8%); this is historically supported by the fact that the dentition is more adapted to a plant and not an animal diet (Ognev 1931). Plant and animal food used by bears is extremely varied and depends on the availability of the food and the season of the year. The bears apparently fast in early spring when they leave their dens and do not find sufficient foods available; they frequently prey on wild animals, particularly ungulates, preferring the hind extremities for their spring meals. On 13 March 1972, we found remains of wild pigs (*Sus scrofa*) weighing from 130 to 150 kg. Sixty-five meters from these carcasses we found traces of a fight between a bear and a wild pig. Judging by the signs the bear weighed about 200 kg. In that same month we recorded an attack by bears on two swine weighing 60 to 70 kg, two year-old sheep and one roe deer. There have been cases of livestock attacked by bears, but very rarely.

We found that the diet of brown bears was varied but that they apparently adhered to their individual preferences. They occasionally eat carrion, often in an advanced state of decomposition. In April bears in high mountain territory eat red bilberries. The hypothesis of Bromlei (1965) on the laxative action of bilberries in the digestive process was confirmed by our observations; the contents of the bilberries are of a liquid consistency. When there is insufficient food from the previous year's crop, the bears must subsist on green aspen shoots, willow, and the prior year's twigs. By the second half of April the bears' diet is enhanced by young, green aspen leaves and also those of birch, willow, various herbs (especially the Carpathian dock), forest fungi and other

TABLE 1. NUMBERS OF OCCURRENCES AND RELATIVE PERCENTAGES OF VARIOUS TYPES OF FOODS IN THE NUTRITION OF BEARS.

Type of Food	Spring		Summer		Autumn		Winter		Total	
	No.	%	No.	%	No.	%	No.	%	No.	%
PLANT FOOD	36	15.5	49	22.0	32	14.6	21	9.7	138	61.8
Shrubs and herb-like plants	9	4.0	17	7.6	4	1.8	2	0.9	32	14.3
Nuts, berries, and other fruit	16	6.6	30	13.4	26	11.9	15	7.0	87	38.9
Leaves	6	2.7	1	0.5					7	3.2
Buds	2	0.9					3	1.3	5	2.2
Mosses, lichens, pine cones	3	1.3	1	0.5	2	0.9	1	0.5	7	3.2
ANIMAL FOOD	26	11.4	20	9.2	19	8.6	20	9.0	85	38.2
Mammals	16	7.1	1	0.5	14	6.3	16	7.2	47	21.1
Insects	8	3.4	14	6.5	1	0.5			23	10.4
Birds	1	0.5	5	2.2					6	2.7
Domestic Animals	1	0.4			4	1.8	4	1.8	9	4.0

green vegetation. Along with these foods, our investigations disclosed the remains of various birds of which we identified feathers of *Tetrao* sp.

The diet of bears in the first part of the summer consists primarily of herbaceous plants. Among these one can observe stems and leaves of forest herbs, corymbose plants such as thistles, French willow, Carpathian sorrel and others.

At this time they apparently prefer to scratch the trunks of spruce and firs. In June, 1972, we observed bears strip off sequential pieces of bark, lick the sap and gnaw the exposed bast fiber with their teeth. Based on evidence of excavated ant hills and traces of wasps, it is concluded that in June bears are active in more open spaces where they also find and eat rich greens.

In the second half of the summer the diet of the bears still contains herbaceous matter as well as whortleberries, strawberries, and later bilberries and raspberries. In the event of an insufficient berry supply, the bears will raid gardens, disperse through orchards, where for some weeks they will feed on bullace, plums, apples and pears; in doing this, they cause extensive damage to trees.

Autumn is the most important period for bears since it is at this time that they complete the buildup of their fat reserves. In September plants coarsen, become less palatable and are rarely found in the bears' diet. At this time the bears collect the remaining raspberries and whortleberries; they eat mature blackberries, mountain ash, fruits of wild apples and pears, blackthorn and dog rose. In high mountain regions they migrate to the upper zone of the coniferous forest and subsist basically on whortleberries.

Closer to winter the diet is reduced in variety and the bears consume bilberries, whortleberries, *Sorbus* spp., apples, willow, blackthorn, dog rose, etc.

Some individual animals begin to fatten on horsemeat. There are cases of feeding on wild *Asarum* (asarabacca).

On 14 November 1972, a wild pig skin was found in the stomach of a bear that had been shot. By the end of autumn cases of bears preying on domestic stock are encountered; four such cases were recorded in the last two years from hunting reserves.

In December the bears den for the winter. Occasionally in winters with little snow and a large harvest of nuts (particularly beechnuts) bears in the Carpathians do not sleep deeply in their dens but spend part of the winter period abroad. Some, especially old males, generally do not hibernate, as was observed in the winter of 1971 and 1972. If there is no harvest of nuts as was the case in the winter of 1972-73 (which was also a winter of little snow), the bears had no opportunity to build up a layer of fat and were denned early; however, a few individuals were seen moving about in the first half of the denning season.

Pregnant females always stay in the den. Observations of bears in winter in the Carpathians is generally confined to the southern slopes (Guryanin 1972; Tatinov 1973). Of all of our observations of dens 58 percent were on the southern slopes and 15 percent on the northern slopes (Table 2). Bears chose natural cover for their winter den site. Most of the dens were constructed in young spruce-beech-fir stands. The elevation of the lowest den was 580 m and the highest 830 m. The dimensions of the den depended on the size of the bear and the type of den. Bears line their dens with dry branches up to 10 cm in width overlaid with herbaceous growth, leaves, moss and fir boughs collected near their dens, generally within a radius of 10 to 15 m. The depth of the bedding is 12 to 18 cm and weight 8 to 12 kg; its composition depends primarily on the availability of natural cover and the exposure of the slope. None of the dens on the mountain slopes were faced into the prevailing winds. The females denned separately from the males.

In the Carpathians during the first part of January the blind, scantily furred cubs are born; they weigh 450 to 500 g. When they leave the den, they weigh almost two kg. The female gives birth to two cubs; one or three occurs rarely, and the birth of four cubs in the Carpathians is extremely rare. Upon encountering humans, the female deserts her den. The cubs left by their mother in heavy frost die within 15 to 20 minutes. Such a case occurred on 22 January 1971, on one hunting preserve.

Some bears in the Carpathians will winter in one den repeatedly over a period of several successive years. New openings in a majority of cases are made by young animals. Frightened out of its den in the winter, one Carpathian bear refused to go back; the next year it proceeded to winter in a different place near the limits of its usual range. The agitated animal did not return to hibernation and traveled approximately 10 km in search of food; it stopped periodically to rest on the snow, breaking off dry branches and some standing trees. If, at that time, there had been a heavy snow (60 to 80 cm) as sometimes occurs in the Carpathians near the end of winter, the bear would likely have been forced to stay in its lair maintaining itself on fat reserves. If the bear remains undisturbed, it will sleep all winter and maintain a positive daily temperature because of the layer of fat. In the Carpathians denning commonly lasts until the middle of March or the first of April; the period of emergence from the dens lasts 5 to 12 days.

It is estimated that the duration of the denning period lasts from 45 to 95 days

TABLE 2. SITE DISTRIBUTION AND DIMENSIONS OF DENS OF THE CARPATHIAN BROWN BEAR LOCATED IN THE SOLOTVIN FOREST PRESERVE OF THE IVANO-FRANKOVSK OBLAST.

No.	2	Name of forest boundary		Site distribution		Type of den	Forestration conditions	Bedding material	Location of exit	Dimensions in cm			
		3	4	5	6					7	8	9	10
<i>I. Manyvskoye Lechnichestvo</i>													
1.	Landmark 'Cave zvir'	S.E.: 17	650	height above sea level	5	hollow	spruce-beech first growth. Density 0.9	leaves, branches of beech to 10 mm in width	S.E.	95	187	16.5	42 x 150
2.	Landmark 'Mlynskaya Hill'	S.E.: 5	680		5	in pine thickets, 4.5 m high	heavy pine forest	conifer boughs, leafy plants	S.E.	118		12	
3.	Landmark 'Waterfall'	S.E.: 16	730		5	fir thickets 4 m in height	spruce-fir stands. Density 1.0	conifer boughs, moss, leafy plants	S.E.	138		13.5	
4.	Landmark 'Skit'	S.E.: 12	580		5	fir thickets 4 to 5 m in height	fir, first growth. Density 1.0	conifer, boughs, moss, leafy plants	S.	126		18	

II. *Gutyanskoye Lesnichestvo*

1. Landmark 'Rapid'	W: 18	700	in pine thickets 4-5 m high	spruce-beech-fir, first growth. Density 1.0	boughs to 10mm thick	S.	155	17
2. Landmark 'Black'	S.E.:10	720	beneath roots of over-turned trees	spruce-beech forest, third growth. Density 0.8	moss, leaves, pine boughs	S.W.	122	14

III. *Syvul'skoye Lesnichestvo*

1. Landmark 'Burdock'	N: 12	780	hollow	spruce-beech forest, third growth. Density 0.6	rotted wood, moss, leaves, twigs	W.	110	16
2. Landmark 'Kuz'minets'	S.E.: 8	790	hollow	spruce-beech stands, first growth. Density 0.9	rotted wood, leaves, twigs, branches	S.W.	105	17.5

IV. *Mezherinskoye Lesnichestvo*

1. Landmark 'Dupdyanka'	S.W.: 16	830	beneath uprooted trees	fir (untrans), first growth		S.E.	138	16
2. Landmark Unnamed	E:17	780		fir, first growth. Density 0.7		N+S	128	15.5

V. *Porogov Lesnichestvo*

1. Landmark 'Plaska'	N.E.:10	810	beneath uprooted trees	fir, first growth. Density 0.6	boughs	N.W.	126	16.5
2. Landmark 'Plaska'	S.E.: 18	760	beneath over-turned tree roots	spruce-beech-fir. Density 0.6	misc. plant material	S.W.	110	14.5

90 × 85

50 × 50

45 × 58
46 × 53

depending on the previous season's food supply, the nutrition of the bear, and the weather.

Females come into heat from the middle of May to the beginning of June. Pregnancy lasts approximately 210 days. Males reach sexual maturity after two years; females breed in their fourth year and give birth to young every other year.

One cannot consider the brown bear a harmful animal except during periods of food shortage in the spring and fall. At this time, they prey upon wild animals and domestic stock, invade cultivated agricultural areas damaging fruit trees and stripping bark from tree trunks. However, the damage to crops is insignificant; cultivated areas on the fringe of the forest near outlying human populations are the only areas affected. Generally only isolated bears prey on cattle. Noise and commotion will usually end their depredations on domestic cattle. Among wild ungulates, only the sick or the injured are the prey of the bear. In this respect bears play a positive role in the health of the wild ungulates of the Carpathians.

The brown bears of the Carpathians are seldom aggressive toward man. In rare cases they will attack a man but only when persistently tracked. In such a case a large and 'experienced' bear may become dangerous. After leaving the den, the female will aggressively protect her young. Upon perceiving danger, the female generally utters a specific noise and the cubs hide. The proximity of man to the family unit at this time can be exceedingly dangerous.

The brown bear is not only an interesting and beautiful animal but a valuable fur bearer. Trade value of the fur stands first among the wild animals hunted in the Carpathians. Its pelt provides beautiful rugs and warm winter clothing. The percent yield of fat and meat from the Carpathian bear is significantly higher than from herbivorous animals. Bear meat possesses excellent taste qualities, and the fat is used in medicinal preparations and is esteemed among the local population. As a subject for sport hunting, the Carpathian bear has no equal. Hunting this animal teaches a man endurance, hardiness, daring and rapid orientation. Under the conditions of the Carpathians the most effective means of hunting the bear is to watch for feeding animals from a tower. It is especially esteemed as a trophy animal.

A study of the growth dynamics and increase in numbers of the brown bear was conducted in Ivano-Frankovsk Oblast. We estimate that the number of bears increases by thirty each year. At present the population density of this species in the forests of Precarpathia is not yet 0.6/1000 ha. Such a density, in our estimation, assuming natural growth, could be reached by 1983-1985.

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Research on the Polar Bear in the USSR

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The polar bear, in one way or another, attracted the attention of Russian researchers even in the last century. Interesting information is contained in early geographic papers and reports on fauna. In the 1930s, a period of intensive study and the economic assimilation of the Soviet Arctic into the USSR brought about research on the taxonomy of polar bears and on the ecology of separate geographic populations. In the post-war years, interest in the polar bear in the USSR increased even more, as shown by a significant number of publications on general questions of the biology of the species and on analyses of distribution, ecology and numbers in several regions of the Soviet Arctic. As in a number of other arctic countries, in the USSR the greatest attention has been paid to the polar bear during the last 10-20 years. The immediate stimulus for research, in a practical sense linked with protection of the species, was the resolution of the Soviet Ministers of the Russian Soviet Federated Socialist Republic in 1956 for total prohibition of hunting. The Polar Bear Specialist Group of the International Union for the Conservation of Nature has also been helpful in stimulating research.

Systematic study of the polar bear in the USSR started in the middle 1950s. This included study of distribution, numbers, population dynamics and structure, ecology, morphology, phylogenesis, Parasitology, and measures for preservation. The present report provides new information.

Research on polar bear ecology is conducted by the Central Laboratory for the Preservation of Nature on Wrangel Island, an area set aside as a game reserve. Since this island is the largest known denning center for pregnant females, polar bear reproduction is studied intensively.

The general number of maternity dens on Wrangel Island was determined to be 150-200 in 1960 (questionnaire reports), 150-200 in 1970 (surface count), 180-200 in 1970 (air and surface count) and roughly 250 in 1973 (air count). Considering the relative stability of the number of dens on different parts of the island which have been observed for 7 or more years, it is possible to conclude that Wrangel Island served as a maternal home for a definite population of polar bears, the number of which in the last 10-15 years has not undergone sharp changes. It can also be concluded that pregnant sows have relatively rigid requirements for the places chosen for dens, and major factors appear to be depth and density of snow cover.

Beginning in 1969, animals have been marked annually in birth dens in one part of the island. Standard metal and plastic ear tags are used, and some adult animals have the tag number duplicated on their rump with large figures in indelible red paint. The number of animals marked thus far is 82, of which, 49 are adult sows and 33 are cubs of the year (Table 1). No bears previously marked on Wrangel Island or elsewhere in the polar basin have yet been recaptured on Wrangel Island. Although the number of marked bears is not great, this may either be interpreted as showing that females do not repeatedly den

in the same location or that tags are short-lived and the marking technique needs perfecting.

TABLE 1. NUMBERS OF POLAR BEARS MARKED ON WRANGEL ISLAND, 1969-1974.

	1969	1970	1971	1972	1973	1974
Adult females	5	6	8	6	7	17
Cubs		1	1		12	19

Experiments lasting many years were conducted on Wrangel Island, primarily in the area of greatest concentration of dens, the Drem-Khed mountains in the north-west part of the island. In this generally square area of about 20 km², 25-50 dens are counted annually. Summarizing the results of these experiments, one can observe that during years of normal arctic conditions, a basic number of sows hibernate on the island in dens during October. In case of late formation of coastal ice, the arrival of females on land and their denning is delayed until the end of November and later. Observations show that the sow generally chooses freshly fallen snow for a den, although use of snow drifts of the previous winter is not excluded. The uneven distribution of snow drifts during the fall causes dens to be unevenly distributed. In the study area, the density of dens sometimes reaches one den per 50 m² (data from 1970 and 1973). Denning females tolerate one another. In 1969, two dens 50 cm apart had a tunnel between them providing the possibility of association between occupants of the two dens.

Most dens are located close to the sea coast on sides of hills with a slope usually of 15-25 degrees. Dens are at various heights but most often on the top third of the slope. The exposure of the slopes on which most dens are constructed changes from year to year, depending on the direction of prevailing winds which in turn determines how snow accumulates.

Dens can consist of an oval chamber about 1.5 m long and wide and 1 m high with a corridor 2-3 m long and 60-80 cm in diameter. However, some dens are more complex with as many as three or four chambers. The greatest length of an observed den was 13 m.

The snow over the denning chamber changes in strength and can be several cm to 3 m and more in thickness. Optimum thickness, apparently, is 50-100 cm.

The corridor, as a rule, has an incline so that the exit is lower than the chamber. This assists in the retention of heat. Females construct and maintain ventilation holes, which apparently play a role in both the regulation of heat and gas exchange. A series of instrument observations completed in 1974 (the instruments were inserted into inhabited, still unopened dens) showed that air temperature in the den varies with external temperature and size of the ventilation opening, although it exceeds the outside temperature (especially under the roof of the chamber) by 5-8 and even 15°C.

The age of the 17 sows with newborn cubs in dens varied from 4 (perhaps even 3) to 12-15 years, with most sows 5-6 years old. Age was estimated from tooth wear. Their weight ranged from 178 to 300 kg. The relationship of the weight of females to their age was not analyzed.

The opening of the den occurs in March-April, most often in the second half of March and the beginning of April. These dates are determined not so much by

degree of maturity of the cubs as by weather conditions and especially by air temperature. As a rule, widespread opening of dens coincides with a rise in the outside temperature to -15 to -20°C and the beginning of a period of stable, windless weather.

The number of cubs coming out per den varies from 1 to 3. The mean litter size for 108 cubs was 1.72. The weight of cubs in newly-opened dens varies from 4-5 to 15-17 kg (average is 10-12 kg). Sexual weight differences at this time are not evident.

Having observed the varying sizes of cubs, we attempted to determine the dates of their birth on Wrangel Island. The period of birth of young extended from early December to late January with most young born during the last half of December and first half of January.

These facts, unavoidably fragmentary here, will cause a series of revisions in existing ideas about polar bear ecology. They can also serve as new proof of the ecological uniformity of the species in the limits of its natural habitat, beyond the dependence on a degree of isolation of separate geographical populations of animals.

The Brown Bear on Baikal: A Few Features of Vital Activity

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The brown bear, *Ursus arctos* L., occurs in all five ranges surrounding Baikal: Khamar-Daban, Ulan-Burgasi, Bargyzinski, Baikal and Primorski. Approximately 1,000-1,200 animals live in a territory of about 60,000 km². The greatest densities occur on the western slope of the Bargyzinski Range between the Malaya Cheremshava and Shirildi Rivers, on the eastern slope of the Baikal between Rita and Kotelnikovski Capes, and on the eastern slope of the Primorski between the Ulan-Khan and Zama Rivers. The Ulan-Burgasi Range has the fewest bears. All the areas have a low human population, extensive mountain taiga, an abundance of food and a prohibition on special hunting for bears.

The shores of Lake Baikal had about twice as many bears 30-40 years ago. Uncontrolled hunting and a series of poor years caused sharp declines in numbers. Hunters who killed more than 100 bears still live on the shores of Lake Baikal. However, measures for preservation of animals and their habitat have caused numbers to increase and densities in areas of concentration reach eight animals per 1000 ha.

The usual habitat of the bear in the ranges surrounding Baikal is the steep slopes of the mountains, river valleys with fallen trees, cliffs, old coniferous forests, places with numerous streams and burned over areas with many berry bushes.

In the second half of October, animals leave feeding places and move toward denning areas. In years of good food, animals enter dens in late October and early November, the time of permanent snow cover. Animals who do not have a den keep searching for a place for its construction.

A bear has rather strict demands for den location. Apparently the main requirement is dry earth. On large expanses of taiga, dens may be clustered. The author discovered three dens on 50 ha and four on 60 ha in the Bargyzinski Range. Bear dens are also known to be concentrated in the Altai.

Dens are constructed under large, flat stones and under roots of mature trees. The den entrance is usually oriented towards the south and west. Its height is 30-65 cm and width is 35-50 cm. The chamber is 110-200 cm long, 65-80 cm high, and 75-150 cm in diameter. In years of poor food, bears den in various places including hay stacks, winter quarters of hunters, fallen trees, and heaps of brush. Animals are alert in such dens and dangerous to anyone who happens to approach.

In one case the author discovered a 'camouflaged' den. Before leaving it, the bear broke six young, living Siberian spruce *Picea obovata* trees, 7 cm in diameter, into pieces 9-100 cm long and laid them together to block the entrance.

An animal uses the same den for several winters; if a den is not used by the original occupant and is in suitable condition, another bear may winter in it.

The bears know well where other dens are located, and a bear who is aroused during the winter may go to several dens trying to drive another bear out of a den so as to occupy it.

Bears leave dens in the middle of April; the peak date for a series of years for the Bargyzinski Range was 16 April. Solitary young animals and those that had poor fat reserves the preceding fall exit first. Females with young are the last to leave.

In good food years, bears acquire fat in late summer and increase body weight 30-35 percent. At the time of exit from the den they still have as much as 25 percent of their weight in fat. This is utilized until fresh grass appears.

In years of poor food supply, some bears do not hibernate and die during severe weather in mid-winter. Others may hibernate late and in poor places, and then come out of hibernation in mid-winter and perish.

A hungry animal is dangerous, both to people and fellow bears. In years of poor food, when bears appear near settlements, they attack domestic animals and people. The author has established more than 70 cases of attacks on people, mainly hunters. In 17 of these, the man died, and in five the man was almost completely eaten. Eleven attacks on humans were in the summer and more than 60 in the winter. Bears actively pursued or ambushed the man in 60 percent of the cases.

In spring or early summer, bears concentrate in forest clearings on steep mountain slopes on all five ranges in the Baikal area. Clearings range from several dozen m² to a hundred ha in size. Bears also concentrate on the shores of Lake Baikal in mid-May and sometimes cross on the ice. They are nocturnal at this time.

The main food of bears when they exit from dens is red whortleberries *Vaccinium vitis-idaea*, remaining from the preceding summer, ants *Formica lasius*, which are just starting to become active, and the nuts of *Pinus sibirica* and *Pinus pumila*, dug out of burrows of chipmunks *Tamias sibiricus*. Bears pursue moose *Alces alces* on the frozen taiga. They feed on green grass as it becomes available. In forest clearings, they feed on *Oxytropis strobilaceae*, *Phlojodicarpus baicalensis* and *Polygonum angustifolium*. On Lake Baikal, they feed on various kinds of animal life including spawning bullheads *Cottidae*. The main food in the fall is berries, cedar nuts and some small mammals.

The Brown Bear in Eurasia, Particularly the Soviet Union

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INTRODUCTION

The brown bear, *Ursus arctos* L., may be viewed in life or death as a very lucky beast in that literally hundreds of research projects and published articles have been devoted to its evolution, taxonomy, global distribution, ecology, and its economic uses. Among the most prominent is a monograph, *Brown Bear*, by Kutyure dated 1954. Another monograph concerning fossilized and living bears on the Soviet Union is presently under preparation by me, so this preliminary report by necessity will only touch upon the topical aspects of bear problems and related subjects.

POPULATION STATUS

Of a questionable nature are the current population status of the Eurasian brown bear, its response to changes in natural habitat, and protective measures required to insure its preservation. In western Europe bears find refuge in forested enclaves primarily in mountainous regions of the Pyrenees, Alps, Appenines and parts of Scandinavia. The largest numbers of brown bears in eastern Europe are generally limited to the Balkans and the Carpathians. They comprise the remnant populations that occur in parts of the Austrian Alps, Yugoslavia, Romania and Bulgaria. The total number of bears estimated by Harper (1954), Kutyure (1954), Curry-Lindahl (1972) and others for Europe, excluding the Soviet Union, during the 1960s was 5, 500-6, 000. In Asiatic Turkey (Asia Minor) there are less than 1, 000 animals while Kutyure reported that during the 1940-1950s there were 2, 500-3, 000 or a few hundred more scattered among the countries of Iran, Iraq, Afganistan and Pakistan. There is little information about the number of bears occupying the southern edge of their habitat in north Burma, Tibet, West China, Manchuria and Korea. Apparently there are but a few thousand animals.

By my inventory, the number of bears found in the Soviet Union during the 1960s was still rather high and reached 100, 000 plus or minus 10, 000 individuals. By the 1970s, the Union for the Management of Hunting and Preservation claimed that the bears were 70, 000 in number. Approximately two-thirds of the world population, or 100, 000 Eurasian brown bears, are thus believed to be in the Soviet Union. There could possibly be a few more. Such a seemingly high number causes complacency regarding their welfare at least over the next decade, but there is indeed no basis for an attitude of calm.

The distribution and density of bears during the last decade is depicted in Fig. 1. Each dot represents 20 individual bears, and the heavy lines constitute the major configuration of natural habitat as it occurred late in the middle ages as evidenced by fossilized remains obtained from the Pleistocene layer. The greatest number and density of bear populations is in a line northwest of

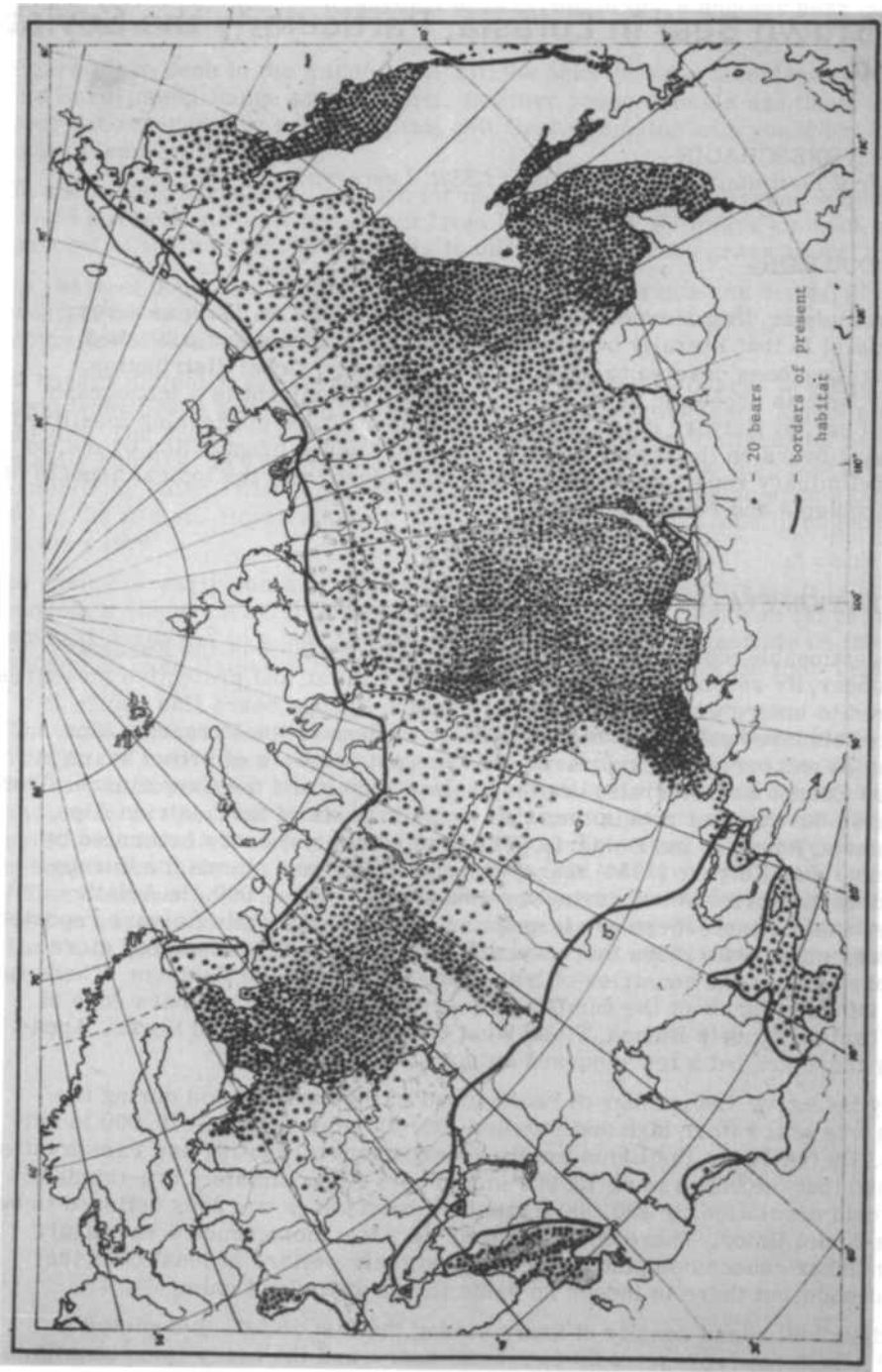


Fig. 1 Natural habitat and numbers of brown bears in the USSR.

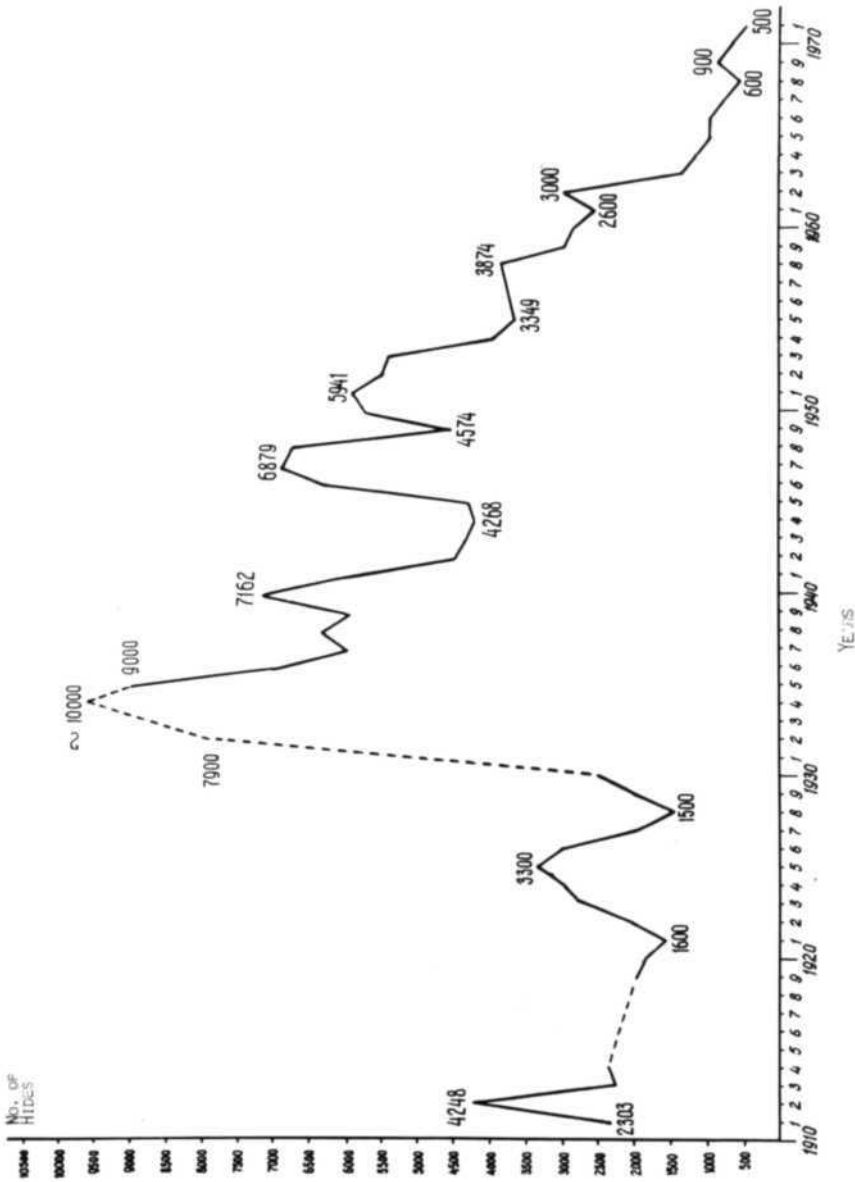


Fig. 2 Number of brown bear hides received at fur exchanges and official stations, 1910-1971.

the administered regions, south from Archangel and Vologadski regions, and the mountainous portions of the Ural, Altai, east Siberia, and especially the Far East regions. There are places in which 4 to 6 individuals occupy 100 square kilometers (10,000 hectares) and such abundance is usually proportionate to the intensity of forest cover. Those regions having the least population density include tundra and marshland habitats as well as the low food-producing lowlands of western Siberia and the central portion of the European part of the USSR.

The natural habitat once found in the European part of the USSR (deciduous forests and forest steppe of the Russian plain) proved to be the most vulnerable. Agricultural development and direct destruction of animals during the last century only has caused the northward shrinkage of their distribution by as much as 2 geographical degrees. Nevertheless, in some northwest regions and republics such as Estonia, Leningradski and Kalininski, their numbers have been maintained the last few years, and even increased in some places as a result of requiring hunting licences. By contrast, the number of bears declined rather quickly in parts of Siberia and the Far East, particularly in the Sakhaline and on Kamchatka. This condition is attributed to industrial expansion, application of military technology, and expeditions. Bears in the Baikal region, Sakhaline and Kamchatka, for example, have declined by approximately one half their former number within the past 20 years.

HARVEST

The number of bear hides recorded at fur exchanges and accumulated by the state during the Soviet period is depicted from 1910 through 1970 in Fig. 2. The

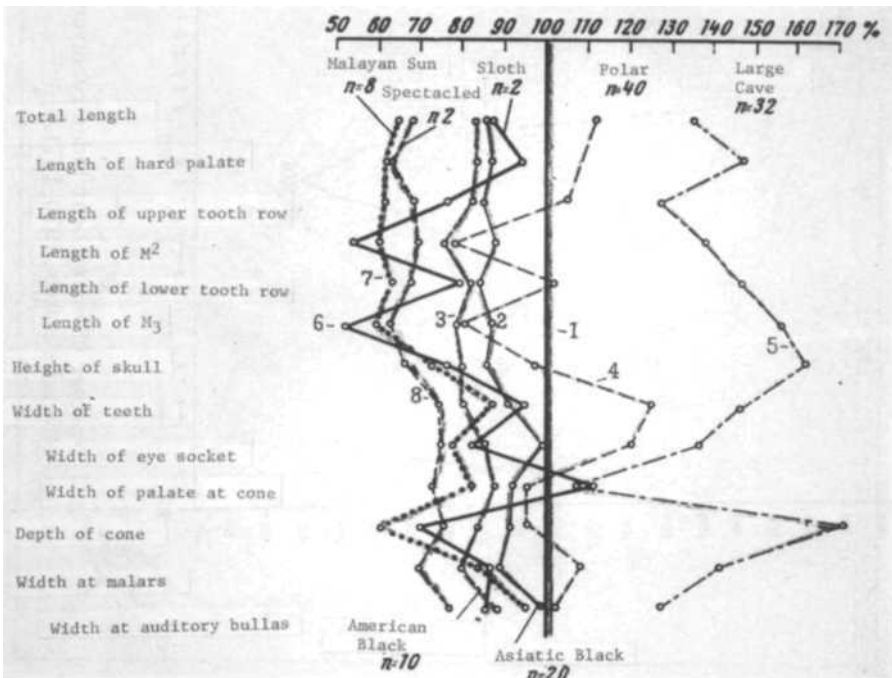


Fig. 3 Percent deviation from the brown bear of skull measurements of other bears.

abrupt fluctuations or 'toothiness' result primarily from variable socio-economic factors such as prices of hides, people moving from the taiga to cities, purchasing of hides by private fur traders, etc. In recent times, records have become quite confused. Nevertheless, information obtained through questionnaires and other means indicate not fewer than 5 to 6 thousand individual bears are harvested by shooting and trapping, mostly snaring. The percentage of commercial use varies from 5 to 15 percent per year according to the administrative area and, in essence, the second figure is the allowed maximum.

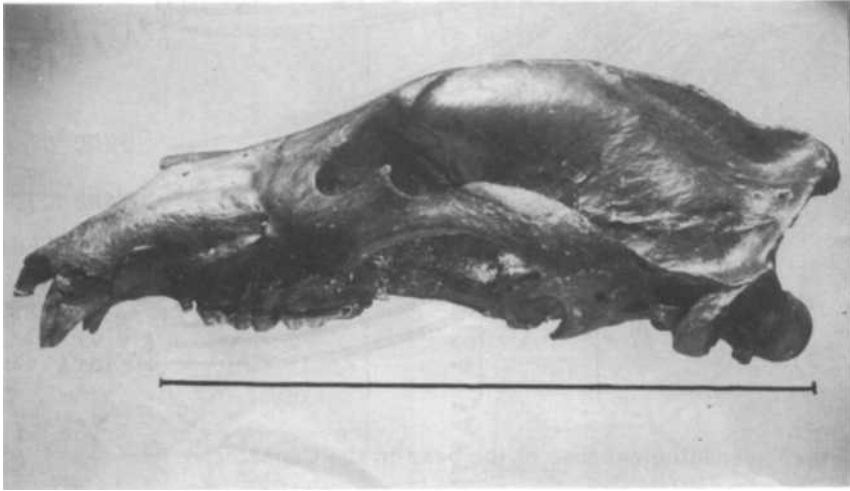


Fig. 4 Skulls of excavated bears: line indicates skull-length of modern brown bear.

- (a) Brown bear from the middle-fourth alluvium of the Volga River.
- (b) Large cave bear from the caves of the Zhigulevski heights.

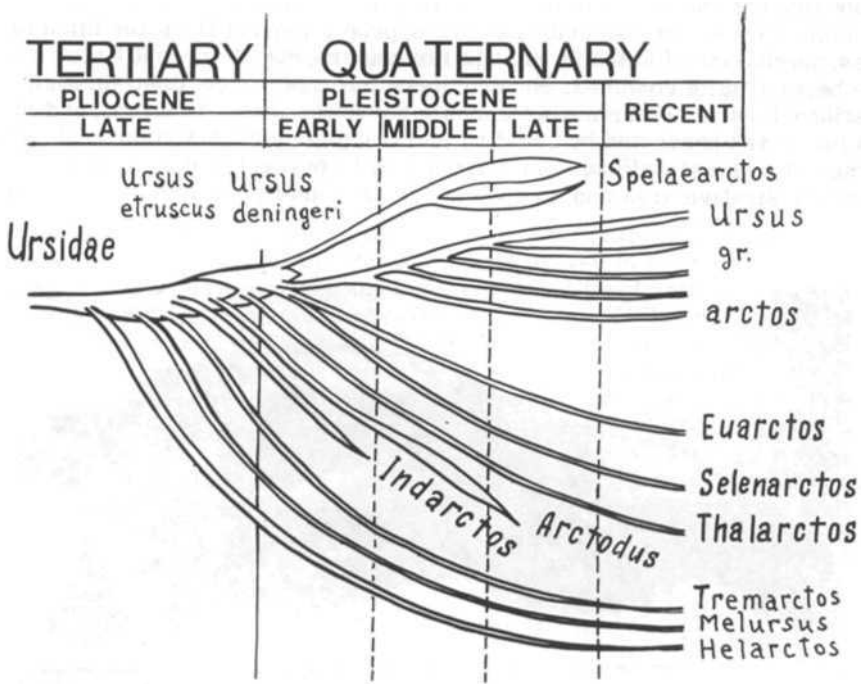


Fig. 5 Genealogical tree of the bear in the Cenozoic.

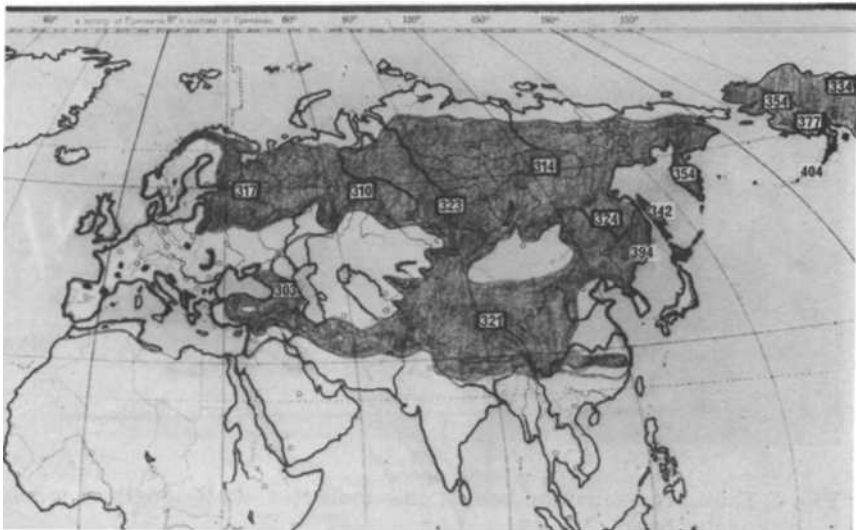


Fig. 6 Natural habitat and geographical variations in brown bear skull length.

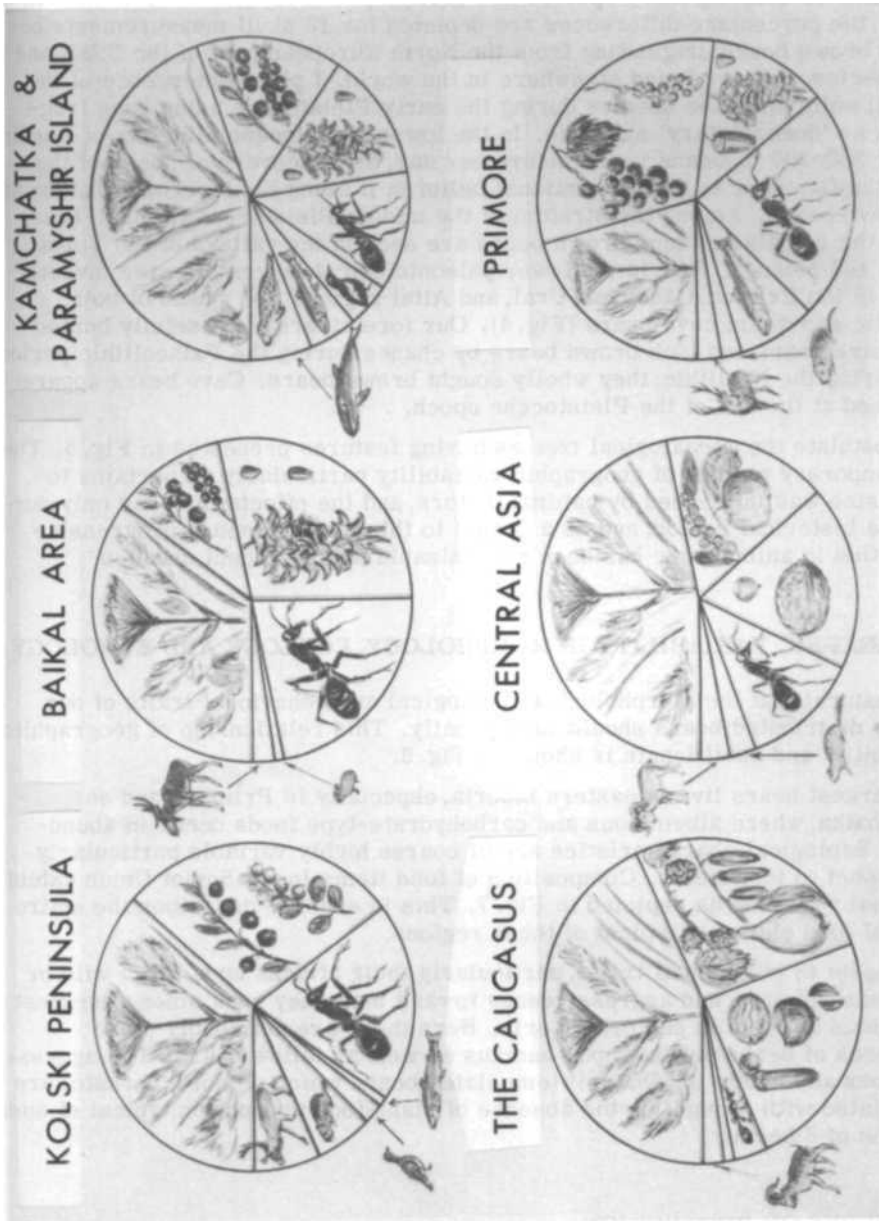


Fig. 7 Food composition of the brown bear in various regions of the USSR.

HISTORICAL ASPECTS

The geological and genealogical tree of the brown bear beginning in the late Cenozoic (Pliocene-Holocene) has been constructed on the basis of morphological traits of contemporary species and certain paleontological materials. In Fig. 3, the percentage differences are depicted for 13 skull measurements between brown bears originating from the North European part of the USSR and six species of bears found elsewhere in the world. I place emergence of the brown, white and cave species during the early Pleistocene using bone fragments as 'documentary' evidence. In the lower Pleistocene alluvium of Dnestra, dating 280-300 thousand years before our day, the discovery of bones of the bear led Deninger to the conventional belief in it being the forerunner of brown and cave bears. Among the stratum of the middle Pleistocene (Mindel-Riss, Riss) the remains of huge brown bears are seen in the valleys of the Volga, Urals and Selenga. And, in the lower paleontological layers of caves investigated in the Crimea, Caucasus, Ural, and Altai regions are skulls of both gigantic and dwarf cave bears (Fig. 4). Our forefathers purposefully hunted only cave bears and took brown bears by chance during the Palaeolithic period but during the Neolithic, they wholly sought brown bears. Cave bears apparently perished at the end of the Pleistocene epoch.

We postulate the genealogical tree as having features presented in Fig. 5. The contemporary picture of geographic variability particularly as pertains to skull size was influenced by natural factors, and the effects man had only during the historical period, and as a sequel to this phenomenon, a progressive reduction in animal size has been recognizable during recent decades.

GEOGRAPHIC VARIABILITY IN MORPHOLOGY, ECOLOGY AND ETHOLOGY

It is natural that the morphological, ecological and behavioral traits of our widely distributed bears should vary greatly. This relationship of geographical variability and skull length is shown in Fig. 6.

The largest bears live in eastern Siberia, especially in Primore and on Kamchatka, where albuminous and carbohydrate-type foods occur in abundance. Ecological characteristics are of course highly variable particularly in respect to food items. Composition of food items in the Soviet Union exhibit regional variation as depicted in Fig. 7. This in essence describes the entire natural food elements typical of these regions.

In respect to ethological traits, particularly their attacks upon large wild or domestic animals, and aggressiveness toward man, they rank among the most voracious animals in eastern Siberia. Here there are noticeably more instances of bears preying upon humans as well as fellow bears. The aggressiveness and habits of 'Shatuni' (emaciated bears which do not hibernate) are associated with drought or the absence of plant-food production typical of some regions of Siberia.

MEASURES OF PROTECTION

During the last decade the Soviet Union has taken protective measures while allowing for the reasonable use of our brown bear resource. Bear hunting is forbidden in Lithuania, Latvia, Estonia, White Russia, the Ukraine, Tataria, Mordovia ASSR, Turkmenia and Khirgizia. Hunting licences have been intro-

duced to many areas and measures have curtailed abusive use of such motorized methods of transport as helicopters and crosscountry vehicles. Bear hunting is permitted in game reserves, and plans are being formulated to develop bear reserves along the southern portion of their natural range and the European part of the USSR.

PART V. BIOLOGY OF BEARS

Paper 36

Reproductive Cycles and Rates in the Grizzly Bear, *Ursus arctos horribilis*, of the Yellowstone Ecosystem

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INTRODUCTION

Since the early 1800s grizzly bears, *Ursus arctos horribilis*, rapidly declined in the contiguous United States to a number that probably does not now exceed 600 or 700 (Craighead and Craighead 1973). They are found only in high mountain country and wilderness areas of our large national parks and forests. In Alaska and western Canada, grizzly bears are still relatively abundant.

Female grizzlies are characterized by a long life span, a relatively late sexual maturity, protracted reproductive cycles and, as adults, high survivorship rates (Craighead *et al.* 1974). Their low reproductive capacity compared to that of other mammals is an evolutionary characteristic that relates to size and power, competence and aggressiveness of mothers, self-sufficiency of cubs, and social facilitation among females with offspring. Because of the long-term continuity necessary to obtain quantitative data on a slowly reproducing mammal, precise reproductive rates have not been obtained for any bear population. Yet information on reproductive rates is essential for intelligent management since neither mortality rates nor population trends can be evaluated without it.

We describe in this paper how reproductive rates were obtained and how this biological parameter relates to the population dynamics of the grizzly bear in the Yellowstone ecosystem.

METHODS

From 1959 to 1971, bears were captured in culvert traps or shot with propulsive syringe darts containing immobilizing drugs. Following capture and immobilization, each grizzly was ear-tagged and individually color-marked. Used in combination with numbered colored ear-tags, several hundred color combinations were possible. Many color-markers lasted 6 or 7 years without replacement and some for the entire study period (Craighead *et al.* 1960).

Computing Reproductive Cycle

To determine age at first pregnancy, animals of known or established age were

observed annually during the mating seasons (Craighead *et al.* 1969). To obtain quantitative data on length of the reproductive cycle, the reproductive histories were recorded for 30 marked females, over extended periods of time. Among these females, all but five were aged by the cementum layer technique (Craighead *et al.* 1970). Litter sizes were determined from annual counts of individually identifiable females with cubs.

The reproductive cycle for a female begins when fertilization occurs during June to mid-July and terminates with weaning (Craighead *et al.* 1969). The cycle for a female or for a population is obtained by dividing the reproductive period in years by the number of cycles. A female with two cycles during a 7-year period, for example, has a reproductive cycle of 3.5; a population with a total of 33 cycles and 99 reproductive years exhibits a 3.00 average reproductive cycle. The reproductive rate was calculated by dividing litter size by length of the reproductive cycle. This is expressed as a number of cubs produced per adult female per year.

Data from the 30 females were grouped into four samples based on number of reproductive cycles. The samples show the variation in reproductive rate that occurs with an increase in the number of cycles used in the computations. Samples 1 and 2 included data from 19 females with the most complete reproductive histories. Sample 3 included the 19 bears from Samples 1 and 2 plus five additional females. The fourth sample included reproductive histories of all 30 females. Nine females were sub-adult when record-keeping began.

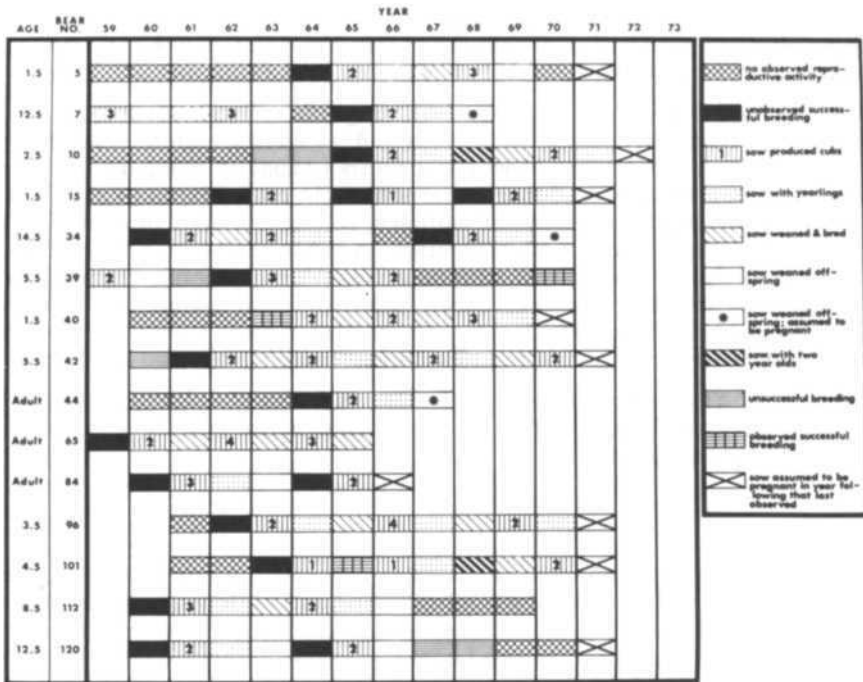


Fig. 1 Method of recording reproductive histories of females. The continuity of observations could be quickly checked for each female each year, as well as the female's reproductive performance.

Number of litters, cubs per litter, length of reproductive cycles, and reproductive period in years, were recorded for each female. The reproductive period for each female is the sum of her reproductive cycles. A cycle is the period in years from pregnancy to pregnancy or to an assumed pregnancy. Assumed pregnancy dates were projected for the females in samples 2, 3 and 4 in order to maximize information on the reproductive chronology of each female. It was assumed that when observation of a given female terminated, pregnancy ensued at the earliest possible date. This assumption tended to minimize values for average length of the reproductive cycle and thus to elevate the reproductive rate. The methodology used to record the annual sequence of reproductive events, with assumed dates of last pregnancy, is shown in Fig. 1.

Determining Age at First Pregnancy

A female was recorded as pregnant following observed copulation resulting in offspring or by extrapolation from observations of females with cubs. A female was considered sexually mature at 5.5 years, the earliest that females were known to produce litters (Craighead *et al.* 1969). We termed the period in years between the earliest recorded pregnancy (age 4.5) and the actual age at which a first pregnancy occurred, the pre-pregnancy period. Among 30 females with reproductive histories, this period ranged from 0 to 4 years. The effect of an extended pre-pregnancy period on length of reproductive cycle for individual females and for the population of females will be considered in calculating values for reproductive cycles.

The age at first pregnancy was recorded for 16 of 30 marked females. Eleven of these (69%) first became pregnant at 4.5, one at 5.5, three at 6.5, and one at 8.5 years of age. Although younger females copulated, none became pregnant before they were 4.5 years old (Craighead *et al.* 1969). The average age at first pregnancy was 5.2 years for 16 females. It was possible, but unverifiable, that some females having protracted pre-pregnancy periods conceived earlier and suffered miscarriages or fatalities of entire litters in the den. The effect on the reproductive rate is, nonetheless, the same as failure to conceive.

RESULTS

Reproductive Cycles

The chronology of events occurring in a cycle varies with the cycle length. The length of a cycle is dependent on when the female weans and how soon thereafter she comes in estrus.

In a 2-year cycle, the female becomes pregnant in June or July, whelps the following February, suckles cubs through summer and winter, weans them as yearlings in the spring, then comes in estrus, breeds, and becomes pregnant following weaning.

In a 3-year cycle, the female becomes pregnant, whelps cubs, attends them as yearlings, dens with them, weans them as 2-year olds soon after leaving the den, and then comes in estrus and breeds to begin another cycle.

In a 4-year cycle, the female follows the 3-year cycle, but after weaning 2-year olds, she either remains anestrous or she comes into estrus but is not fertilized. She is bred the following year and becomes pregnant. In longer cycles, the female may remain anestrous or for various reasons fail to bring forth cubs.

TABLE 1. REPRODUCTIVE RATES OF 19 MARKED FEMALE GRIZZLY BEARS (33 REPRODUCTIVE CYCLES) 1959-1972.

Bear No.	Age Marked	No. of Repro. Cycles in Years				Total Cycles	Repro. Period in Years	Date of Last Known Pregnancy	No. Cubs	Repro. Rates
		2	3	4	5					
5	1.5		1			1	3	1967	2	0.667
7	12.5		1	1		2	7	1965	6	0.857
10	2.5			1		1	4	1969	2	0.500
15	1.5		2			1	6	1968	3	0.500
34	14.5	1			1	2	7	1967	4	0.571
40	1.5	2				2	4	1967	4	1.000
42	5.5	1	2			3	8	1969	6	0.750
65	Adult	2				2	4	1963	6	1.500
84	Adult			1		1	4	1964	3	0.750
96	3.5		2			2	6	1968	6	1.000
101	4.5	1		1		2	6	1969	2	0.333
120	12.5			1		1	4	1964	2	0.500
125	5.5		3			3	9	1970	8	0.889
128	10.5	1	2			3	8	1969	10	1.250
144	0.5			1		1	4	1970	2	0.500
150	4.5			1		1	4	1966	3	0.750
172	11.5	1	1			2	5	1967	4	0.800
173	2.5		1			1	3	1969	2	0.667
175B	Adult		1			1	3	1962	2	0.667
Totals		9	16	7	1	33	99		77	

Reproductive cycles of 19 marked females were calculated from known pregnancies as shown in Table 1. The number of cycles per female varied from one to three and totalled 33 for all 19 animals during a cumulative reproductive period of 99 years. Sample 1 contains no assumed pregnancies, so usable data on cycles, reproductive period and litter size are minimal. The reproductive cycle varied from 2 to 5 years. Of the 33 cycles, 9 were 2 years; 16, 3 years; 7, 4 years; and 1, a 5-year cycle. Three-year cycles were more prevalent than 2-year cycles (64 to 36 percent). For some females the reproductive period consisted of a single reproductive cycle, but for others it included two or more cycles.

An average reproductive cycle of 3.00 years is obtained when the total of reproductive periods in years for all 19 females (99) is divided by the total number of cycles (33). This parameter can then be refined by including pre-pregnancy data. For example, among 19 females recorded in Table 1, five were older than 4.5 years at first pregnancy. The average reproductive cycle of

TABLE 2. REPRODUCTIVE CYCLE OF 30 MARKED FEMALE GRIZZLY BEARS (68 REPRODUCTIVE CYCLES) 1959-1972.

Bear No.	Age* Marked	No. of Repro. Cycles in Years						Total Cycles	Repro. Period In Years	No. Cubs	Repro. Rates
		2	3	4	5	6	7				
5	1.5		1	1				2	7	5	0.714
T	12.5		2	1				3	10	8	0.800
10	2.5		1	1				2	7	4	0.571
15	1.5		3					3	9	5	0.556
34	14.5	1	1		1			3	10	6	0.600
39	5.5		1	1	1			3	12	7	0.583
40	1.5	2	1					3	7	7	1.000
42	5.5	2	2					4	10	8	0.800
65	Adult	3						3	6	9	1.500
84	Adult	1		1				2	6	5	0.833
96	3.5		3					3	9	8	0.889
101	4.5	2		1				3	8	4	0.500
112	8.5		1			1		2	9	5	0.556
120	12.5			1			1	2	11	4	0.364
125	5.5		4					4	12	10	0.833
128	10.5	2	2					4	10	13	1.300
144	0.5	1						2	6	4	0.667
150	4.5			1	1			2	9	5	0.556
163	1.5	1						1	2	2	1.000
172	11.5	1	2					3	8	7	0.875
173	2.5	1	1					2	5	3	0.600
175	10.5	1	2					3	8	4	0.500
175B	Adult		2					2	6	4	0.667
200	3.5			1				1	4	2	0.500
44	Adult						1	1	7	2	0.286
140	8.5				1			1	5	3	0.600
141	1.5		1					1	3	2	0.667
160	Adult					1		1	6	2	0.333
180	11.5		1					1	3	3	1.000
187	1.5		1					1	3	1	0.333
Totals		18	32	10	4	2	2	68	218	152	

*Bears designated as 'Adult' were assumed to be at least 4.5 years of age.

TABLE 3. COMPARISON OF FOUR CALCULATIONS OF REPRODUCTIVE CYCLES AND RATES OF MARKED FEMALE GRIZZLIES.

	Sample Group			
	1	2	3	4
Number of Marked Females	19	19	24	30
Number of Reproductive Cycles	33	52	62	68
Reproductive Period in Years (Adjusted)	99(110)	156(167)	191(202)	218(231)
Total Number of Cubs	77	119	139	152
Average Litter Size	2.33	2.29	2.24	2.24
Average Unadjusted Reproductive Cycle	3.00	3.00	3.08	3.21
*Adjusted Average Reproductive Cycle	3.33	3.21	3.26	3.40
Reproductive Rate for Population of Marked Females	0.700	0.713	0.687	0.659

*Adjusted by including pre-pregnancy data.

3.00 was adjusted for the 11 years that these females were not pregnant. With this adjustment ($99 \text{ years} + 11 = 110/33 = 3.33$), the average reproductive cycle is 3.33 years.

By assuming when each of 30 females would become pregnant following her last litter (see Methods), it was possible to use a larger number of cycles and reproductive years to compute reproductive rate.

With longer reproductive histories to examine, changes occurred for individual females in average length of the reproductive cycle and in reproductive rates. In sample 2, 52 cycles representing 167 reproductive years yielded an average reproductive cycle of 3.21.

In sample 3, 24 females having 62 reproductive cycles during a combined reproductive period of 202 years gave an average reproductive cycle of 3.26 years.

A fourth sample of 30 females (Tables 2 and 3) yielded 68 reproductive cycles, a reproductive period of 231 years, and an average reproductive cycle of 3.40 years. Data used to calculate average reproductive cycles for marked females included in the four data samples are summarized in Table 3. The values of 3.33, 3.21, 3.26, and 3.40 years for reproductive cycles indicate the range occurring in this parameter with changes in sampling. They also indicate that a representative reproductive rate for a population of long-lived animals can be obtained only from a relatively large sample of animals over an extended period of time since the accuracy of this biological parameter is dependent on an accurate measurement of cycle length.

Litter Sizes

The thirty marked females produced 68 litters. Nine were 1-cub litters; 38, 2-cub; 18, 3-cub; and 3, 4-cub litters. Fifty-six and twenty-six percent were 2-

TABLE 4. COMPARISON OF REPRODUCTIVE RATES OF 19 MARKED FEMALE GRIZZLIES (EXCLUDING PRE-PREGNANCY DATA).

Bear No.	Repro. Rates from 33 Repro. Cycles	Repro. Rates from 52 Repro. Cycles	Change in Repro. Rates with Change in Sample Size	
			33 R.C.	52 R.C.
5	0.666	0.714		+0.048
7	0.857	0.800	-0.057	
10	0.500	0.571		+0.071
15	0.500	0.555		+0.555
34	0.571	0.600		+0.029
40	1.000	1.000		0.000
42	0.750	0.800		+0.050
65	1.500	1.500		0.000
84	0.750	0.833		+0.083
96	1.000	0.888	-0.112	
101	0.333	0.500		+0.167
120	0.500	0.364	-0.136	
125	0.888	0.833	-0.055	
128	1.250	1.300		+0.050
144	0.500	0.666		+0.166
150	0.750	0.555	-0.195	
172	0.800	0.875		+0.075
173	0.666	0.600	-0.066	
175B	0.666	0.666		0.000
Totals	14.447	14.620	-0.621	+0.794
			+0.173	+0.173
	R.R. =0.760	R.R. =0.769		

and 3-cub litters, respectively. The average litter size for the females recorded in each sample are shown in Table 3. These parameters and those for length of cycle were used to compute reproductive rates for the population.

Reproductive Rates

In sample 1, reproductive rates for individual females ranged from a low of 0.333 to a high of 1.500. The low represented two cubs produced in two cycles totalling 6 years, whereas the high resulted from six cubs produced in two cycles of 4 years. Of the 19 females, 4 exhibited reproductive rates of 1.000 or higher (Table 1). The average rate for all 19 females was 0.700 (Table 3).

In sample 2, we calculated reproductive rates for the same 19 females but used a longer time period. We increased the length of the reproductive period

TABLE 5. CALCULATION OF AVERAGE REPRODUCTIVE RATE FOR 30 ADULT FEMALES.

Cycle Length (yrs)							Total Cycles	Repro. Period (yrs)		No. Cubs	Repro. Un-adjusted	Rate Adjusted
2	3	4	5	6	7	Un-adjusted		Adjusted				
18	32	10	4	2	2	68	218	(+13)231	152	0.697	0.658	

Calculations

$$\frac{\text{Total Cubs}}{\text{Total No. Litters}} = \frac{152}{68} = 2.24 = \text{Average Litter Size}$$

$$\frac{\text{Total Reproductive Period in Years}}{\text{Total Number Cycles}} = \frac{218}{68} = 3.21$$

= Unadjusted Reproductive Cycle

$$\frac{\text{Total Cubs}}{\text{Total Reproductive Period in Years}} = \frac{152}{218} = 0.697$$

= Unadjusted Reproductive Rate

218 + 13 = 231 (Total Reproductive Period in Years Adjusted by Pre-Pregnancy Data)

$$\frac{\text{Adjusted Total Reproductive Period in Years}}{\text{Total Number Cycles}} = \frac{231}{68} = 3.40$$

= Average Reproductive Cycle

$$\frac{\text{Total Cubs}}{\text{Adjusted Total Reproductive Period in Years}} = \frac{152}{231} = 0.658$$

examined from 110 to 167 years. Total cub production then showed an increase from 77 to 119 and number of reproductive cycles 33 to 52. Calculating reproductive rates with these parameters altered the rates for individual females (Table 4). Three rates remained unchanged, 10 increased by an average of 0.079, but 6 decreased by 0.104, for a 0.009 overall average increase in all rates. This gave a 0.713 average reproductive rate for all 19 females in sample 2 compared to 0.700 for the same females in sample 1 (Table 3).

In the third sample, the number of marked females was increased to 24 and a reproductive rate calculated from a total of 62 cycles and 202 reproductive years (191 plus 11 years pre-pregnancy). This gave a reproductive rate of 0.687.

In sample 4 involving 30 females, a reproductive cycle of 3.40 years, and a reproductive period of 231 years, gave a reproductive rate of 0.658 (Table 5).

A comparison of reproductive rates based on only one recorded reproductive cycle per female (Table 2) illustrates how the cycle length and litter size affect the reproductive rate of individual females. As an example, one female had a very low reproductive rate (0.286) because of a long 7-year cycle, while

another had a moderately high reproductive rate (0.600) despite the production of three cubs during a 5-year cycle. The 0.667 reproductive rate of still another female exceeded the average for all females (0.658) because a 3-year cycle compensated for her low production of two cubs. The average reproductive rate was 0.482 for six females, each with only one reproductive cycle.

Because even minor changes in reproductive rate affect the population growth of a slowly reproducing species, four different rates were calculated to show the variation that could occur. We believe the reproductive rates from sample 4 shown in Table 3 are more accurate than those from samples 1, 2 and 3, because they represent the reproductive behavior of a large number of females over a longer period of time than the other samples. The higher rates of 0.700 and 0.713 obtained with samples 1 and 2 are due to higher values for litter size and may represent optimum rates attained over relatively short reproductive periods.

Maximum and Minimum Reproductive Rates of Marked Females

Maximum and minimum reproductive rates for individual females or a group of females are useful because they indicate the potential of a population to grow or to decline. A population exhibiting compensatory reproduction following a population decline should contain females with high reproductive rates. Similarly, a declining population under environmental stresses could be expected to have females with low reproductive rates. Both maximum and minimum reproductive rates for grizzly bears in Yellowstone are shown so that data obtained in the future can be compared with these parameters.

Maximum reproductive rates of individual bears, including variations resulting from changes in sampling, are presented in Table 6. For example, female No. 128 exhibited a reproductive rate of 1.250 during a period of 8 reproductive years and 1.300 in a 10-year period. Female No. 96 had a reproductive rate of 1.000 during 6 reproductive years, but this declined to 0.889 over a period of 9 years. Although the data indicate that one female exhibited a reproductive rate of 1.500 during a 6-year period, it is highly unlikely that she could sustain this throughout her entire reproductive life. Data suggest that a maximum for several females averaged 1.17 or, in round figures, about one cub per adult female per year. A reproductive rate of this magnitude for a population of females would indicate a potential for that population to grow if mortality was not excessive.

Although the minimum reproductive rate recorded for an individual female was 0.286, this was for only one reproductive cycle and was not considered representative. Bears with minimum rates as calculated for samples 1, 2, and 3 are shown in Table 7. The reproductive rate for female No. 120 averaged 0.364 over an 11-year period. The average of four females in samples 2 and 3 was 0.498; therefore, an average minimum reproductive rate among marked females was approximately half the maximum or, in round numbers, 0.5 cub per adult female per year. A rate of this magnitude among female grizzlies in Yellowstone would clearly indicate a declining population even if man caused mortalities were kept to a minimum (Craighead *et al.* 1974).

The maximum and minimum reproductive rates presented illustrate the range in this parameter and clearly show that a valid long-term reproductive rate for a population of grizzly bears must be obtained from a large sample of females observed over a long period of time.

TABLE 6. MAXIMUM REPRODUCTIVE RATES ILLUSTRATED BY CERTAIN GRIZZLY BEARS FOR WHICH MORE THAN ONE REPRODUCTIVE CYCLE WAS OBSERVED, 1959-1972.

Bear No.	Sample 1 (19)	Sample 2 (19)	Sample 3 (24)
40	1.000	1.000	1.000
65	1.500	1.500	1.500
96	1.000	0.889	0.889
128	1.250	1.300	1.300
Average	1.188	1.172	1.172

TABLE 7. MINIMUM REPRODUCTIVE RATES ILLUSTRATED BY CERTAIN GRIZZLY BEARS FOR WHICH MORE THAN ONE REPRODUCTIVE CYCLE WAS OBSERVED, 1959-1972.

Bear No.	Sample 1 (19)	Sample 2 (19)	Sample 3 (24)
101	0.333	0.500	0.500
120	0.500	0.364	0.364
10	0.500	0.571	0.571
15	0.500	0.556	0.556
Average	0.458	0.498	0.498

Reproductive Rate for Ecosystem Population

The reproductive cycle of 3.40 and rate of 0.658 are average parameters for 30 marked females over a 12 year period. To obtain a reproductive rate that would more accurately represent the entire population of grizzly bears inhabiting Yellowstone National Park and adjacent areas, we increased the sample size. This was accomplished by combining data from an additional 25 marked females omitted from reproductive cycle calculations because of observational discontinuities. These data were valid for calculating litter size and when combined with data from the 30 females, gave a long-term reproductive rate of 0.626 for the population. This long-term rate, derived from annual counts of 55 marked and recognizable females with litters extending over a 15-year period, we consider to be the most accurate long-term average rate for the population between 1959 and 1970.

Reproductive Longevity

One female was 14.5 years old when marked, and produced her last litter of

TABLE 8. REPRODUCTIVE PERFORMANCE OF 30 FEMALE GRIZZLIES, 1959-1972.

Bear No.	Age Marked*	Repro. Years Prior to Pregnancy	Age at First Pregnancy	Age at First Recorded Pregnancy	Sequence of Cycles in Years 1st 2nd 3rd 4th	Repro. Period in Years	Age When Last Observed	Age When Last Litter was Produced
5	1.5	2	6.5	6.5	3 4	7	12.5	10.5
7	12.5	—	—	11.5	3 4	10	21.5	19.5
10	2.5	4	8.5	8.5	4 3	7	14.5	13.5
15	1.5	0	4.5	4.5	3 3	9	12.5	11.5
34	14.5	—	—	14.5	2 5 3	10	24.5	22.5
39	5.5	0	4.5	4.5	4 3 5	12	16.5	12.5
40	1.5	0	4.5	4.5	2 2 3	7	10.5	9.5
42	5.5	2	6.5	6.5	2 3 3 2	10	15.5	15.5
44	Adult	—	—	—	7	7	Min.	10.5
65	Adult	—	—	—	2 2 2	6	Min.	10.5
84	Adult	—	—	—	4 2 2	6	Min.	9.5
96	3.5	0	4.5	4.5	3 3 3	9	12.5	11.5
101	4.5	2	6.5	6.5	2 4 2	8	13.5	13.5
112	8.5	—	—	8.5	3 6	9	17.5	12.5
120	12.5	—	—	12.5	4 7	11	22.5	17.5
125	5.5	1	5.5	5.5	3 3 3 3(2)	12(11)	15.5	15.5
128	10.5	—	—	10.5	3 2 3 2	10	19.5	19.5
140	8.5	—	—	10.5	5	5	12.5	11.5
141	1.5	1	5.5	5.5	3	3	7.5	6.5
144	0.5	0	4.5	4.5	4 2	6	9.5	9.5
150	4.5	0	4.5	4.5	4 5	9	12.5	9.5
160	Adult	—	—	—	6	6	Min.	9.5
163	1.5	0	4.5	4.5	2	2	5.5	5.5
172	11.5	—	—	11.5	3 2 3	8	19.5	17.5
173	2.5	0	4.5	4.5	3 2	5	8.5	8.5
175	10.5	—	—	10.5	3 2 3	8	17.5	16.5
175B	Adult	—	—	—	3 3 3	6	Min.	10.5
180	11.5	—	—	11.5	3	3	14.5	12.5
187	1.5	1	5.5	5.5	3	3	7.5	6.5
200	3.5	0	4.5	4.5	4	4	8.5	5.5
Totals		13			100 72 39 7	218 + 13 = 231		

*Bears designated as 'Adult' were assumed to be at least 4.5 years of age.

TABLE 9. SEQUENCE OF CYCLE LENGTHS FOR 30 FEMALE GRIZZLIES, 1959-1972.

Bear No.	Sequence of Cycles in Years				Sequence of Litter Sizes				Cubs Produced/Year			
	1st	2nd	3rd	4th	1st	2nd	3rd	4th	1st	2nd	3rd	4th
5	3	4			2	3			0.67	0.75		
7	3	4	3		3	3	2		1.00	0.75	0.67	
10	4	3			2	2			0.50	0.67		
15	3	3	3		2	1	2		0.67	0.33	0.67	
34	2	5	3		2	2	2		1.00	0.40	0.67	
39	4	3	5		2	3	2		0.50	1.00	0.40	
40	2	2	3		2	2	3		1.00	1.00	1.00	
42	2	3	3	2	2	2	2	2	1.00	0.67	0.67	1.00
44	7				2				0.29			
65	2	2	2		2	4	3		1.00	2.00	1.50	
84	4	2			3	2			0.75	1.00		
96	3	3	3		2	4	2		0.67	1.33	0.67	
101	2	4	2		1	1	2		0.50	0.25	1.00	
112	3	6			3	2			1.00	0.33		
120	4	7			2	2			0.50	0.29		
125	3	3	3	3	2	3	3	2	0.67	1.00	1.00	0.67
128	3	2	3	2	3	3	4	3	1.00	1.50	1.33	1.50
140	5				3				0.60			
141	3				2				0.67			
144	4	2			2	2			0.50	1.00		
150	4	5			3	2			0.75	0.40		
160	6				2				0.33			
163	2				2				1.00			
172	3	2	3		3	1	3		1.00	0.50	1.00	
173	3	2			2	1			0.67	0.50		
175	3	2	3		1	2	1		0.33	1.00	0.33	
175B	3	3			2	2			0.67	0.67		
180	3				3				1.00			
187	3				1				0.33			
200	4				2				0.50			
\bar{h}	100	72	39	7	65	49	31	7				
\bar{x}	3.33	3.27	3.00	2.33	2.17	2.23	2.38	2.33	0.65	0.68	0.80	1.00

TABLE 10. LENGTH OF CYCLE VERSUS NUMBER OF CUBS PRODUCED, 1959-1972.

	2-Yr	3-Yr	4-Yr	5-Yr	6-Yr	7-Yr
1.	2	2	2	3	2	2
2.	2	3	2	2	2	2
3.	2	2	3	2	$h = \bar{4}$	$h = \bar{4}$
4.	2	2	2	2	$\bar{x} = 2.0$	$\bar{x} = 2.0$
5.	1	3	2	$h = \bar{9}$		
6.	2	2	3	$\bar{x} = 2.25$		
7.	2	3	2			
8.	4	2	3			
9.	2	3	3			
10.	3	2	1			
11.	2	1	$h = \bar{23}$			
12.	1	2	$\bar{x} = 2.30$			
13.	1	3				
14.	2	1				
15.	3	2				
16.	2	1				
17.	2	3				
18.	3	2				
19.	$h = \bar{38}$	4				
20.	$\bar{x} = 2.11$	3				
21.		2				
22.		2				
23.		2				
24.		2				
25.		3				
26.		2				
27.		2				
28.		3				
29.		4				
30.		3				
31.		1				
32.		2				
		$h = \bar{74}$				
		$\bar{x} = 2.31$				

two cubs at the age of 22.5, weaning them when she was 24.5. Two females produced litters when they were 19.5 years old and two others when 17.5 (Table 8). The greatest age attained by a female was 25 years; therefore, the data suggest that reproductive longevity approximates physical longevity and that most adult females could produce offspring as long as they lived. The minimum breeding age is 4.5 years, but a female cub born into the population requires an average of 6.3 years to whelp her first litter. With an average reproductive cycle of 3.40 years and 2.24 average litter size, a 25-year old female would experience 6 reproductive cycles and produce 13 cubs.

Sequence of Reproductive Cycles

We examined data to determine if any sequence of reproductive cycle lengths was more prevalent than others among the 30 females. The sequence of reproductive cycles varied greatly among individual females (Tables 8 and 9). For example, one female's first reproductive cycle was 3 years and her second, 4 years. Another female had a sequence of 3,4, and then 3.

Among females with at least two reproductive cycles, cycle length consisted of 12 combinations: 6 occurred once, 4 were repeated, and 2 (3-3 and 3-2) occurred four times each.

Among females with 3 reproductive cycles, 9 combinations occurred. Seven occurred once, while 2 sequences (3-3-3 and 3-2-3) occurred three times each. Since (3-3 and 3-2) occurred four times each in two-cycle sequences, one would expect them to predominate, as they did, in three-cycle sequences. The significance of these repetitive patterns is unclear, but they definitely relate to physiological differences which are responses to extrinsic factors such as food, climate and population density. Variations in both cycle length and litter size appear to be natural population-regulating mechanisms. However, Table 9 shows no relation between cycle length and litter size, so compensatory processes may not be highly developed.

Length of Cycle Versus Cubs Produced

A Spearman Rank Correlation Coefficient (S.R.C.C.) was computed to determine if length of reproductive cycle was related to number of cubs produced per litter (Table 10). No significant correlation was obtained; the 'rho' value equalled +0.124, a statistically insignificant positive correlation.

EVALUATION OF PROCEDURAL BIAS ON RESULTS

To determine whether procedural biases were present in evaluations of reproductive cycle, reproductive rate and litter size, the data for these parameters were tested statistically.

Productivity Related to Age of Females

Ages of the 30 females varied from 0.5 to 14.5 years when marked; eleven were between 0.5 and 3.5 years, 10 were 4.5 to 5.5 years, and 9 were between 8.5 and 14.5. If productivity was dependent on age of the female, then the age composition of a sample could affect the values obtained for reproductive cycles and reproductive rates. This was tested by arranging data on number of

TABLE 11. PRODUCTIVITY OF 28 FEMALE GRIZZLIES RELATED TO AGE, 1959-1972.

Age Class	No. of Litters	No. of Cubs	Ave. No. of Cubs	Age Class	No. of Litters	No. of Cubs	Ave. No. of Cubs
5½	13	28	2.2	14½	2	5	2.5
6½	4	6	1.5	15½	5	10	2.0
7½	5	11	2.2	16½	2	5	2.5
Total 5½-7½	22	45	2.0	Total 14½-16½	9	20	2.2
8½	4	8	2.0	17½	3	7	2.3
9½	11	26	2.4	18½	0	0	0.0
10½	1	3	3.0	19½	2	5	2.5
Total 8½-10½	16	37	2.3	Total 17½-19½	5	12	2.4
11½	4	8	2.0	20½	0	0	0.0
12½	6	15	2.5	21½	0	0	0.0
13½	3	6	2.0	22½	1	2	2.0
Total 11½-13½	13	29	2.2	Total 20½-22½	1	2	2.0

litters and number of cubs produced by 28 females into one-year age groups (5.5 to 25.5 years of age). A S.R.C.C. was calculated to compare individual age of post-parturient females with number of cubs per litter. The 'rho' value was -0.021 , a statistically insignificant negative correlation.

Other correlation coefficients compared adult age-groups with number of cubs per litter. These tests determined whether females were more productive during certain periods of life. Grouping female grizzlies into six 3-year age categories (Table 11) and ranking them against numbers of cubs gave a 'rho' value of $+0.132$. The six groups were then consolidated into 3 arbitrary age categories of reproductive females: young (5.5-9.5 years); prime (10.5-17.5); and old (18.5-22.5). A S.R.C.C. calculation produced a 'rho' value of $+0.118$ when age categories were ranked with number of cubs in litters. Neither of these positive 'rho' correlations were statistically significant. We concluded that age of females in our sample did not appreciably affect litter size.

Variations in length of reproductive cycles for individuals and between individuals, and variation in the sequential combinations of reproductive cycles for individuals, indicated that a relationship might exist between a female's age and the length of her reproductive cycles. A S.R.C.C. calculated to examine this relationship resulted in a 'rho' equal to $+0.256$, which is not statistically significant. Correlation between the female's age at her last litter and the length of her last reproductive cycle was also found to be statistically insignificant. The coefficient of correlation was $+0.025$.

From our statistical analyses, we concluded that age of the females sampled

TABLE 12. NUMBER OF IMMOBILIZATIONS RELATED TO REPRODUCTIVE PERFORMANCE FOR 12 ADULT FEMALE GRIZZLIES, 1959-1970.

Bear No.	Age Marked	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	Total	Age 1st Observed Litter	Repro. Rate
7	12.5	1	—	1	—	2	—	—	—	1	—	—	—	5	12.5	0.800
23	14.5	—	2	—	—	1	1	1	—	1	—	1	—	7	15.5	0.600
39	5.5	—	1	1	—	1	1	—	—	1	2	5	—	12	5.5	0.583
42	5.5	—	1	—	—	1	1	—	—	1	3	—	—	7	7.5	0.800
65	Adult	—	1	1	—	—	—	—	—	—	—	—	—	2	Min.	1.500
84	Adult	—	—	1	—	—	—	—	—	—	—	—	—	1	Min.	0.833
112	8.5	—	—	1	—	—	—	—	1	2	3	—	—	7	9.5	0.556
120	12.5	—	—	1	—	—	—	—	1	—	—	—	—	2	13.5	0.364
125	5.5	—	—	—	1	—	—	—	—	—	—	—	—	1	6.5	0.833
128	10.5	—	—	—	1	1	—	—	—	1	—	1	—	4	11.5	1.300
172	11.5	—	—	—	—	—	1	—	—	1	—	—	—	2	12.5	0.875
175	10.5	—	—	—	—	—	1	—	—	1	—	—	—	2	11.5	0.500
Totals		1	5	6	2	6	5	1	2	9	8	7	—	52		

TABLE 13. NUMBER OF IMMOBILIZATIONS RELATED TO REPRODUCTIVE PERFORMANCE FOR 15 SUB-ADULT FEMALE GRIZZLIES, 1959-1970.

Bear No.	Age Marked	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	Total	Age 1st Litter	Repro. Rate
5	1.5	1	1	1	—	—	—	1	—	1	1	—	—	6	7.5	0.714
6	0.5	1	2	2	—	—	2	1	—	—	—	—	—	10	7.5	Killed-Blastocysts Recovered
10	2.5	1	—	1	—	—	1	—	—	1	—	—	—	4	9.5	0.571
15	1.5	1	—	1	—	—	—	—	—	—	—	—	—	2	5.5	0.556
29	0.5	1	—	2	—	—	—	1	—	—	—	—	—	4	6.5	0.250
40	1.5	—	2	1	1	1	2	2	2	2	3	1	—	17	5.5	1.000
81	2.5	—	—	1	—	—	—	1	—	—	—	—	1	3	6.5	0.250
96	3.5	—	—	1	1	3	—	—	—	1	—	—	—	6	5.5	0.889
101	4.5	—	—	1	—	—	1	—	—	3	2	—	—	7	7.5	0.500
200	3.5	—	—	—	—	—	—	1	—	1	1	—	—	3	5.5	0.500
187	1.5	—	—	—	—	—	1	1	1	1	2	—	—	6	6.5	0.250
163	1.5	—	—	—	—	1	—	—	—	3	—	—	—	4	5.5	1.000
144	0.5	—	—	—	—	1	—	1	4	—	—	1	1	8	5.5	0.667
150	4.5	—	—	—	—	2	1	—	—	1	—	—	—	4	9.5	0.556
173	2.5	—	—	—	—	—	1	—	—	1	—	—	—	2	5.5	0.600
Totals		5	5	11	4	8	9	9	7	15	9	2	2	86		

caused no significant bias in our calculations of litter size, length of reproductive cycle, or reproductive rate.

Immobilizations Related to Reproductive Rate

Female grizzlies were drugged with succinylcholine chloride or phencyclidine hydrochloride to obtain reproductive and other types of information. Females captured as adults were immobilized 1-12 times each, and females captured as sub-adults were immobilized 2-17 times.

To test the possibility that frequent use of drugs may have altered long-term productivity, we correlated the number of immobilizations with the reproductive rate for each of 12 adult and 14 sub-adult females. A correlation coefficient between number of immobilizations and reproductive rates of 12 adult females (Table 12) was not statistically significant ('rho' value of -0.332). A similar test for 14 sub-adult females (Table 13) yielded no significant correlation between number of immobilizations per female and reproductive rate ('rho' value of $+0.345$). A third S.R.C.C. indicated no significant correlation between number of immobilizations per female before age 5.5 and the age at which these females first littered ('rho' value of $+0.496$). We concluded that drugs did not significantly alter reproduction and did not bias the data.

Food Supply Related to Reproductive Rates

Both intrinsic and extrinsic factors affect reproductive rates but are difficult to isolate and analyze. Lack of comparative data prevents us from thoroughly evaluating whether the food available at the long-established open pit garbage dumps increased the reproductive rate of female grizzlies or changed the carrying capacity of the pristine habitat. We have much evidence, however, that the abrupt closing of garbage dumps in Yellowstone during 1969 and 1970, did stress the population and that this coincided with lower reproductive rates (Craighead *et al.* 1974). Feeding habits of many females were observed when reproductive histories were recorded. We cannot, at this time, show a statistically significant correlation between food supply and the reproductive rates of specific females. However, a drop in the annual reproductive rate of the population during 1970-72, can be related to a marked decrease in food supply associated with the abrupt closing of open pit garbage dumps (Craighead *et al.* 1974). Studies of other animals have shown that a decrease in nutritional level can affect reproductive success (Cheatum and Severinghaus 1950; Beuchner 1955; Knowlton 1972). Jonkel and Cowan (1971) presented inconclusive data suggesting an increased black bear reproductive rate coinciding with an increase in food.

The major food types used by grizzlies in the Yellowstone ecosystem were green vegetation, roots and tubers, berries, pine nuts, small rodents, large herbivores, and garbage. Relatively slight annual fluctuations occurred in the availability of green vegetation, roots, tubers and garbage, while great variations occurred annually in the other major foods (Craighead *et al.* in press). With garbage available to bears, the nutritional level of the Yellowstone population was more stable and this may have elevated reproductive rates. Our data suggest that for a period of years, a lowered reproductive rate associated with the decreased food base is more probable than a rising rate attributable to compensatory density-dependent factors.

DISCUSSION

We have shown that reproductive parameters of Yellowstone grizzlies are highly variable. Ages at first pregnancy ranged from 4.5 to 8.5 years, reproductive cycles from 2 to 7 years, litters from 1 to 4 cubs, and reproductive rates from 0.286 to 1.500 for the individual females studied. Presumably, flexibility of these biological parameters should enable the species to adjust to environmental factors that affect the population favorably or unfavorably. However, for a long-lived species exhibiting delayed maturity these compensatory reproductive processes (increases in litter size, decreases in length of reproductive cycle, and/or higher survivorship rates for sub-adult bears) would act slowly. On the other hand, population regulating mechanisms (infanticides from aggressive males and hormonal activity regulating the intervals between estrus in females) are factors that can offset compensatory processes. Infanticide was low (eight records). The great variability in the sequences of reproductive cycles could be important in regulating reproduction, but it will be difficult to draw conclusions from this information until similar data are obtained from other populations and norms established.

The grizzly bear is at the top of its food chain, and under primitive conditions has had few natural enemies, partially explaining the relatively low reproductive rate. In modern times, man has developed the capability of inflicting rapid and heavy mortality. There is no scientific evidence that the grizzly bear has the capacity to compensate for the high mortality rates inflicted by man. On the contrary, Craighead *et al.* (1974) have shown that the Yellowstone grizzly cannot sustain a high death rate for even a short period of time without critically lowering the population level. Any abnormal mortality such as undue control by man or excessive hunting, or both, should be viewed with concern because it can cause a rapid irreversible decline in population size. The historic decline of the grizzly bear in the western United States has probably resulted from the species' low reproductive rate and its inability to cope with man-induced mortality and drastic habitat changes. The grizzly has been able to survive only in large national parks and national forest wilderness areas where spacious habitats have, until recently, insulated the species from excessive mortality. If threatened with high mortality rates, the grizzly will face extinction just as surely as it did in California some 50 years ago.

Where mortality rates are known to be high (Yellowstone ecosystem) or are of uncertain status (Bob Marshall-Scapegoat Wilderness), we believe it would be prudent for game managers to apply the long-term average reproductive rates presented in this paper. To assume higher rates for other populations, in the absence of any other long-term scientific evidence, is to take unjustifiable risks with a threatened species.

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Telemetry Experiments with a Hibernating Black Bear

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INTRODUCTION

During the winter of 1966-67 the body temperature of a male black bear (*Ursus americanus*) was telemetered in winter sleep under natural denning conditions (Craighead *et al.* 1971). To improve equipment and techniques for studying the physiology and behavior of bears under natural conditions, a captive black bear was used to continue the investigations during the winter of 1971-72. This paper describes the experiments and the results.

Other investigators (Essler and Folk 1961; Folk *et al.* 1965, 1968, 1972; Hedge *et al.* 1965) have studied the physiology and hibernation behavior of captive bears under simulated natural conditions. Our own long-range objectives are to develop the means of obtaining ecological, behavioral and physiological data from unrestrained hibernating animals in the wild through the use of recent electronic and technological advances, including earth-orbiting satellites (Craighead *et al.* 1971).

The specific objectives of the work described here were to develop and test telemetry equipment suitable for monitoring a typical physiological parameter (body temperature) by satellite; to refine immobilizing and handling techniques; to visually observe a bear throughout the hibernation period and correlate its behavior with body and den temperatures; and to outline surgical techniques for implanting telemetry transmitters in the body of a wild black bear.

METHODS

Simulated den conditions

A male black bear cub approximately 8 months of age was obtained from the Montana State Fish and Game Department in October 1971, and on 11 November 1971 was placed in a concrete block building containing (1.8 x 2.4 x 2.4m) cells with no windows and steel mesh doors. An interconnecting doorway with a sliding gate permitted us to move the bear from one cell to another. Ambient light was reduced to a level simulating the interior of a den covered with snow.



Fig. 1 An infrared scope (shown here without the light-blocking drape) was used to observe the hibernating bear (Fig. 1A) without disturbing him.

Enough light entered around the door jambs for the animal to probably distinguish night from day much as he might from within a natural den. A 1 x 1 x 1.2 m wooden box was placed in one cell to provide an enclosure. Loose straw was put in the cell for bedding material. The bear constructed a bed by dragging straw into the box. Food and water were discontinued after 15 December when the bear became noticeably lethargic and was feeding irregularly.

Instrumentation

Detailed records were kept of the bear's activity and body temperature, the



Fig. 1A

den temperature, local barometric pressure, disturbances, and other factors which might influence hibernation behavior. Temperature in the den room was recorded using a Ryan Thermograph, a clockwork-driven chart recorder which provides a continuous record for 30-day periods. Temperature and relative humidity were also recorded with a Casella hydrothermograph placed 10 m from the den room. Having found no significant differences between the temperature records at the two sites, we removed the Ryan recorder from the den after the first month of operation to eliminate disturbances during the changes of charts.

The bear's body temperature was measured with a temperature-sensitive telemetry transmitter implanted in the abdominal cavity. Data from the transmitter were recorded by equipment near the den room. The recording equipment was designed to be compatible with a satellite data-collection system (the IRLS experiment on the Nimbus-3 satellite). Although it was possible to transmit our data via the satellite this was not attempted since we had earlier demonstrated the feasibility (Craighead *et al.* 1971).

Barometric pressure was obtained from daily Weather Bureau records. Variations over the short distance separating the den and the Missoula recording station were insignificant.

The bear was observed with the aid of an infrared weaponsight loaned to us by the Department of the Army (Fig. 1). The scope was mounted on a tripod and trained on the den box. A black cloth draped over the scope prevented light from entering the den during daytime observations. Observations were made daily to determine the animal's degree of lethargy, changes of position, and whether he had urinated or defecated.

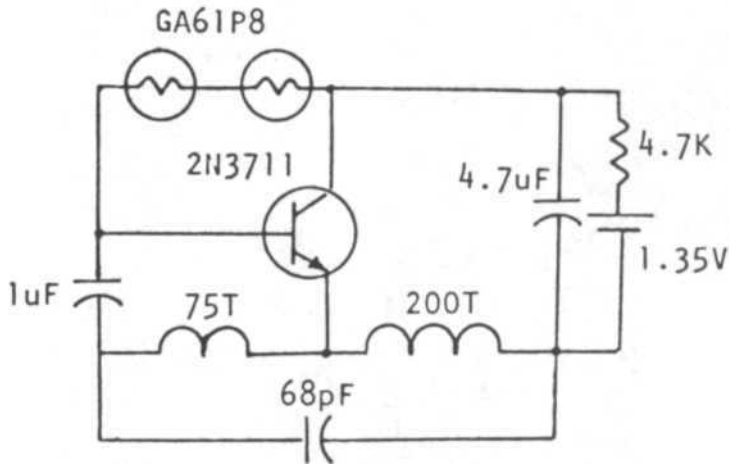


Fig. 2 Circuit for body temperature telemetry transmitter used on a hibernating black bear.

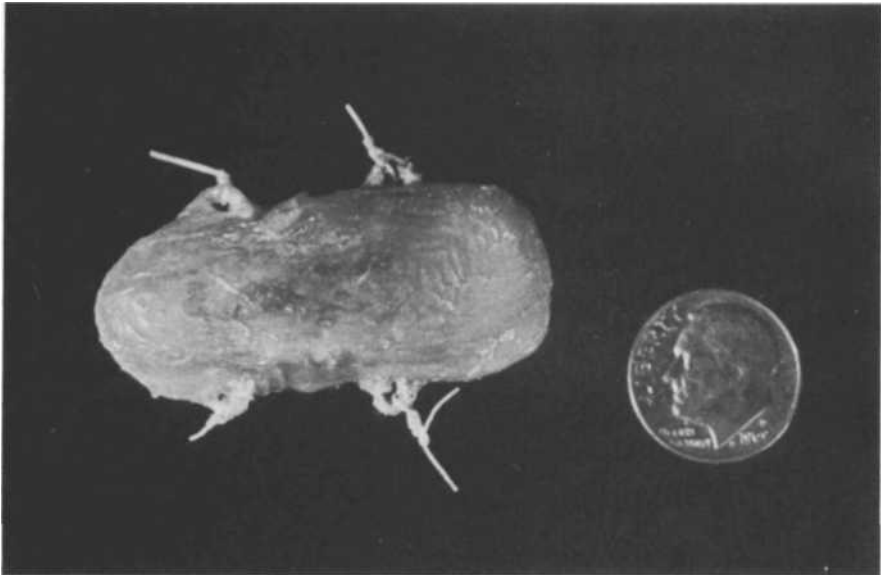


Fig. 3 Body temperature telemetry transmitter after removal from the bear in April. It was attached to the peritoneum with sutures to keep it in a known location.

Temperature transmitter

The circuit of the temperature-sensitive transmitter is a simple 1 MHz blocking oscillator with a pulse rate determined by two thermistors in the collector-base path (Fig. 2) and is similar in design to units used by Mackay (1970) and Goodman (1971). A Hg-625R cell provides an estimated lifetime of several years (at 37°C). Previous work with this transmitter had proven it to be reliable and accurate (Craighead *et al.* 1971).

Transmitter components were imbedded in epoxy for mechanical support and protection. The transmitter assembly was then waterproofed with a mixture of beeswax and paraffin. An outer covering of Dow-Corning Type-A Medical Silastic was used to prevent tissue reaction when implanted in the bear's body. The completed unit was 4.5 x 2 x 1 cm in size and weighed 12.8 g (Fig. 3).

The transmitter was calibrated in a constant temperature water bath and its thermal time constant measured by subjecting it to an abrupt temperature change of 10°C. The thermal time constant was found to be 1.3 minutes in well-stirred water. The temperature indicated by the transmitter in 4 time constants (5.2 minutes) was 98.2 percent of the final value. This is equivalent to an error of less than 0.2°C.

The transmitter was recalibrated in the water bath after removal from the bear. We found no measurable shift in the temperature calibration.

Body temperature recording equipment

Signals from the temperature transmitter in the bear's abdominal cavity were picked up by a circular loop antenna (14 turns of No. 24 wire, 50 cm in diameter) placed on the floor of the den directly under the bear's bed. The antenna was connected to a standard broadcast band receiver in an adjoining room by a 9 m cable. Pulses from the transmitter detected by the receiver were converted to direct current by a pulse rate converter (Varney 1974) and recorded on a Rustrak model 288 chart recorder at a chart speed of 2.5 cm per hour. A block diagram of the recording setup is shown in Fig. 4.

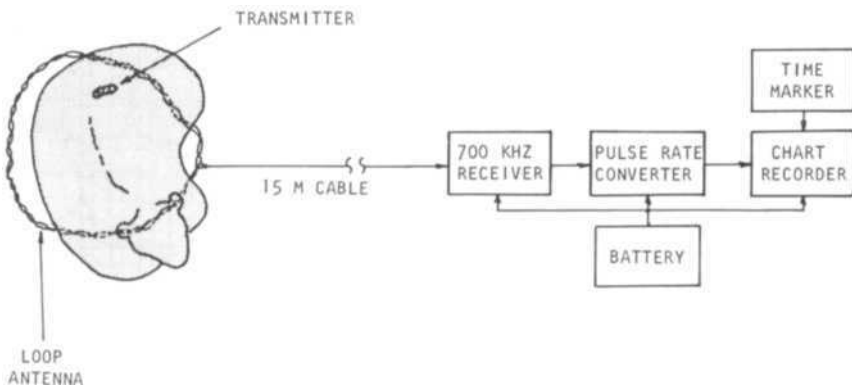


Fig. 4 Body temperature recording equipment used on a hibernating black bear.

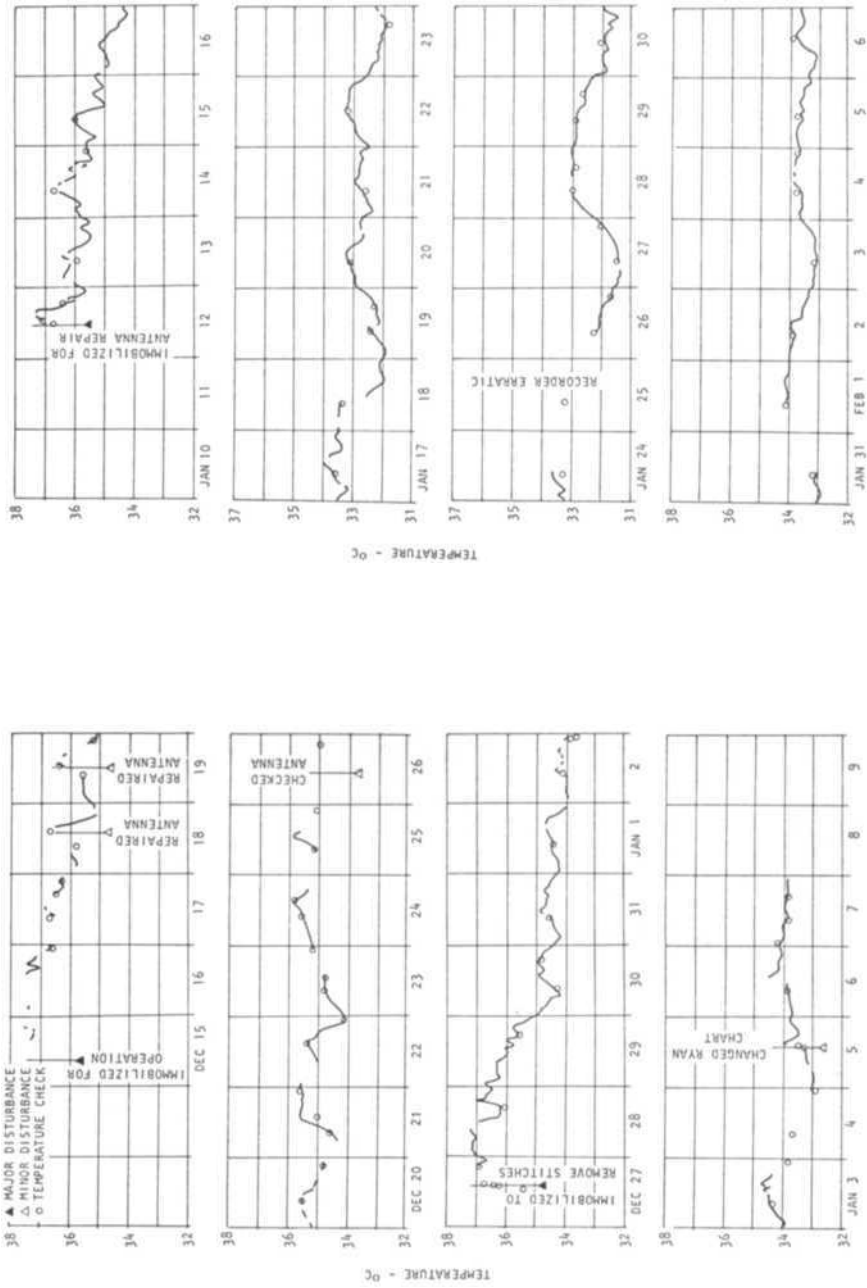


Fig. 5 Daily body temperature data of a hibernating black bear.

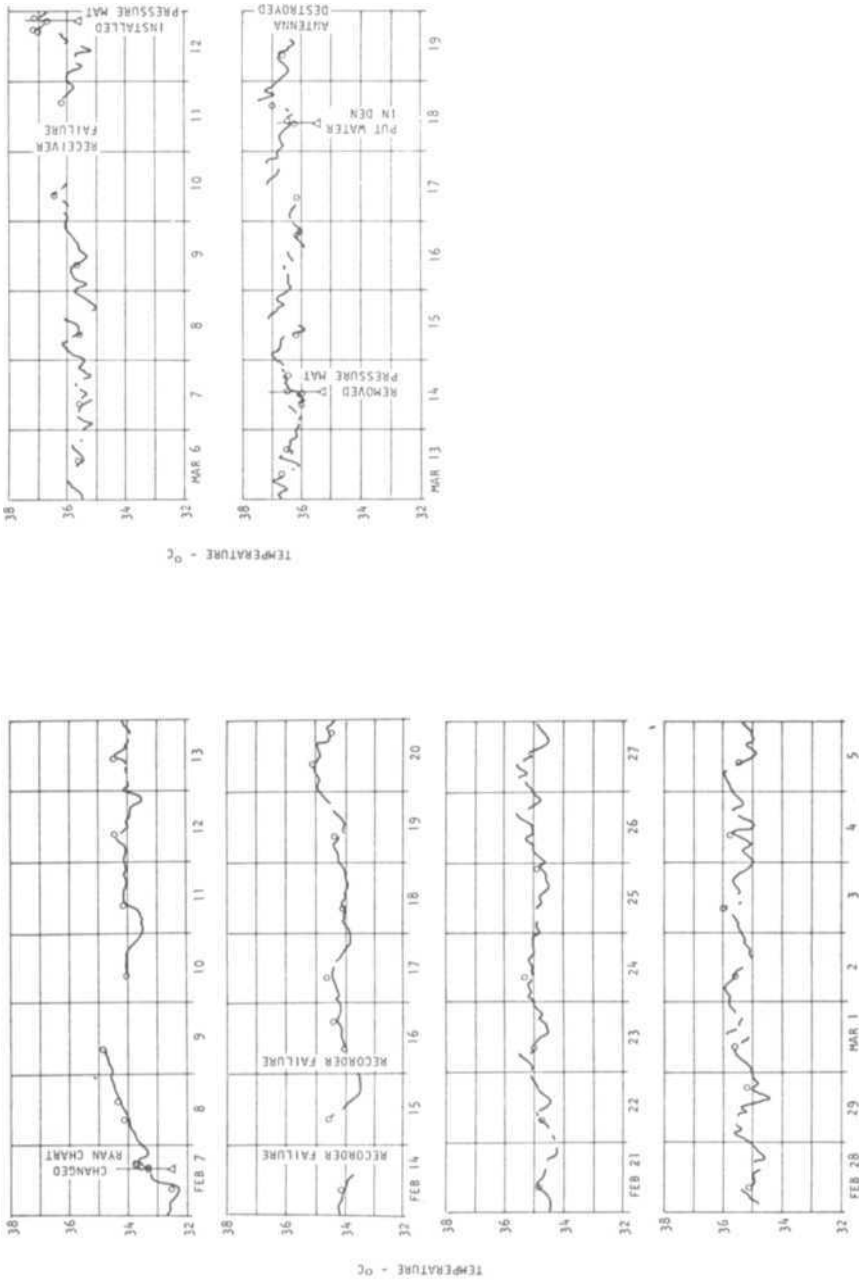


Fig. 5 Daily body temperature data (cont'd.).

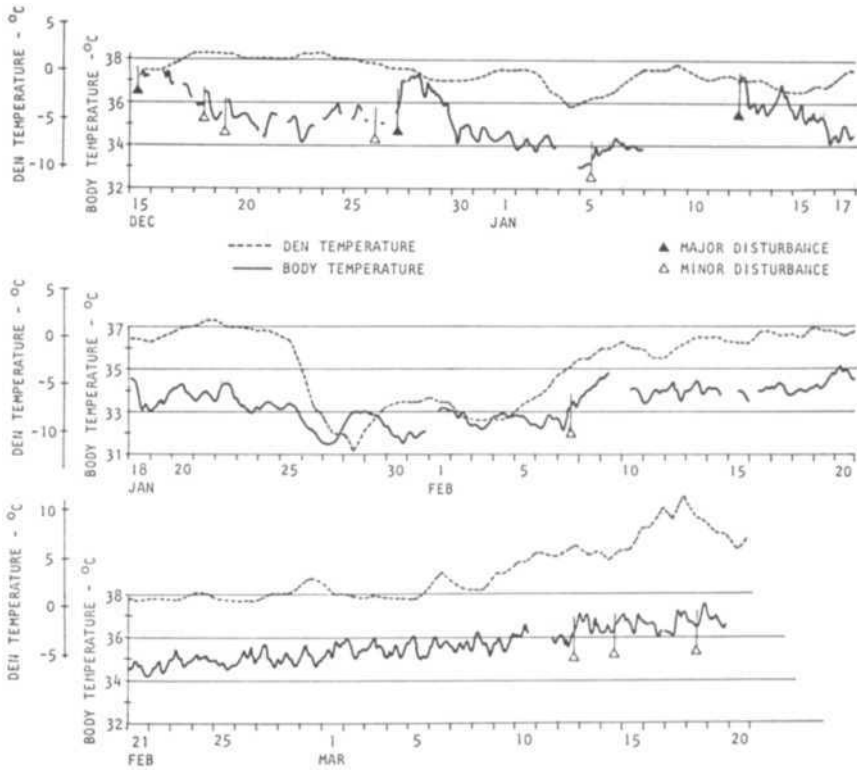


Fig. 6 Body temperature and ambient den temperature for a hibernating black bear.

Surgical procedures

We immobilized the bear to implant the temperature transmitter by firing a syringe dart containing 45 mg of phencyclidine hydrochloride (Sernylan) in a 100 mg/cc solution into the shoulder muscles. An additional 15 mg was administered after the dose took effect and the bear taken immediately to a local veterinary clinic for the operation.

The bear was placed in a slightly head-down position on the operating table to prevent saliva from blocking air passages. A 0.125 grain dose of atropine was given to reduce salivation. The belly was shaved with an electric clipper, washed, and disinfected. A 10 cm incision was made through the skin and fat along the midline from just below the umbilicus to 3 cm anterior to the penis. This location (the *linea alba*) was selected because it is relatively free of large blood vessels and would present fewer problems if field surgery were attempted.

An incision through the peritoneum into the abdominal cavity permitted placing of the transmitter (which had been sterilized overnight in Zephiran chloride [1 : 1000]) into the abdominal cavity. It was anchored to the peritoneum in four places with nylon sutures. The peritoneum was then sutured with chromic cat gut, Furacin powder sprinkled into the incision, and the skin sutured with heavy nylon. A 2 cc injection of penicillin-streptomycin was

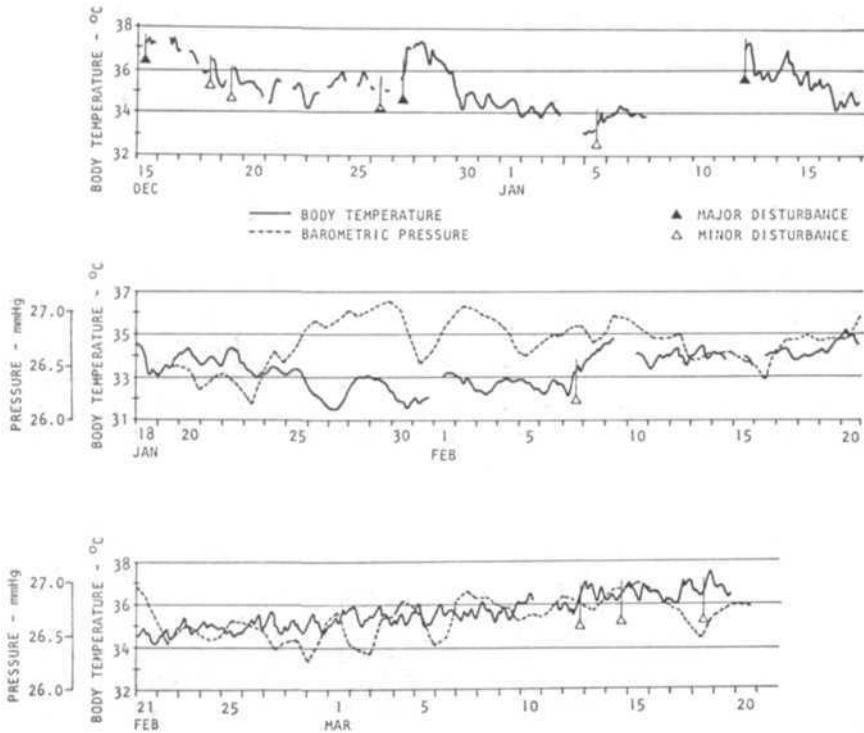


Fig. 7 Body temperature and barometric pressure recorded for a hibernating black bear.

given at the conclusion of the operation. The entire procedure took about 45 minutes.

We immobilized the bear 12 days later (27 December) to examine the incision and to remove the external stitches. Healing was normal, but a slight inflammation was present in the caudal portion of the incision. Topical application of Combiotic, combined with a 2 cc intramuscular injection, were used to combat the infection. The incision was checked again on 18 January and had completely healed. Regrowth of hair on the belly was slower than expected.

We followed the same operating procedure in removing the transmitter from the animal on 5 April. Examination of the peritoneum revealed that the transmitter had been encapsulated in a thin layer of scar tissue. We detected no adverse tissue reaction or inflammation.

Body temperature data

Temperature data from the implanted transmitter were recorded continuously for more than 3 months (Fig. 5). To check on the automatic recording system, we made manual counts of the transmitter pulse rate with a stop-watch during daily equipment checks. Some gaps occur in the data when the bear was out of his bed or oriented unfavorably to the receiving antenna; these occurred more frequently at the beginning and end of the hibernation period and provide an index of the animal's activity while entering into and emerging from deep

sleep. Data gaps due to equipment problems, rather than animal movements, are noted on the graph.

Disturbance to the bear such as anal temperature determinations and other procedures necessitating trespass into the den are also apparent on the graph. The same data in a more compressed form are plotted against den temperature in Fig. 6, and barometric pressure from 19 January to 20 March in Fig. 7.

Day-night rhythms

Diurnal changes in body temperature were not pronounced though they occasionally did occur for short periods (e.g. 30 Dec-2 Jan. and 20-22 Jan., Fig. 5). Such changes were on the order of 0.5 to 1°C. During other periods, they either did not occur at all or, if present, were obscured by larger trends due to other factors. Folk and Essler (1961) reported day-night body temperature rhythms of the black bear in captivity and Craighead and Craighead (1967) recorded similar results from a wild black bear in a natural den.

Responses to disturbances

The largest and most significant changes in body temperature occurred in response to disturbances, and varied relative to duration and intensity of the disturbance. On three occasions when the bear was immobilized, his temperature rose 2°C in a period of 2 hours.

When disturbances were less severe (for example, when we entered the den for a minute or two to change charts in the temperature recorder or to repair a disconnected leaf) temperature readings increased typically 0.5°C. Body temperatures behaved erratically, rising and/or falling for several days afterward.

Response to cold

Data from the period between 24 January and 10 February are particularly interesting (Fig. 6). A severe storm moved into the Missoula area with sub-zero temperatures and high winds. Accordingly, the temperature in the den began to drop on 25 January. The bear's temperature dropped as the den temperature declined. On 27 January the body temperature of the bear reached a low of 31.8°C, approaching the lowest temperatures reported in the literature (Hock 1957). Then, although den temperature continued to drop, body temperature rose abruptly to 33°C. This cycle was repeated between 30 January and 1 February. We suspect that a spontaneous arousal mechanism was operating, with 32°C being the lower limit the bear could safely tolerate; a metabolic increase ensued when this limit was approached. If this behavior is typical of all black bears and grizzlies, it may serve as an alternative to the regular periodic awakening that occurs in other mammalian hibernators, but which has not been demonstrated in bears.

In general, long-term body temperature trends followed variations in ambient temperatures. This is particularly evident in Fig. 6 for the period between 5 February and 20 March. A gradual increase in den temperature took place during that time and was accompanied by a 3°C increase in body temperature.

Influence of barometric pressure and relative humidity

We believe that variations in barometric pressure had little effect on temperature or activity of the bear but data were not conclusive. No correlation be-

tween body temperature and pressure is evident in Fig. 7 from 20 January to 20 February. There was a gradual increase in pressure from 21 February to March which was paralleled by a rise in body temperature, but this was probably due to increases in den temperature occurring during the same period rather than to pressure changes. Relative humidity data taken during the hibernation period did not appear significant.

Comparison of rectal and abdominal temperatures

On three occasions we took a series of rectal temperatures for comparison with the telemetered abdominal-temperature data. This was done during periods of immobilization when the sutures were removed on 27 December, when repairs were made to the den antenna on 12 January, and when the transmitter was removed on 5 April.

Rectal temperatures were taken with a glass-mercury thermometer inserted approximately 9 cm into the rectum. The thermometer was allowed to stabilize for 2 minutes after insertion before readings were taken. Abdominal readings were recorded by placing a portable radio beside the bear and timing the transmitter pulse rate with a stopwatch.

Rectal temperature readings ranged from 1.3°C below to 0.3°C above the abdominal readings (Fig. 8). Data are insufficient for generalizations, but

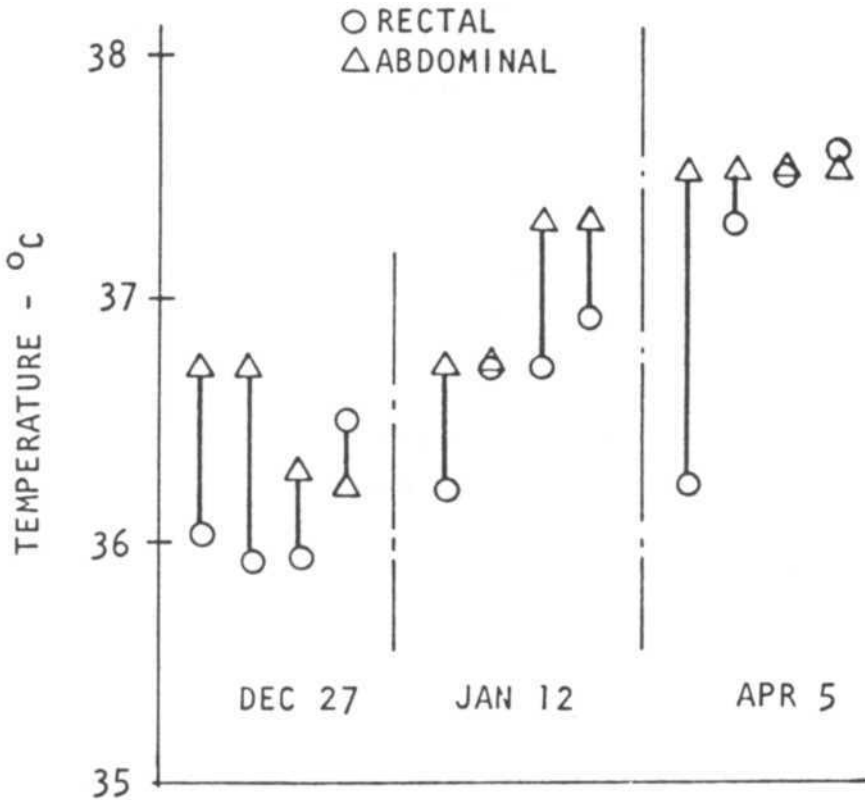


Fig. 8 Comparison of rectal and abdominal temperatures of a hibernating black bear.

give a rough idea of the variation to be expected between the two methods and permit evaluation and correlation of rectal temperature data obtained during previous field studies.

Weight loss during hibernation

The bear was weighed whenever possible during the experiment to determine rate of weight loss during hibernation (Fig. 9). The bear weighed 34 kg in November when placed in the den to acclimatize. Feeding was continued, and weight increased to 42.5 kg at the time of the implant operation on 15 December. Food and water were not offered after that time. The bear became dormant, and his weight declined gradually during the winter to a low of 30.8 kg when the temperature transmitter was removed on 5 April. This represents a weight loss of 11.7 kg or 27.5 percent. During the 112-day period from 15 December to 6 April, the average weight loss was 0.1 kg per day. Feeding was resumed on 7 April, and the bear's weight increased to 41 kg by 19 April. In 12 days the bear regained weight at an average rate of 0.85 kg per day.

A load-cell weighing system was evaluated for future use in more detailed studies of weight loss and metabolism. It consists of a reinforced plywood platform supported by three load cells which produce an output voltage proportional to the weight on them. They are connected to readout equipment that can be located at any desired distance. The system provides both a meter readout and a continuous chart record of the total weight on the platform. The platform is mechanically solid compared to a conventional spring or balance system, with downward deflection for a 45 kg load being only 0.76 mm. The system is accurate to within 0.5 percent of the full scale load

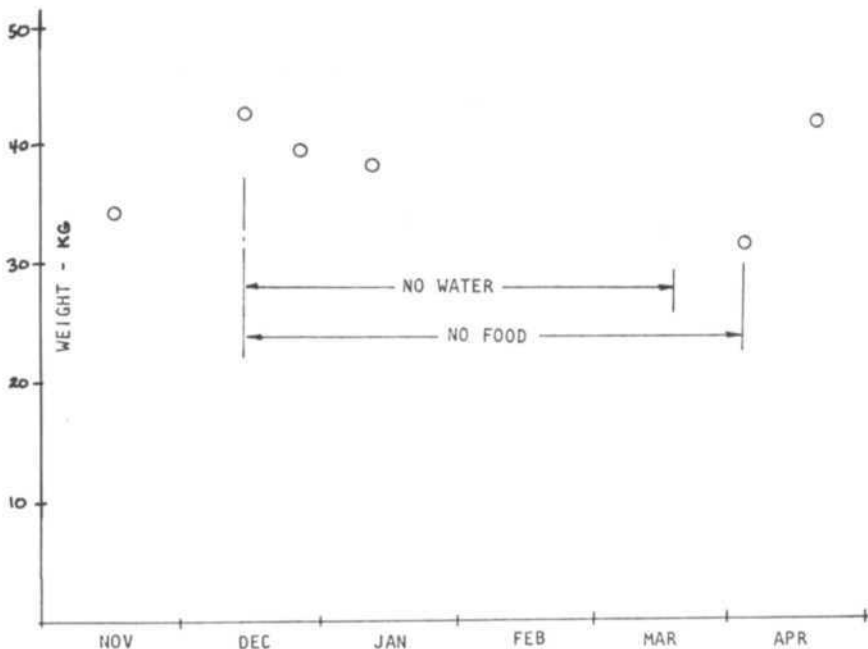


Fig. 9 Changes in weight of a hibernating black bear between November 1971 and April 1972.

of 45 kg, or 0.23 kg. Larger loads can be accommodated by using less sensitive load cells.

Tests of the weighing system were satisfactory and indicated that this technique holds promise for future studies. In further experiments with hibernating captive bears, a weighing platform could be placed beneath the bed to give an accurate, continuous record of weight loss during winter that would permit correlation of weight loss with temperature changes and metabolic increases during spontaneous arousal. Measurements could be made on a year-around basis by placing the platform where the bear would walk across it periodically. It could also be used to quantify activity at the beginning and end of the hibernation period by recording amount of time spent in the bed. It may be possible to use the system in the den of a wild hibernating bear, although construction of an unobtrusive platform and its installation in a natural den would pose problems.

Activity monitoring

In future experiments with wild bears in natural dens, it will be valuable to measure shifts of position and movements of the animal within the den. Information about such movements can be obtained with the temperature monitoring system used in this experiment. The range of the transmitter is limited to about 1 m, so data were not obtained when the bear was not lying in his bed directly over the loop antenna. An examination of the temperature record for signal dropouts gave a general indication of activity or inactivity of the bear. This was not foolproof, however, since signal loss can also occur when the transmitter is aligned orthogonally to the receiving antenna.

From observation with the infrared scope we concluded that the bear probably did not urinate or defecate during a period of 96 days, thus supporting Folk's conclusions (1972).

Release of bear

The bear gradually became less lethargic during March and began leaving its bed for short periods during the latter part of the month. On 19 March he located the antenna cable and disrupted transmission. Since the animal was nearly out of hibernation, we terminated the experiment and removed the temperature transmitter from the bear on 5 April.

The bear was immobilized again on 19 April to remove stitches from the abdominal incision. The temperature telemetry transmitter that had been removed earlier was inserted rectally and a continuous temperature recording was made for 2 hours to observe the effect of the immobilizing drug on temperature regulation. The indicated temperature remained nearly constant at 38.5°C. The bear was held until 15 June, then fitted with a radio-location collar and released.

DISCUSSION

While we attempted to simulate the natural conditions of hibernation in order to develop and improve our telemetry equipment and monitoring techniques, many factors differed from a completely natural situation and probably influenced the information obtained. Experience gained in temperature monitoring changed some of our initial ideas about den-monitoring methods and suggested new lines of development and investigation.

Implanting the temperature transmitter in the abdominal cavity would be a very ambitious undertaking under adverse field conditions in midwinter. We concluded that it would be preferable to conduct any necessary implant surgery early in the fall when it would be possible to capture a wild bear and hold it a few days for observation and recovery. This would reduce the risk to the animal and increase our confidence in the resulting data by providing a longer period between surgery and the beginning of hibernation. Before release, the bear would be fitted with a radio collar and radiotracked until it entered a den for winter. With the temperature transmitter already implanted there would be no need for surgery in the field.

If necessary, it is feasible to implant telemetering devices subcutaneously without attempting to enter the body cavity. Such surgery is relatively minor and has little effect on the animal even when done in midwinter. Temperatures obtained from a subcutaneous implant differ somewhat from deep body temperature recordings (Craighead *et al.* 1967), but differences can be minimized by selection of the proper location (near good blood supply and under a thick coat of fur or layer of fat). It should also be possible to obtain good EKG potentials from a subcutaneous implant by running leads under the skin for short distances from the transmitter.

The rapid rise in body temperature and changes in behavior of the bear in response to disturbances while in a lethargic condition, indicate that frequent visits to a natural den would disturb the animal and would influence results of behavioral or physiological monitoring. This was confirmed by earlier field experience. On all occasions when bear dens were visited and examined, the bears were alerted or partially aroused from lethargy by our presence. On five occasions bears emerged from the dens; one animal did not return. Therefore, instrumentation must be designed for unattended operation over long periods of time. Satellite monitoring has a distinct advantage in this respect.

Some bears emerge from their dens for short times during early spring. A time-lapse camera installed outside a den and triggered when the bear moved away from a proximity detector inside the den, would photograph the bear at intervals revealing early post-hibernation behavior.

Heart rate may provide a better measure of lethargy and response to disturbance than body temperature. However, measurements of body temperature and their relationship to ambient den temperatures and heat conservation mechanisms under natural conditions are basic to a thorough understanding of how bears hibernate. The fact that the bear exhibits minor drops in body temperature compared to other hibernators, arouses quickly when disturbed, and spontaneously in response to low ambient temperatures, becomes active enough to leave a den or defend itself, and can quickly regain body weight following winter sleep, all suggest the bear has evolved a highly efficient hibernating mechanism. It will require sophisticated electronic monitoring equipment to precisely record the hibernating process under natural conditions of denning. We believe this can be best accomplished using satellite technology.

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assisted throughout the project in handling and maintaining the bears, and in radio-tracking them after release. Dr. B.W. O'Gara provided us with assistance in caring for the bears, the implant surgery was done by Conrad Orr, DVM, and John Mitchell made many helpful suggestions.

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Physiology of Hibernating Bears

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INTRODUCTION

This paper will consider the technique of physiological measurements in bears during their 'winter-sleep'; it will consider whether the term hibernation is justified in the case of bears; and it will review experiments showing the physiological changes in hibernating bears. We have also taken the opportunity to review all conspicuous papers on any aspect of physiology of bears; it is significant that these could be listed on about one page of this paper. Much more attention should be given to the unique physiological mechanisms of bears by experimental physiologists.

METHODS

In a previous report, the proof of a small reduction in body temperature and a large reduction in heart rate of bears during 'winter-sleep' has been presented (Folk *et al.* 1972). Eight bears were instrumented with the implanted Iowa radio-capsules originally designed by Professor Warren O. Essler; this equipment was described earlier (Folk & Copping 1973). The series consisted of two polar bears, three black bears and three grizzly bears. Several of these animals were instrumented three or four times during their lifetimes. The small reduction in body temperature during the many months of 'winter-sleep' of bears amounts to a decrease of no more than 5°C. Our attention has been devoted to the more interesting cardiovascular adjustment. Gradually, over a period of two to four weeks, the sleeping heart rate of the bear becomes lower and lower, changing from a summer heart rate of 54 bpm in young bears to a winter sleeping level of 24 bpm (a reduction to 43 per cent of summer rate), and in older bears from a summer sleeping heart rate of 40 bpm down to 10 or 8 bpm (a reduction to 25 per cent of summer rates). In our initial experiments, the long life, short-range transmitters usually had a life of only six months. This meant that transmitters placed in the summer would have a battery which would become depleted during the bear's dormancy period in the winter. Because of this condition in the implanted transmitter, some investigators have asked us whether the low heart rates attained were due to the change in the mercury battery of the transmitter during the last month of its activity. We have never carefully explained in the literature that this is by no means the case. For the following reasons, it can be categorically stated that low heart rates in bears in winter are always accurately recorded with the Iowa transmitter up to within one day of the cessation of the life of the transmitter. In the

first place, the circuit was carefully planned by Professor Warren Essler so that there was no diminution in signal from the transmitter near the end of the battery life; the battery was selected to represent an all-or-none situation. Secondly, an inherent characteristic of the circuit is a marked change in frequency in the last 24 hours of the life of the battery. In every instance, we have observed this change in frequency followed by cessation of signal from the animal within 24 hours. For example, the actual tuning on the classic ARC-5 receiver may be as follows: using the audio-speaker or a recorder, the heart rate is obtained by tuning to a frequency between 294 kHz and 298 kHz. In the middle of this range there is a null point that does not give a signal. Using the same receiver with all conditions being the same, we could listen to or record the heart rate of a bear for as long as two years at this same frequency. Furthermore, in other types of hibernators such as woodchucks, rates of 7 bpm changing within a few hours to 300 bpm, are always faithfully recorded. However, on a particular day, at the end of the lifetime of the circuit, we would find the transmitter functioning at a level 10 kHz lower. Always within 24 hours of such an event, the circuit would be dead due to depletion of the mercury battery. On several occasions, bears in winter sleep were aroused and normal heart beats were recorded. Usually this was not intentionally done, simply be-

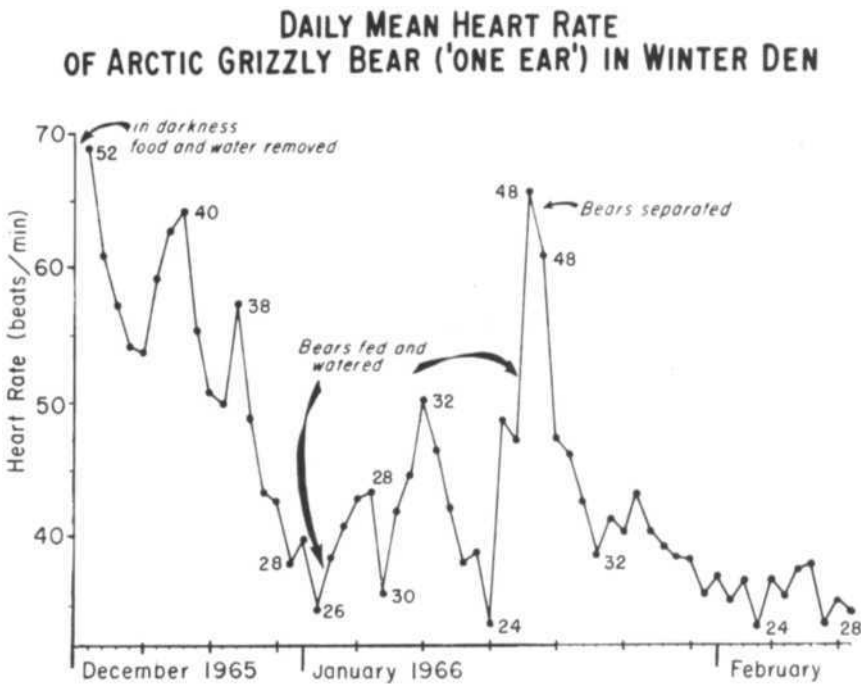


Fig. 1 Daily mean heart rate and lowest sleeping heart rate of arctic grizzly bear (One Ear) in winter den. The figures on graph are sleeping heart rates. In this experiment there was no attempt to keep the bear quiet and unfed until 17 December. Its sleeping heart rate had been about 52 bpm. When darkness, cold temperatures, quiet conditions were provided, its sleeping heart rate was reduced to 24 bpm. When disturbed, summer sleeping heart rates were again recorded during the night-time period.

cause it seemed valuable and even unusual to even get bears to go into deep winter sleep and we were reluctant to disturb them. One of several examples is here presented (Fig. 1). Recordings were made on a two-year-old grizzly during the summer and winter. The summer sleeping heart rate and the heart rate during 'winter-sleep' are relatively high in two-year-old animals; this could be predicted since in the natural state, two-year-old grizzlies usually are with the mother and will probably be nursing during 'winter-sleep'; at least Murie (1963, p. 38) observed sows nursing the same young in the fall and the following spring. In the particular case presented in this illustration, the heart rate during summer sleep was 56 bpm. Gradually over a period of five weeks, the heart rate of the animal (kept without food and water) reduced to 24 bpm. The animal was in the care of an Eskimo guide and naturalist, Pete Sovolic; because of lack of information about physiology of hibernation, he became alarmed that the two grizzly bears might starve to death (only one was instrumented). At this point he fed and watered the animals. Presumably they both ate and drank, and they resumed summer heart rates both during sleep and activity. However, no more food and water were given to them during the winter, and within a few weeks the instrumented animal again was showing a heart rate of 24 bpm. The above proof of a physiological reduction in heart rate followed by summer types of heart rates was also demonstrated with polar bears (Folk *et al.* 1972). In summary, we can say definitively that a heart rate during winter sleep of 10 bpm recorded again and again by our equipment over a month's time represents exactly and precisely the physiological condition of the heart of the bear.

DOES THE TERM 'HIBERNATION'¹ APPLY TO BEARS?

There is some value in comparing in detail the winter dormancy of small, typical mammalian hibernators with the condition found in bears. The first comparison concerns the initial stages of going into dormancy. The small mammalian hibernator does this rapidly and does not even need to be cold-acclimated in order to accomplish this physiological change (Folk 1974, p. 302). Bears, on the other hand, take at least two weeks to change their physiological condition (Folk *et al.* 1972).

Next consider the condition of the small mammalian hibernator over a four-month period of cold exposure. Early naturalists observing this hibernator in a free environment or in the laboratory might have repeatedly observed 'complete dormancy in a tight rolled-up position' for many weeks at a time. Because of lack of electronic recordings, the impression at first was created that the animals remained dormant for several months. This is by no means the case. As far as we know, all small mammal hibernators repeatedly become normothermic and active every few days; 13-lined ground squirrels become active, on the average, every four days; a few will remain dormant with a body temperature of about 5°C for as long as 10 days. What do these small mammalian hibernators do when they become normothermic? Although there are hundreds of investigators of mammalian hibernation at this time in the history of biology, there is an incredible lack of information as to what physiological events take place in between the bouts of dormancy. Accordingly, an experiment is presented here to specifically answer this question in the case of two species of dormice. The procedure was quite simple: in a double-door refrigerator with complete air circulation, maintained at 5° ± 1°C, the animals were maintained all winter in large cages with open mesh bottoms. Each of three dormice hibernated in a small mass of cotton in one corner of its cage.

Fresh carrots and rat chow were provided on the other side of the cage. Fresh white paper was changed daily under the cage. Over each animal in dormancy there was placed a few thin strips of tissue paper and flakes of sawdust. We have previously determined in our laboratory, and other investigators have shown, that when small mammalian hibernators awake from dormancy and become active, they always clean these indicators from their fur. The results were consistent: deposition of feces and urine and feeding took place regularly between bouts of hibernation (Table 1). For example, the specimen of *Glis glis* awoke approximately every three days (on one occasion after nine days). On every occasion except one, he deposited feces, urinated and ate. The only exception was that in one case he did not deposit urine.

TABLE 1. PHYSIOLOGICAL ACTIVITY BETWEEN BOUTS OF HIBERNATION IN DORMICE

	Length of Bout		No. of Bouts	Present Between Bouts:		
	Mean	(Range)		Feces	Urine	Feeding
Edible Dormouse <i>Glis glis</i>	3	(2-9) days	17	16	15	16
Garden Dormouse <i>Eliomys quercinus</i>	(1) 4	(2-10) days	15	13	14	14
	(2) 3	(2-6) days	4	3	3	3

Let us compare this situation with bears. We had a unique opportunity to do the same sort of experiment with two two-year-old polar bears, one adult black bear, and one four-year-old grizzly bear. In each case the animals were recorded in deep 'winter-sleep' for at least one month and in one case for 4.5 months; this means that they assumed the typical position of 'winter-sleep' in a curled-up position with the top of the skull pressed against the bedding and the nose near the tail. These observations were made by having an electric light bulb in each cage with rheostat outside. The black bear and the grizzly bear were observed with through-the-door lenses as used in some apartment houses. The polar bears were observed by closed circuit television. We do not have proof that the three species of bears remained in the curled-up position for one to four months, but on no occasion were they seen to be walking around the cages or away from their place of bedding down. During about 50 per cent of the observations, the bears would raise their heads when a dim light was turned up gradually. Much more attention should be paid to such experiments. We consider it possible that in similar experiments, it might be demonstrated that a bear in 'winter-sleep' does not change his position for several months; this introduces the question of how the animal avoids cramped muscles and continues circulation to tissues of the limbs.

The remarkable condition of these bears under these circumstances is not the long period of time they remain in the 'nest' but the fact that we obtained evidence of the lack of urination or defecation for at least a 4.5 month period. At the end of all experiments, which were begun with absolutely clean cages, we examined all surfaces, took apart all bedding and found that there was no urine or feces present. Because the temperature was well below freezing, the urine would have been preserved. When the grizzly bear was taken out of winter sleep which had lasted 4.5 months, he was placed in a cage with a heavy mesh bottom under which there was a plastic sheet to collect urine. The animal still did not urinate for two days (Table 2). Other investigators have demonstrated that for even longer periods than this 4.5 months, bears in winter sleep

do not defecate, urinate, drink or eat even when food and water is available. Thus we see the remarkable difference between small mammal hibernation and the hibernation of the bear.

TABLE 2. URINE VOLUMES OF BEAR AFTER HIBERNATION.

Dates	Time	Volumes	Type of Sample	Comment
Nov.14- April 4	—	No urination	—	In hibernation
April 5	8:00 am	No urination	—	Moved from den
April 6	—	No urination	—	—
April 7	10:30 am	160 ml	—	1st urination, 4.5 mos.
April 7	4:00 pm	21 ml	24 hour (181 ml)	Moved to large enclosure
April 17	3:00 pm	116 ml	single emptying	Analyzed
April 27	2:00 pm	140 ml	single emptying	Analyzed
June 10	—	2010 ml	24-hour	Not analyzed
July 15	—	2080 ml	24-hour	Analyzed

We must also realize that in the case of the bear, there may be shunting of blood so that some compartments receive little blood flow. This is consistent with the observation by Hock (1966c) that the oxygen consumption of bears is reduced by 50 per cent during winter sleep. We suggest that a comparison can be made between the reduction of heart rate during the diving of marine mammals, and the winter sleep of bears. The same advantage which diving mammals find in a reduced heart rate may be applicable to the bear in winter sleep; we say it is possible that the bear may 'dive' into hibernation in the winter (Anschuetz 1971; Folk *et al.* 1973), making itself into a 'heart-lung-brain preparation'.

Although it is generally assumed that bears can quickly reach an active state when stimulated during 'winter-sleep', there is one known case observed by Wakefield (1974, pers. comm.) in Pennsylvania where a black bear was found in 'winter-sleep' above ground. Several men surrounded the bear and prodded it, and for 20 minutes it did not even raise its head. Eventually it did become active and ran away rapidly.

It should be pointed out that renal and digestive activity in denning bears is reduced greatly. We can say in humor, that at least these two organ systems are more 'in hibernation' than is the case with small mammalian hibernators. Assessing the entire picture of the condition of dormancy of the bear in mid-winter, we would like to propose that there is really no conspicuous reason not to apply the term 'hibernation' to bears as well as small mammalian hibernators. Bears are unusually well adapted as they *stay* dormant and do not consume or eliminate.

PHYSIOLOGICAL CHANGES IN HIBERNATING BEARS

Many blood samples have been taken by Nelson (1973) and his team from black

bears in hibernation, but under anesthesia. They demonstrated that because the bear does not urinate, metabolic water from fat is produced in sufficient quantities to satisfy water needs. Throughout the winter, the water content of plasma and of red blood cells remains constant. The bear does not produce those products of protein metabolism that require urinary excretion. The animal relies on body fat stores so that lean-body mass apparently remains constant. The blood concentration of total protein, urea and uric acid remains unchanged throughout the winter; as may be expected, however, creatinine concentration increases more than two-fold during hibernation. Nelson's team found no evidence of intestinal storage of nitrogen produced from protein catabolism. They also proved that urea is formed but the cycle of urea metabolism functions so as to recycle nitrogen back into the body pool (Nelson *et al.* 1975). The animal would not be able to tolerate the condition of a continuous net amount of urea produced each day.

In one experiment we were able to collect urine samples from the grizzly bear mentioned above after 4.5 months of deep hibernation. After removal from the den, the animal was maintained on a heavy grill over plastic sheeting. The animal and the plastic were hosed down and then drenched with large volumes of distilled water. An observer remained beside the cage at all times of the day and night. If the animal defecated, the hosing and distilled water treatment was repeated. When the animal urinated, the sample was collected from the plastic funnel and immediately frozen. By this means, all 'first' samples after hibernation were collected, and two control samples after the animal had been fed. The analyses of these urine samples confirm in the grizzly bear the observation made by analysis of blood by Nelson *et al.* (1973). The urea from a 4.5 month bladder filling during hibernation was only one gram, compared with 55 grams from a 24 hour control sample (Table 3). Our results also confirm those of D.C. Brown *et al.* (1971). However, the samples collected by both Nelson and by Brown were obtained from anaesthetized bears.

TABLE 3. ANALYSES OF HIBERNATING AND CONTROL URINE SAMPLES FROM FOUR-YEAR-OLD GRIZZLY BEAR.

	Hibernating	Control
Time of bladder filling	4.5 months	24 hours
Volume	181 ml	2080 ml
Total nitrogen	1.43 gm	34.00 gm
Urea	0.98 gm	55.05 gm
Ammonia	72.20 mg	1785.00 mg

What is the weight loss during hibernation? Some of our bears lost 27 per cent of their body weight during hibernation, whereas some other authors have indicated that their specimens lost only 15 per cent. Note that Nelson *et al.* (1973) stated that the loss of weight is merely from body fat stores and that there is no loss in lean-body mass. It should be recognized that the lactating bear in winter represents a special case; Nelson has explained some of the details of this physiological challenge (1971).

SUMMARY

It has been an accepted premise by some biologists that the three species of North American bears (polar, black and grizzly) do not experience mammalian hibernation. The conclusion of this paper, based upon an eight-year study of bears, is exactly the opposite. We believe that the hibernation observed in bears is an example which in the evolutionary sense is more perfected than that of small mammals; furthermore bears maintain their modified state for a much longer period than is the case with any other mammal.

ACKNOWLEDGEMENTS

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Reproductive Biology of Female Brown Bears (*Ursus arctos*), McNeil River, Alaska

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INTRODUCTION

Brown bears *Ursus arctos* congregate in Alaska's McNeil River State Game Sanctuary in July and early August to feed on salmon (*Oncorhynchus* spp.) traveling up rivers to spawn. The area has been closed to brown bear hunting since 1955, and in 1967 it received permanent protection by the Alaska State Legislature as a sanctuary for study and observation of brown bears. Because bear hunting is prohibited in the sanctuary and is infrequent in surrounding areas, bears of McNeil River form a virtually un hunted population. The area is well known for its concentration of bears, and the Alaska Department of Fish and Game limits by permit the number of photographers and observers that can enter it at one time. There are no roads or settlements in the area, and it can be reached only by aircraft and boat.

The Alaska Department of Fish and Game has captured, marked and observed brown bears at McNeil River in most years since a study emphasizing reproductive biology was started in 1963. Information has also been obtained on population composition, food habits, effects of human activity in the sanctuary on bears, and methods for capturing and handling animals. Emphasis of future studies will be to observe marked females to obtain more reproductive data.

STUDY AREA

The McNeil River State Game Sanctuary includes 185 km² on the lower west side of Cook Inlet at the base of the Alaska Peninsula (Fig. 1). The area is characterized by precipitous mountains; short, swift streams; and a narrow coastal plain. Most mountains are less than 1,200 m above sea level with upper elevations consisting of glaciers and snow, bare rock, and alpine plant communities. Alders (*Alnus* spp.), the dominant vegetation between 300 m and sea levels, are interspersed with grasses, forbs and tundra. Extensive grass and sedge flats occur near salt water.

McNeil River, the major drainage, originates from an unnamed glacier and

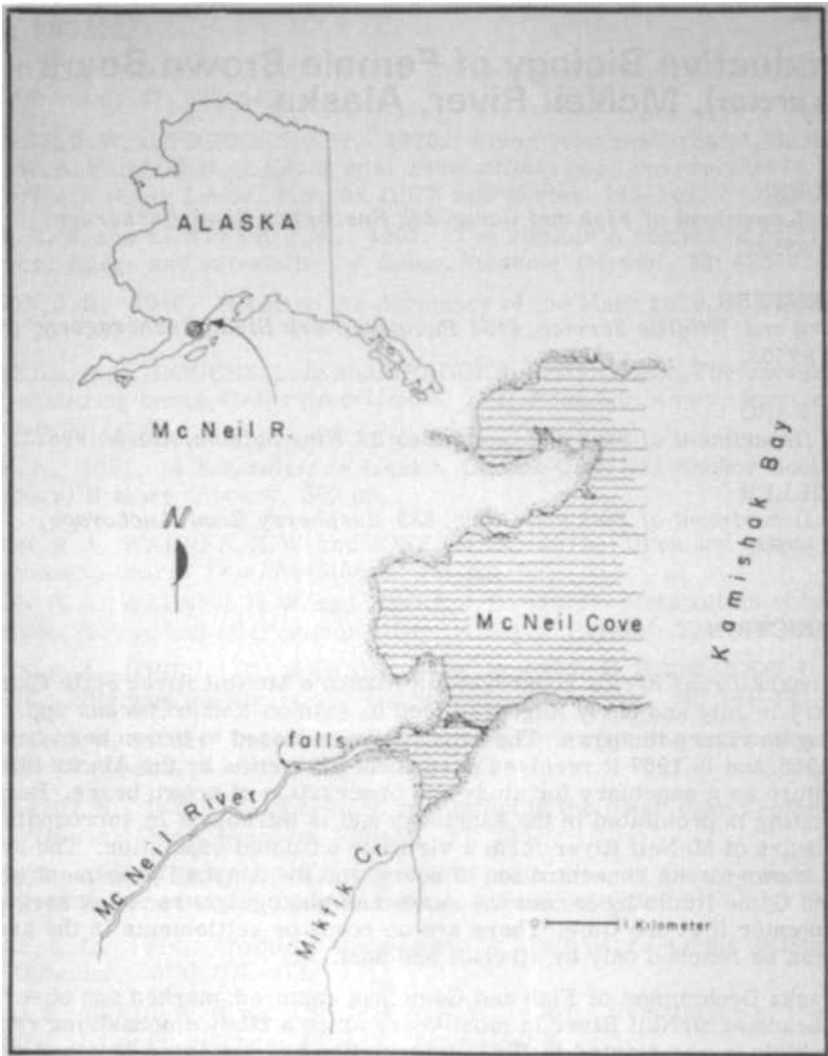


Fig. 1 Map of McNeil River and Alaska location map.

flows 34 km to the intertidal McNeil Lagoon. McNeil Lake drains into the river about 18 km above its mouth. The river flows over a series of boulders 1.8 km upstream from McNeil Lagoon to form McNeil Falls, a 100 m long section of turbulent water which is a partial obstacle to migrating salmon. Bears congregate here to capture primarily chum salmon (*Oncorhynchus keta*) and occasionally silver salmon (*O. kisutch*). Mikfik Creek, also part of the study area, flows about 3 km to McNeil Lagoon. In some years bears feed on chum, red (*O. nerka*) and pink (*O. gorbuscha*), salmon in Mikfik Creek.

METHODS

Bears were captured when free-ranging by injecting immobilizing drugs intra-

muscularly with projectile syringe guns. The first drugs used were succinylcholine chloride (Anectine) as an immobilizing agent and pentobarbital sodium an anesthetic (Lentfer *et al.* 1967). In recent years bears were more satisfactorily immobilized with 1.65 mg/kg of phencyclidine hydrochloride (Sernylan), mixed with 50-100 mg of promazine (Tranvet or Sparine) to counteract undesirable side effects of phencyclidine (Seal and Erickson 1969).

Bears were marked with ear tags and numbers tattooed on the inner lip and groin. To facilitate field identification of individuals, nylon flagging and polypropylene rope markers were attached to ears with ear tags, and nylon collars were placed on some adults.

Females with swollen and turgid vulvas were considered to be in estrus, and those with dark mammae larger than 10 mm in diameter and length as having suckled young. A rudimentary premolar was taken from bears older than known age cubs and sectioned to estimate age (Mundy and Fuller 1964; Craighead *et al.* 1970; Willey, 1974).

From 1963 through 1972, 60 individual animals were immobilized a total of 102 times. Marked animals not recaptured were often identified by examining collars and ear markers and tags with binoculars and spotting scopes.

RESULTS

Breeding Season

Observations, starting usually the first week in July, were too late to determine the start of breeding. The latest that males were observed following females in estrus was 10 August.

Minimum Breeding Age

Five (Identification Nos. 03, 905, 57, 124, 1814) of eleven 3.5-year-old females captured had swollen vulvas indicating physiological changes related to the estrous cycle (Tables 1 and 2). Observations during the 2 years following capture indicated that none of these five females was accompanied by young that could have been conceived when the females were 3.5 years old. Among eight 4- to 7-year-old females, three (03, 905, 05) conceived for the first time when 4.5 years old; three (17, 57, 1803) conceived for the first time when 5.5 years old; one (126) conceived for the first time when 6.5 years old; and one (13) conceived for the first time when 7.5 years old. Mammae characteristics suggested that two other females (19A, 124) conceived for the first time when 4.5 years old.

Maximum Breeding Age

The oldest female with cubs (No. 14) conceived in 1971 when 14.5 years old (Tables 1 and 2). Her maximum breeding age can be determined only by observations in future years. Female No. 22 had nursed young previously when captured or observed each of the following 6 summers.

Family Breakup and Frequency of Litters

Thirteen litters of brown bears at McNeil River provided definitive information on age at which young separated from females. For three litters, young

13.5	O-IE	O-WOY	O-MS	O-WOY	C-WY	-WC	O-WOY
14.5	O-WOS	-	O-WC	-	O-MS	O-WY	
15.5				O-WC	-		
16.5				O-WY			** C-WOY
17.5				O-WOY			C-IE
18.5							O-WOY
19.5							O-WOY
20.5							C-WOY
21.5							C-WOY
22.5							O-WOY

C = Captured.

O = Observed.

- = Not observed.

IE = In estrus.

N = Not in estrus.

WOY = Without young.

MS = Mated successfully resulting in a litter the following year.

FL = First litter.

WC = With cubs.

WY = With yearlings.

W2Y = With 2-year-olds.

* = Estimated age.

** = Condition of mammae indicates female had whelped previously.

TABLE 2. REPRODUCTIVE SUCCESS OF KNOWN AND ESTABLISHED AGE MCNEIL RIVER BROWN BEARS.

Age	No. of Females Mating Successfully	No. of Females not Mating or not Mating Successfully*	Sample Size
2.5	0	16	16
3.5	0	15	15
4.5	5**	10	15
5.5	3	5	8
6.5	3	4	7
7.5	6	0	6
8.5	1	0	1
9.5	2	1	2
10.5	3	2	5
11.5	1	2	3
12.5	1	3	4
13.5	1	3	4
14.5	1	1	2
15.5	0	0	0
16.5	0	1	1
17.5	0	2	2
18.5	0	1	1
19.5	0	1	1
20.5	0	1	1
21.5	0	1	1
22.5	0	1	1

* Females with cubs or yearlings not included in these figures.

** Includes 2 females which probably bred successfully based on condition of mammae.

accompanied females at 0.5 year but not at 1.5 years; for nine litters, young accompanied females at 1.5 years but not at 2.5 years; and for one litter, young accompanied the female through 2.5 years of age. In five other cases, 1.5-year-olds were with females but observations were not made the next year to determine if family breakup had yet occurred. It was not possible to determine the fate of young after family breakup because most were not marked and therefore could not be identified in later years.

For twelve observations of intervals between successful breeding, one was 2 years, seven were 3 years, two were 4 years, and two were 6 years.

Litter Size, Mortality, and Mixing

Mean size and range of 41 litters of cubs observed at McNeil River were 2.5 and 1-4 respectively. Mean size and range of 69 litters 1.5 years old and older were 1.8 and 1-4. This was a 13 percent reduction in litter size from cubs to older litters. Observations of thirteen litters 2 consecutive years provided a direct measure of loss of young between 0.5 and 1.5 years. Mean litter size of 2.0 cubs (26 cubs/13 females) decreased to 1.23 yearlings (16 yearlings/13 females), a 38 percent reduction in litter size from 0.5 to 1.5 years of age.

Three instances of cub loss were observed. In one instance a female with three cubs was carrying a salmon from the river to an alder patch on higher ground. One cub in the lead took a different trail than the others and was not seen again. The female was later seen with the other cubs and never appeared to be searching for the third cub. In another instance three cubs became separated from their mother when she was attempting to drive off a large male. She found one cub immediately and another 3 days later. After a week, she still had only the two cubs. No other females were observed with an extra cub. In the third instance a dead cub was found at a feeding area with a large wound on the ventral portion of the neck, apparently inflicted by another bear.

Exchange of cubs among different maternal females was observed. In 1974 three females, each with three cubs were first observed, came together and changed litter complements almost daily. There were times, however, when a group remained together for as long as 2 days. When cub interchange was first observed, females appeared to be under stress. In one instance, a female tried to stop the litter with her from leaving with another family group. She managed to keep one cub by grasping it in her mouth and tossing it down a hill. As the summer progressed and cub interchange continued, the females appeared to accept litter mixing as a normal activity. Each female was never observed with less than one or more than six cubs at one time. There was one observation of a female nursing six cubs. Mixing of litters continued to the end of the field season, and it was not possible to determine the final status of each family group.

Sibling Breakup

Two male siblings were inseparable the summer they were marked as 1.5-year-olds after they had separated from their mother. The next summer they were nearly independent of one another and only occasionally associated for short periods. The bears were completely independent of one another the following two summers when 3.5 and 4.5 years old.

Three marked female siblings remained together as yearlings and 2.5-year-olds, with one individual dominant at 2.5 years. This animal only occasionally associated with the other two when they were 3.5 years old and never during the following summer. The other two only occasionally associated when they were 4.5 years old and did not associate when 5.5 years old.

DISCUSSION

Breeding by brown bears at McNeil River probably starts about the same time as at Kodiak Island, Alaska, where breeding activity has been observed from the last half of May through mid-July (Hensel *et al.* 1969). Breeding activity has been observed later (10 August) at McNeil River than elsewhere. Craighead *et al.* (1969) state that grizzly bears in Yellowstone National Park, Wyoming,

mate from 26 May to 9 July. Mundy and Flook (1973) report breeding activity of grizzly bear in Canadian mountain parks from 30 April to 25 June. Pearson (1972) states that grizzly bears in southwestern Yukon Territory, Canada, breed from mid-June until late July.

Brown bears at McNeil River most commonly conceived for the first time when 4.5 and 5.5 years old. The oldest age at first breeding was 7.5 years. Age of sexual maturity for female brown bears is reported as 3-6 years on Kodiak Island (Hensel *et al.* 1969), 4-5 years in Yellowstone Park (Craighead *et al.* 1969), and 7 years in the Yukon Territory (Pearson 1972).

The oldest McNeil River female observed with young conceived in 1971 when 14 years old and could have conceived again in 1974. Other older females can also be identified, and maximum breeding age observations will continue in future years. On Kodiak Island a 16.5-year-old female brown bear conceived. She and her two 1-year-old cubs were in poor condition when killed at a garbage dump in January (unpublished data, Alaska Department of Fish and Game files; R. L. Rausch, pers. comm.). Possibly she would not have been able to raise these young or another litter. Females 15 to 18 years old are fairly commonly harvested on the Alaska Peninsula, but females older than 18 are not.

Separation of young from females at McNeil River normally occurred between 1.5 and 2.5 years of age. Observations were not made late enough in the summer and fall or early enough in the spring to determine if separation normally occurred shortly before denning when young were 22 months old or after denning when they were 29-30 months old. On Kodiak Island, Hensel (pers. comm.) found very few 22-month-old bears still with the mother late in the fall just before denning.

A 3-year breeding interval for females, the most common at McNeil River, is the same as that for females on Kodiak Island (Hensel *et al.* 1969), in Glacier National Park (Martinka 1974), and in Yukon Territory (Pearson 1972). Mundy and Flook (1973) assume breeding intervals of 3 and 4 years for female grizzly bears in Canadian mountain parks. Craighead *et al.* (1969) state that young females in Yellowstone Park breed in alternate years, and older bears may show greater intervals between breeding.

Mortality at McNeil River between litters 0.5 year old and litters 1.5 years old and older appeared to be greater among those identified in consecutive years (38 percent mortality for 13 litters) than among those observed more than 1 year but not identified (13 percent mortality for 110 litters). This may be because sample size of identified litters was smaller and because family groups identified in consecutive years spent a greater proportion of time feeding at the falls, thereby increasing chances of cub mortality resulting from interaction with other bears.

Aerial counts reported by Glenn (1973) further south on the Alaska Peninsula provide information on mortality of young. Counts were flown in August. Three hundred and forty-two litters were observed and grouped in two categories; sows with cubs and sows with young one year of age and older. In these counts young 1, 2 and 3 years of age were grouped because these age classes could not be accurately differentiated from the air. A 9 percent reduction in litter size was reported. Reduction from cub to yearling mean litter size reported elsewhere is 10 percent for 201 litters observed on Kodiak Island (Hensel *et al.* 1969), 0 percent for 154 litters observed in Canadian mountain parks (Mundy and Flook 1973), and 0 percent for 65 litters observed in Glacier National Park (Martinka 1974). Craighead and Craighead (1970) report that 27

percent of cubs (sample size not given) in Yellowstone Park do not survive to age 1.5 years. The higher mortality at both McNeil River and Yellowstone Park may be related to congregating of bears and resulting intraspecific strife at feeding areas.

Intraspecific strife has been observed elsewhere. In mid-October on the lower Alaska Peninsula a large bear was seen eating a cub. A female with a frightened cub on her back was in an alder patch about 100 m away (Glenn 1971). On Kodiak Island, Troyer and Hensel (1962) investigated four cases of brown bears killing and eating other bears, three of them cubs.

Cub adoption, perhaps only temporary, has been previously observed at McNeil River. Erickson and Miller (1962) report that two females, each with three cubs, came together and then separated, with one cub accompanying one female and five cubs accompanying the other female. The female with five cubs was observed repeatedly until studies terminated 2 weeks later. The following summer no females were observed with more than three yearlings, and since neither female was marked it was not possible to determine if each female regained her original young or if loss occurred. Mixing of litters and cub adoption could be both beneficial and detrimental to maintenance of populations. Cubs might be provided for by another female if they should lose their mother. On the other hand, a female that adopted extra cubs from another female might not be able to raise all individuals of her oversized litter. Cubs that lost their mother might survive on their own.

Johnson and LeRoux (1973) report that a grizzly bear became self-sufficient at 7 months of age after its mother was killed.

SUMMARY

The Alaska Department of Fish and Game marked 21 female brown bears at McNeil River on the upper Alaska Peninsula to obtain life history information. Data were obtained in July and August in most years from 1963 through 1974. Some females experienced first estrus at 3.5 years, but did not conceive until older. First successful breeding occurred most commonly at 4.5 years. The oldest McNeil River female known to produce cubs conceived when 14.5 years old. The normal interval between litters was 3 years. Litters contained 1-4 young. Mean size of 41 litters of cubs was 2.1 and of 69 litters 1.5 and 2.5 years old was 1.8.

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Paper 40

Clinical, Epidemiological and Parasitological Features of the *Trichinella* strain (ATS)

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INTRODUCTION

The problems of the taxonomic individuality of natural arctic *Trichinella* strain (ATS) attacks (in connection with the phenomena of the clinical epidemiological peculiarities of trichinosis in humans produced by this strain) have been studied (Ozeretskovskaya and Uspenskiy 1957; Ozeretskovskaya 1956, 1968). Further, there has been established a sharp destruction of the process of encapsulation in muscle of larvae in humans and their massive kill in the course of the first months of invasion (Ozeretskovskaya *et al.* (1966). The experimental study of ATS from the polar bear (*Thalarctos maritimus*) on Franz Josef Land showed a stable, low invasibility of ATS for laboratory rodents and higher sensitivity to specific chemicals in comparison with the laboratory strain of *Trichinella* (LST), obtained by prolonged passage of synanthropic (pig) strains of *Trichinella* in laboratory rodents. The method of disc electrophoresis in polyacrylamide gel also established that there were peculiarities of protein content of ATS larvae and protein shifts in blood serum caused by strains invasive for laboratory animals in comparison with LST and certain other strains of *Trichinella* (Ozeretskovskaya *et al.* 1969a, 1970).

On the basis of reproductive isolation tests, laboratory strains of *Trichinella* were initially distinguished from those from domestic animals of synanthropic foci, from wild mammals of the European and Asiatic parts of the Soviet Union, and from predators of the African continent (Britov 1971). A position was advanced based on the presence of three varieties of parasite, which were further elevated to the rank of species (Britov and Boyev 1972). Along with ATS, native strains of *Trichinella* from wild mammals of all parts of the Eurasian and North American continents were added to *Trichinella nativa* sp. nova. At the same time the native African strain from hyenas was named *Trichinella nelsoni* sp. nova and was also discovered in the southern Ukraine (Britov and Boyev 1972). Later, evidence was produced regarding the possibility in interbreeding these enumerated three strains of *Trichinella* (Komandarev 1973; Meerovitch 1973, pers. comm.; Bessonov 1974).

CLINICAL EPIDEMIOLOGICAL FEATURES OF ATS

We studied 242 cases of human trichinosis of which 18 cases of infection were caused by ATS. In 15 patients the disease was contracted from the meat of the brown bear (*Ursus arctos*); seven cases in arctic and subarctic areas of the European continent; eight cases in the Asiatic parts of the Soviet Union. Three patients contracted trichinosis from the meat of the polar bear of the Novosibirsk Islands. Among the remaining 224 patients, 140 were from endemic foci of trichinosis in Western and Central regions of the European part of the Soviet Union. In 84 cases, the infection was caused by native strains of

Trichinella passed through domestic swine (STS). Of the 84 patients, 53 were infected by meat of domestic swine which had fed freely in the territory of the Caucasus Preserve—the North Caucasian Strain of *Trichinella* (NCST). In 7 cases the infection was contracted from swine which were reared in the territory of the Moscow-Oksk Preserve and in 24 cases from swine reared on meat from fur-bearing caged animals in the Karelian isthmus.

A study of the clinical-epidemiological and parasitological features of human trichinosis from ATS showed its definite differences from STS trichinosis and trichinoses caused by other strains from temperate and southern sections of the European part of the Soviet Union. For ATS trichinosis is characterized by a prolonged incubation period, relatively low muscular invasiveness (Table 1) and together with a severe course of illness marked general signs of sensitization and severe organ pathology (Table 1). The most significant difference of ATS trichinosis from trichinosis in endemic foci is the prolonged convalescent period and the frequent development of a chronic invasion phase, not a property of STS trichinosis. This phase can involve angiomycotic cardiopathies, a chronic phenomenon of gastroduodenitis, and cerebral disturbance with psychotic reactions (Ozeretskovskaya *et al.* 1966, 1972, 1974; Ozeretskovskaya 1968).

The principal chronic course of the disease during infection with ATS appears to be an incomplete process of encapsulation of the infective organism in the muscles. In the course of the months following infection, in place of a formation characteristic of STS trichinosis, a dense fibrous capsule is observed instead of a massive kill of parasites, with violent perifocal and diffuse cellular infiltration (Fig. 1) (Ozeretskovskaya *et al.* 1966, 1969a, 1970). High titers of specific antibodies illustrate the hypersensitivity of the patients (Table 1).

The significance of the break-up of the process of encapsulation in the pathogenesis of ATS trichinosis is confirmed by the very severe course of invasion. Therapy of patients with glucocorticoids supplementarily suppress the formation of the parasite capsule (Ozeretskovskaya *et al.* 1966). There are good effects in therapy of ATS trichinosis with a specific chemical—thiabendazol (Ozeretskovskaya *et al.* 1969a, 1970; Faynfeld 1973). At the same time the specific chemical preparation thiabendazol (a derivative of benzimidazol) is less active on the muscle stage of STS trichinosis in comparison with the intestinal stage, as a consequence of the difficulty of penetration of the preparation through the fibrous capsule, and has authentically higher effectiveness in ATS trichinosis (Ozeretskovskaya *et al.* 1969a, 1970).

PARASITOLOGICAL FEATURES OF ATS

A study of ATS and its natural hosts—the polar bear and the polar fox (*Alopex lagopus*)-by Vranghel showed that there is a peculiar process of capsule formation occurring in the circulation of the parasite in its natural biocenosis (Pereverzeva and Veretennikova 1973). In contrast to the two-layered fibrous-hyaline capsules of the parasite in animals of temperate areas (Govoroz 1895; Geller 1934; Berezantsev 1960, 1962; Pereverzeva 1966), capsules of ATS trichinosis in muscles of polar bears and polar foxes have a non-typical form, multilayered with unequal hyaline regeneration of encapsulated portion of the sarcoplasm (Fig. 2a & b). An associated network of equal-dimensioned protective capsules of STS *Trichinella* and wild, temperate strains through ATS trichinosis show distinctions between hyaline layers, often obliterating vessels (Fig. 2c). Upon heating, a significant part of the larvae become non-invasive. Hyalinated cicatrices are observed in sections in place of earlier

TABLE 1. COMPARATIVE CHARACTERISTICS OF HUMAN TRICHINOSIS CAUSED BY THE SYNANTHROPIC STRAIN (STS), ARCTIC (ATS), AND SWINE PASSAGED NATIVE (PPST) OF *TRICHINELLA*.

Trichi- nella strain	Number of patients	Intensity of muscle invasion (larvae/g)	Incubation period	Eosiniphilia of the blood in %		Titer of serological reaction at the height of illness		Lethal outcomes	
				in incuba- tion	at height of illness	agglutination	precipitation		no.
ATS	18	30.5±5.9- 36.0±1.4	34-200		30.0±4.54- 50.0±12.3	1:32-1:128	1:256-1:1024	0	0
STS	140	17.4±2- 25.5±1.7	22-600	2.93±68	22.0±4.16- 33.45±3.8	1:4-1:32	1:64-1:128	0	0
PPST	84	9.2±2.1	500-22500	1.88±0.35	16.76±2.09	% negative* -1.4	% negative* -1.4	12	14.3

*SKST trichinosis

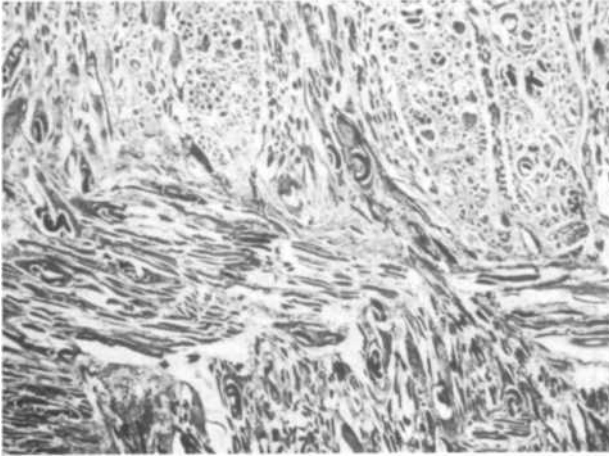


Fig. 1(a)



Fig. 1(b)



Fig. 1(c)

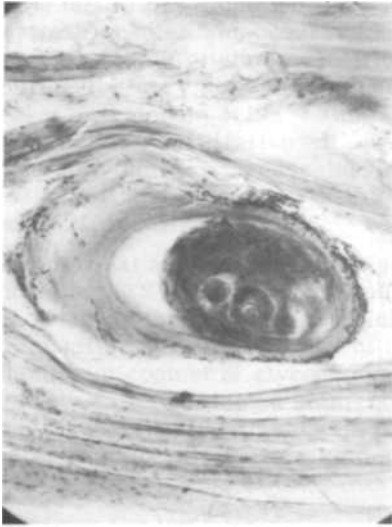


Fig. 2(a)

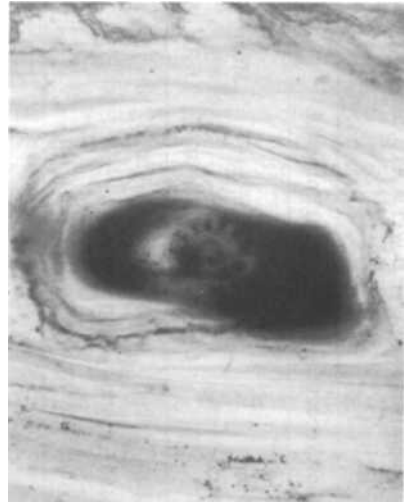


Fig. 2(b)

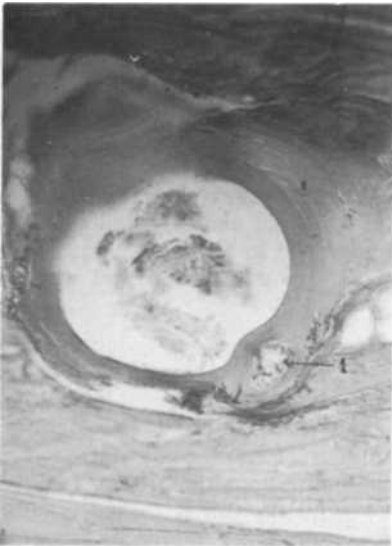


Fig. 2(c)

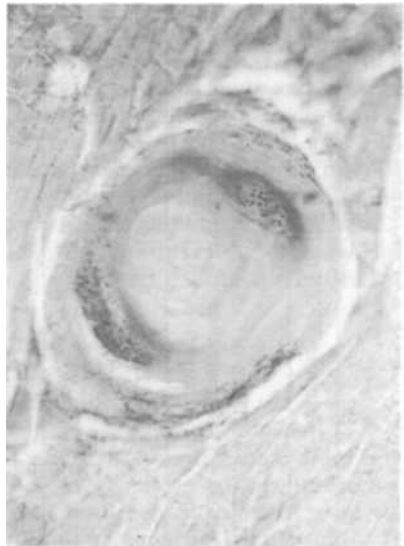


Fig. 2(d)

killed *Trichinellae* (Fig. 2(d)). not observed by us and other researchers in muscles of wild and domestic animals infected with temperate strains of *Trichinella*. Analogous peculiarities of capsule structure were discovered (Pereverzeva and Veretennikova 1973) in studies of polar bear muscles from Franz Josef Land and from arctic regions of Canada (materials of Dr. G. Dzhonkel). The capsule of ATS *Trichinella* differs morphologically from the capsule of native strain *Trichinella* found in various specimens of wild fauna of the Central European part of the Soviet Union—the wolf (*Canis lupus*), the fox (*Vulpes vulpes*), the raccoon dog (*Nyctereutes procyonoides*), etc. (Zimoroy 1963; Pereverzeva 1966).

TABLE 2. COMPARATIVE CHARACTERISTICS OF EXPERIMENTAL TRICHINOSIS IN WHITE MICE INFECTED WITH ATS, SEPST, AND LTS.

Trichinella strain	Intestinal Trichinella			Muscle Trichinella			Blood according to days after infection							
	Viability on the seventh day of invasion in % of entries	Period of* elimination from the intestine	Time of* appearance in muscles	Number in muscle	In diaphragm	Leucocytes	% Lymphocytes	% Monocytes	7	21	60	7	21	60
ATS	13-15	14-15	10-12	158	2765	16300	16200	8000	41	61	60	8	8	7
SEPST	15	10-12	12-13	845	1768	13400	11000	6900	73	70	53	14	7	5
LTS	54	25-28	6-7	2360	10355	4700	4500	16200	63	57	41	3	5	15

*Days after infection

During laboratory studies of ATS trichinosis, low association of larvae with intestinal muscles was observed and rapid disappearance of intestinal parasites (Table 2). Cellular infiltration around the intestine by *Trichinella* is significantly more powerful than during invasion by LTS and contains a higher percent of lymphoid cells. Later *Trichinella* appear in the muscles with violent cellular infiltration with predominantly lymphocytes around larvae, seeded into the skeletal muscles, disrupting the process of encapsulation and massive kill and resorption of *Trichinella* in muscle (Table 2) (Pereverzeva *et al.* 1971,1973).

Morphological and histochemical study of muscle sections from animals invaded by ATS show slower development of parasites in comparison with LTS. Thus, in three weeks after infestation, the larvae have a cylindrical form with insufficient differentiation of internal structure (Fig. 3a), extremely insignificant content of glycogen and absence of mucopolysaccharides. Simultaneously, in LTS-infected animals by the fifteenth day a majority of larvae are already spirally twisted with organogenesis concluded; they contain a greater quantity of glycogen, acid and neutral mucopolysaccharides reflecting the active metabolism of the parasite (Fig. 3b).

Aside from the later formation of connecting capsules of ATS larvae (30-35 days instead of 20-25 days with LTS) there is undefined, absent or very weak development of a hyaline layer even 2-3 months after infection (Fig. 3c), while, with larvae of LTS, a double-layered capsule forms by the 4th week. The insufficiency of the protective function of the capsule in ATS causes a violent cellular reaction around the larva and in the interstitial tissue of the muscle, resulting in the destruction of the normal development and metabolism of parasites leading to a massive kill and lowered intensity of invasion (Fig. 3d and Table 2) (Pereverzeva 1966; Pereverzeva *et al.* 1971, 1973). Invasiveness of ATS larvae in its passaging in white mice is substantially lower in LTS infection (Ozeretskoyevskaya *et al.* 1969a 1971). The development of STS in laboratory animals has patterns in common with the development of ATS. However, peculiarities of the morphology and biochemistry of intestinal and muscular *Trichinella* are significantly less expressed (Table 2) (Pereverzeva 1966).

DISCUSSION

The materials presented here confirm that ATS has specific characteristics, individually defined development, and is a unique parasite with obligate and incidental hosts. It was possible to guess that features of the course of ATS-trichinosis in humans and laboratory animals are linked to its difficulty in adapting to organisms not common to the usual biocenosis of this strain. However specific the development of muscle *ATS-Trichinella* in obligate hosts, it is definitely different from *Trichinella* of the natural SEPST strain and leads to the conclusion that specific ATS can quickly be characterized by its genetic aspects.

Our clinical, epidemiological and experimental studies allow us to conclude that ATS displays genetically low immuno-suppressive activity—a property determining the possibility of one organism sharing a habit with another foreign to it in antigenic relation. In recent years we have obtained a variety of indirect and direct indicators of immuno-depressive activity of *Trichinella* (Svet-Moldavskiy *et al.* 1969, Chimishkyan *et al.* 1974). It was established that *Trichinella* separate out of the host organism low molecular weight compounds



Fig. 3(b)



Fig. 3(d)



Fig. 3(a)



Fig. 3(c)

having the capacity for agglutinating leucocytes and producing a cytopathic effect. Analogous activity is shown by extracts of *Trichinella* from muscles (Tanner and Gaubert 1972). The immuno-depressive activity of *Trichinella* is especially pronounced 24-40 days after invasion (Chimiskyan *et al.* 1974), that is at the stage of massive encapsulation of the *Trichinella* larvae.

Low immuno-depressive activity of ATS-*Trichinella* determines the sluggish development and early evacuation of intestinal parasites, a later period of implantation of migrating larvae in the muscle, imperfections of the encapsulation and massive kill in the early period after infection on a background of active angiomyositis. The indicated biological peculiarities of the strain determine the features of the clinical course of ATS infection—prolonged incubation period, severe course of the disease (despite low intensity of invasion), and its transition to a chronic stage. The low immuno-depressive activity of ATS-*Trichinella* produces violent cellular infiltration with sharp predominance of lymphocytes around the intestinal and muscular *Trichinella* in experiments and in patients infected with ATS (Ozeretskovskaya *et al.* 1966, 1969a, 1970, 1974; Pereverzeva *et al.* 1971, 1973). Evidence of low immuno-depressive activity of ATS is shown in the uncommonly high titers of specific antibodies during the 6-12 months after infection (Ozeretskovskaya and Uspenskiy 1957; Ozeretskovskaya 1958; Ozeretskovskaya *et al.* 1974). The indicated property explains the useless effect of steroid hormones in ATS-trichinosis, the immuno-depressive effect of which facilitates the breakdown of encapsulation of larvae in the muscles and the hypersensitivity of the host organism and the shift of the disease to a chronic state (Ozeretskovskaya *et al.* 1966, 1974; Ozeretskovskaya and Tumol'skaya 1972).

Of special interest in the discussion of various immuno-depressive activity are STA and PPTS trichinosis. Favorable course of the invasive process of STS infection determines the moderate immuno-depressive activity of strains of *Trichinella* of endemic foci and the 'balanced' relationship in the host-parasite system. Under these conditions are guaranteed the quick and absolute encapsulation of larvae in muscles, securing the host from hypersensitivity and facilitating biological protection of both members of the system (Ozeretskovskaya 1968, 1970; Ozeretskovskaya *et al.* 1974). Simultaneously PPTS and especially SKTS trichinosis displays an uncommonly high immuno-depressive activity determining the malignant course of invasion and kill of the host (Ozeretskovskaya *et al.* 1969b, 1974). Together with this, SKTS is distinguished by low invasiveness in relation to laboratory rodents (Ozeretskovskaya *et al.* 1969a, 1970). Trichinosis is caused by STS and wild strains from the African continent and in *O. Sumatra* also is distinguished by low invasiveness with respect to laboratory rats and also yields a lethal outcome upon infection of humans (Forrester *et al.* 1961; Nelson and Mukundi 1963; Ozeretskovskaya *et al.* 1966, 1974), thus closely resembling the characteristics of PPTS trichinosis strains in the USSR. The high immuno-depressive activity of PPTS secures rapid and complete encapsulation of larvae in muscle, despite the uncommon intensity of invasion. The complete formation of the larval capsule in the muscle despite the death of the host ensures the preservation of the parasite as a consequence of the presence of wide dietary interspecies links, cannibalism and necrophagy. Simultaneously in high arctic latitudes, with relatively scanty numbers of mammals—hosts of *Trichinella*—they are limited in consequence to the possibility of transmission and invasion through food links among them and, therefore, the *Trichinella* accumulate in the largest predators and marine mammals. The presence of aggressiveness from ATS ought to have been leading to the kill of the parasite as a species.

It is possible that the metabolic peculiarities of ATS determine features of the biochemism of muscle tissues of polar mammals. It is known that upon infection with STS and native strains, bands of *Trichinella* larvae never appear in the cardiac muscle (Merkushev 1954; Matoff and Komandarov 1965). Simultaneously we (Pereverzeva and Veretennikova 1973) found in the cardiac muscle of two out of three polar bears from Vrangel Island 0. 5-1 larvae/gram of tissue.

In recent times data have been obtained that indicate that *Trichinella* selectively settle in the so-called 'tonic' muscles, rich in imidazole compounds, especially imidazole alkylamines, histamines, etc. (Ozeretskivskaya and Bekish 1969; Bekish 1972). Invasion by *Trichinella* is accompanied by a sharp drop of imidazoles in the skeletal muscles, also of anzerine and carnozine and a marked increase in the histamine content (Bekish 1972). It is known that natural imidazoles are connected with a high level of energy processes in the skeletal musculature (Severin 1965). It is possible to suggest that in conditions of high arctic latitudes the biochemistry of the skeletal musculature and cardiac differ from the biochemistry of muscles of mammals in temperate latitudes. Later the biochemical features of ATS may be elucidated and will explain the difficult adaptation to animals of the average spectrum and to man.

Not excluding the ATS, we distinguished two natural arctic strains—a high arctic strain from polar bears, possessing strength of ecological isolation in features of biochemistry of land mammals, the weakest immuno-depressive activity, and a strain from lower arctic latitudes from the brown bear. However, clinical-immunological features of disease and incomplete encapsulation of *Trichinella* in muscles in both cases are displayed in equal degree (Ozeretskivskaya *et al.* 1966, 1969b, 1974). Britov and Boyev (1972) agree to a new species *Trichinella nativa* sp. nova. ATS with other natural strains of *Trichinella*, often in synanthropic foci, in the separation of native African strains of *Trichinella* into another new species *Trichinella nelsoni* sp. nova, according to the authors not irradiating in the vicinity of man and weakly pathogenic for him, appears somewhat artificial. First of all, it is known from a series of outbreaks of human trichinosis in Africa that intensive infection of humans with lethal outcome has occurred (Forrester *et al.* 1961). Further, the morphological and functional muscle capsules of larval SEPTS strain and other native strains of *Trichinella* are similar. Finally, it is hard to explain the reasons for isolated occurrences of the African strain of *Trichinella* in the southern Ukraine, that, nevertheless, are recorded by the authors themselves.

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Paper 41

Denning Ecology of Grizzly Bears in Northeastern Alaska

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INTRODUCTION

In arctic Alaska the grizzly bear, *Ursus arctos*, is at the northern limit of its range; the period of food availability during the summer season is short, reproductive potential is low, and populations may be more susceptible to the pressures of human development and sport hunting than they are in other regions.

As one aspect of a cooperative research program to determine the basic parameters of grizzly bear population size, structure and movement patterns in northeastern Alaska, denning was studied during April-November 1972, 1973 and 1974 (Reynolds 1974; Quimby 1974; Quimby & Snarski 1974; Curatolo & Moore, in press). The primary objectives of this segment of the study were to locate dens, delineate denning habitat and determine if the availability of den sites was a population limiting factor.

STUDY AREA

The study area is in the eastern Brooks Range along the southwestern border of the Arctic National Wildlife Range. It includes the Canning and Ivishak Rivers which flow north into the Arctic Ocean and the Junjik River and East Fork of the Chandalar River which flow south into the Yukon River and thence to the Bering Sea. The country is characterized by rugged mountains rising to 1700 m, cut through with river valleys up to 3 km wide at elevations from 300 to 900 m and interspersed with steep rolling hills in portions of the area. There are scattered stands of stunted white spruce *Picea glauca* on the south side of the divide but none on the north; otherwise the vegetation is similar: willows *Salix* spp., poplars *Populus* spp. and scattered *Shepherdia canadensis* in the river valleys; horsetails, *Equisetum* spp. and *Eriophorum*., in moist areas; and *Dryas* communities predominating in drier habitat.

PROCEDURES

Systematic aerial searches of small drainages for caves or material excavated from dug dens revealed 20 dens. Fourteen dens were located by tracking bears in the snow, some for long distances, during spring and autumn. The contrast of

excavated earth against vegetation or newly fallen snow resulted in the locating of eight dens from aircraft by biologists conducting other studies in our study area. Seven bears fitted with radio transmitters were found in dens. Three grizzly bear dens were located after interviews with native residents of Arctic Village.

RESULTS AND DISCUSSION

Den site Selection and Structure

Fifty-two dens were located including 29 active dens (23 dug and 6 in caves) for which the winter of use was known and 23 inactive dens (16 dug and 7 in caves) for which the year of use could not be determined.

Inclement weather, especially snowstorms during autumn, has been hypothesized as a major factor in stimulating denning activity (Craighead & Craighead 1965, 1972a; Jonkel & Cowan 1971). Observations during this study generally agree with this hypothesis.

In 1973, den construction was preceded by a major snowstorm and followed by a number of light snowfalls on successive days. The dates of den excavation were judged by the accumulation of snow on the material removed from the den and by the age of the tracks leading to the sites. Ten of the 14 active dens (71 percent) which were found during the fall were dug between 5 and 12 October. Intensive searches for dens were continued until 25 October but few fresh tracks were encountered after 12 October. However, four dens were located between 26 October and 7 November by other biologists in or adjacent to the study area; the dates of construction for these were unknown but at least one appeared to have been recently made. Similarly, in 1974, of eight bears whose summer movements were monitored, six denned between 3 and 9 October, a period characterized by cold temperatures and Snowstorms, one denned on 29 September and one between 15 and 31 October.

Of the 52 dens, 47 (90 percent) were on southerly slopes, 4 (8 percent) were on northerly slopes and 1 (2 percent) was on an easterly slope. The den sites, excluding three coastal plain dens, had a mean elevation of 1040 m (S.D. = 240) above sea level and a mean elevation of 180 m (S.D. = 150) above the valley floor. Most dens were on slopes of 20 to 35 degrees.

A considerable difference in the exposure of the slope used for denning exists between geographic areas. Craighead & Craighead (1972) found bears in Yellowstone National Park denning on north facing slopes at altitudes from 3100 to 2700 m. Lentfer *et al.* (1972) found the greatest proportion of bears on Kodiak Island denned on north facing slopes at 550 m and on the Alaska Peninsula on east facing slopes at 400 m. Our study showed bears in the Brooks Range had a definite preference for south facing slopes, possibly selecting sites which would melt the earliest and expose available forage. Bears in more southerly locations may be selecting sites which protect them from mid-winter thaws which would flood or dampen the den (Craighead & Craighead 1972a), a situation which rarely occurs in the Brooks Range.

A more probable explanation for the southern orientation of den sites is related to Brooks Range soil characteristics. These mountains lie within the zone of continuous permafrost (Péwé 1966). The soil on the north facing slopes may melt down only 30 to 60 cm from the surface while south slopes may melt to 2 m (Kline, pers. comm.). Permafrost soils of small particle size and high water content have a greater hardness than well-drained coarse soils (Péwé

1966), which would be easier to excavate. Bears appear to select terrain characterized by steep slopes for drainage, south facing slopes for the maximum depth of thaw and rather coarse soil substrates. These characteristics would aid in den construction in autumn, but also make collapse of the den more likely after the spring thaw; and indeed all dug dens visited during the summer had collapsed.

Permafrost may also keep bears from digging dens earlier in the season. Craighead & Craighead (1972a) found bears constructed dens up to 2 months before finally entering the den for winter hibernation. Conversely, in this study, bears appeared to construct dens almost immediately before entering for hibernation. Since the maximum depth of thaw occurs in autumn it may be easiest to construct dens immediately before hibernation rather than months earlier when frozen soil may make excavation difficult or impossible.

The selection of moderate to steep slopes for den sites may also aid in construction of a heat trap where the chamber is higher than the entrance (Craighead & Craighead 1972a, 1972b) and for ease in getting rid of excavated material (Lentfer *et al.* 1972).

In this study area grizzly bears either dug dens or used natural rock caves for hibernation. In other parts of North America, reported brown and grizzly bear den sites have been dug (Murie 1963; Craighead & Craighead 1972a, 1972b;

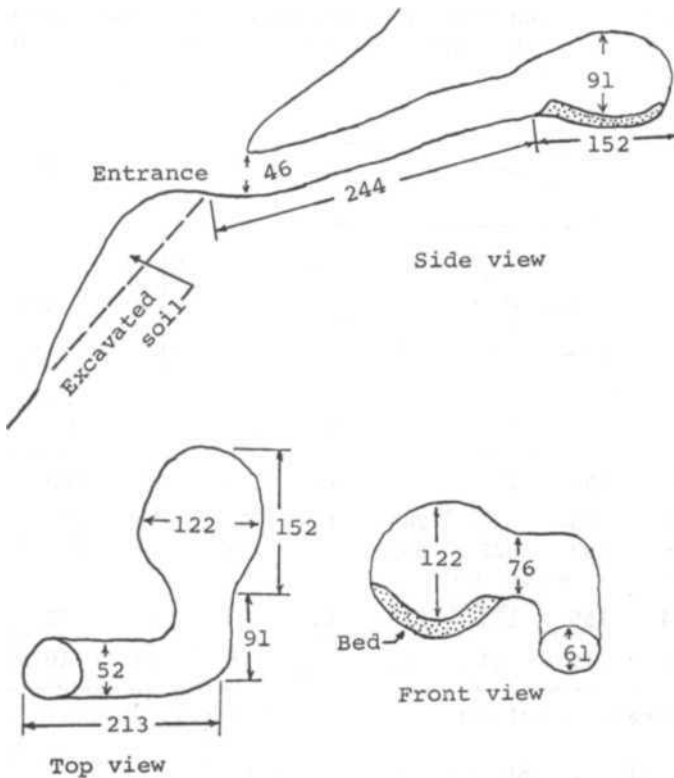


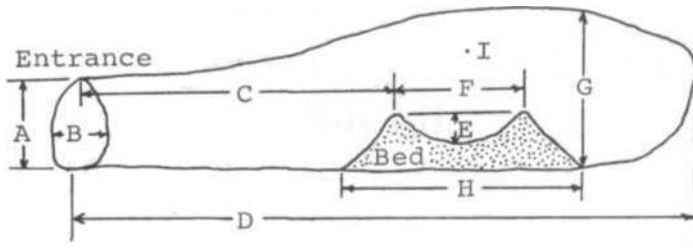
Fig. 1. Two dug grizzly bear dens, eastern Brooks Range, Alaska. (Dimensions in centimeters)

Lentfer *et al.* 1972), although Lentfer *et al.* (1972) noted receiving reports of utilization of caves on Kodiak Island and the Alaska Peninsula. Black bears, *Ursus americanus*, are more likely to dig dens under rocks, logs, trees or to utilize caves (Erickson *et al.* 1964; Jonkel & Cowan 1971; Craighead & Craighead 1972a). The European brown bear, *Ursus arctos arctos*, is reported to den in caves, hollow trees and dense vegetation (Couturier 1954).

Most dug dens collapsed before we were able to examine them; only one intact dug den and one which was partially collapsed were measured. On-the-ground observations showed that most dens closely followed the descriptions of Craighead & Craighead (1972a, 1972b) and Lentfer *et al.* (1972). The two that were found relatively intact were representative of the den structure shown in outline by collapsed dens (Fig. 1). Both dens were constructed with an upward leading tunnel between the entrance and the bed chamber, which provided an effective dead air space. Twigs, roots, grass, shrubs and moss were scraped into the chamber to form a nest-like bed.

Dimensions of cave dens are given in Fig. 2. All den sites had vegetation at or adjacent to the cave mouth; bears scraped and collected this vegetation, similar to that found in dug dens, into the den to construct beds. One of these beds, however, was constructed completely from the feces of porcupines, *Erethizon dorsatum*, which had previously occupied the cave.

Craighead & Craighead (1972a, 1972b) discuss the warm micro-environment which develops in the den when snow covers the entrance and creates an effective insulating layer of snow and dead air. In the Brooks Range snowfall is very light, and temperatures may reach -50°C for weeks at a time; maintenance



	A	B	C	D	E	F	G	H	I*
Mean	125	189	232	506	27	107	88	189	149
Range	52- 216	55- 293	0- 625	289- 899	15- 46	70- 168	55- 122	131- 217	25- 70
Standard deviation	64	155	177	235	12	37	21	58	55
No. in sample	11	11	11	11	8	6	10	10	11

*I—width of cave above center of bed

Fig. 2. Composite side view sketch and dimensions (in centimeters) of 11 grizzly bear rock cave dens and hibernation beds, eastern Brooks Range, Alaska.

of a warm microclimate within the den would seem to be important for sustaining fat reserves and the animal's well being. The construction of beds up to 30 cm thick with walls extending as high as 47 cm serves as an insulative barrier to the cold; other adaptations to conserve body heat include construction of the bed above the level of the entrance and, in the case of some dug dens, pushing vegetation into the entrance from the inside, effectively reducing the size of the mouth of the den. However, in some cave dens, beds were close to and at the same height as the entrance, allowing air to circulate freely; these had only a bed of vegetation to conserve body heat.

Movement

Den sites were located within or closely adjacent to the area used by grizzlies during spring, summer and autumn. Of the eight bears whose home ranges were determined in 1974 by radio telemetry or visual observation none migrated outside their summer or autumn range to den (Curatolo & Reynolds, in prep.). When eight bears whose home ranges were not known were tracked to dens during the fall of 1973, the straightline distances traveled before den sites were reached were 3.2, 3.2, 4.8, 6.5, 8.1, 9.7, 12.9 and 54.8 km. Another bear was tracked from its summer and early autumn range 51.6 km to its denning area but its den was not found. Thus, two of these nine bears moved a considerable distance to reach denning areas, possibly beyond their summer ranges.

Two types of home ranges have been reported in other areas: one in which a single area was used throughout the year for foraging and denning, and one in which the summer and early autumn foraging area was connected by a migratory corridor to an early spring and late autumn area that contained the den (Berns & Hensel 1972; Craighead & Craighead 1972a).

Our study showed that seven of eight bears had known home ranges of the single area type and that seven of nine bears with unknown home ranges were tracked to dens which appeared to still be within their home ranges due to the short distances traveled. Thus it appears that most grizzlies in our study area did not have different seasonal ranges connected by a migratory corridor, but used a single, well-defined area throughout the year.

Den Related Activities

No re-use of dug dens was found in this study, although rock cave dens may have been used more than once. Both Lentfer *et al.* (1972) and Craighead & Craighead (1972a) cited one instance of possible den re-use, but there is little doubt that most bears construct new dens each year since seepage and erosion tend to collapse dug dens in the spring and summer (Lentfer *et al.* 1972). Although individual dens may not be used more than once, there is some evidence that bears may use the same general area for more than 1 year (Craighead & Craighead 1972a).

In 1973, bears abandoned five den sites after they were tracked to them by helicopter. One bear abandoned two of these sites after it had been disturbed on 7 October and again on 8 October. Bears appeared to be most prone to abandon dens when disturbed during or shortly after den construction. However, dens could be located without causing abandonment by approaching them carefully and spending little time in the area. No dens were abandoned in 1974.

Two cases of possible den-related mortality were recorded. The remains of a 2-year-old bear were found in a small and poorly constructed cave den. The other case involved the report of a large bear feeding on the carcass of another bear. Inspection of the site showed that the bear, probably a male, had discover-

ed an occupied den and had either killed the occupants (a sow and at least one yearling) or had discovered them dead within the den. Pearson (1972) cites an instance in which a male killed a female at a den. Lentfer *et al.* (1972) found no instances of den mortality; neither had Craighead & Craighead (1972a), but they believe that old bears may die in the den.

Denning Habitat Availability

If the availability of denning habitat was a population limiting factor it would have its greatest effect on the low foothills and coastal plains where permafrost is closest to the surface. Although bears whose home ranges were primarily in the mountains foraged in this area during certain times of the year, few bears established home ranges entirely in the region; this was probably due more to the lateness of thaw, slow disappearance of snow and low food resources than to availability of denning sites. Well-drained sites near stream banks may be important for denning for the few bears that winter in this area.

In the mountains and foothills, denning took place over wide areas on both the north and south slopes of the Brooks Range. There did not seem to be specific areas of denning where habitat was limited although south facing slopes were preferred and some caves may be re-used in successive years. Thus it appears at this time that denning habitat is not a limiting factor on the grizzly bear population in northeastern Alaska.

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Paper 42

Parasites of Bears: A Review

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INTRODUCTION

This paper is an attempt to summarize the available information on parasites of bears. Knowledge of ursine parasites has expanded considerably since the subject was reviewed by Stiles and Baker in 1935; more than 90 additional reports on the subject have been published, and at least 43 additional parasites have been reported. In this paper, available information is summarized for each of 77 species of parasites, including (1) species of host, (2) pathological effects, (3) whether hosts were captive or wild, (4) the proportion of the bears from a given geographic location that were infected, and (5) sources of information. Parasites also are listed by host. Topics discussed include transmission of trichinosis and parasitism during hibernation.

PROTOZOA

Hair and Mahrt (1970) reported two new species of coccidia from wild black bears (*Ursus americanus*) in Alberta, Canada. They examined 52 fecal samples and found oocysts of *Eimeria albertensis* in four and oocysts of *E. borealis* in three of them. Coccidia also were reported from the USSR, where *E. ursi* was reported from the brown bear (*Ursus arctos*) (Yakimoff and Matschoulsky 1935) and *Isospora fonsecai* was reported from the red bear (*Ursus arctos isabellinus*) (Yakimoff and Matschoulsky 1940). Couturier (1954) thought Coccidia and Infusoria make bears slightly ill. Stiles and Baker (1935) reported a haemosporidean parasite (*Babesia* sp.) from an unidentified bear in a zoo at St. Petersburg, Florida. Marchionini (1967) claimed that bears (species not given) could act as intermediate hosts for *Leishmania* sp., which is the protozoan agent of dermal leishmaniasis, a disease of man in the Middle East.

TREMATODES AND ASSOCIATED RICKETTSIA

Flukes (*Dicrocoelium lanceatum*) were found in the bile ducts of 8 of 12 adult Himalayan bears (*Selenarctos thibetanus*) in southeastern USSR (Bromlei 1965). Worley *et al.* (1976) found flukes (*Echinostoma revolutum*) in 2 of 31 wild grizzly bears (*Ursus arctos horribilis*) in Montana. A third fluke, *Nanophyetus* (= *Trogloremata*) *salmincola*, was reported from a wild brown bear from eastern Siberia (Filimonova 1966) and from experimentally infected black bears from the north-western United States (Simms *et al.* 1931, Farrell 1968, Poelker and Hartwell 1973).

Farrell (1968) reported that metacercariae of *Nanophyetus salmincola* live in certain species of fish, including the salmonid species eaten by bears. The metacercariae carry two types of rickettsia-like organisms which they transmit to fish-eating mammals. One is *Neorickettsia helminthoeca*, to which the bear is refractory; the other has no generic name but is known to cause Elokomin fluke fever (EFF) in black bears. Farrell (1968) experimentally infected nine wild-caught black bears with metacercariae of *N. salmincola*. Eight of them exhibited diarrhea and refused to feed on the ninth to twelfth days following infection. Appearance of these animals varied from mild lethargy to lateral recumbancy from which they were aroused only with difficulty. The ninth bear was captured in an area where it probably already had been exposed to EFF, and it was immune to the disease. Six of the bears were sacrificed for further studies during the acute phase of illness. One of these had approximately 64,000 flukes in the small intestine and showed bile blockage with necrosis of the gall bladder sufficient to have caused death. The two bears that were not sacrificed made uneventful recoveries without treatment.

CESTODES

Cyclophyllidean Tapeworms

Jonkel and Cowan (1971) found *Taenia saginata* in several droppings from wild black bears in northwestern Montana. Horstman (1949) reported *T. pisiformis* from a wild black bear in Colorado. Rausch (1954) and Rausch *et al.* (1956) reported *T. krabbei* and sterile specimens of *T. hydatigena* from captive black bears in Alaska. *Taenia krabbei* also was found in 2 of 21 wild grizzly bears (*Ursus arctos*) in northwestern Canada (Choquette *et al.* 1969). Taeniid cestodes (cf. *Multiceps serialis*) were found in a wild black bear in Minnesota during a population explosion of the snowshoe hare (*Lepus americanus*), which is the usual intermediate host of *M. serialis* in that state (Rogers 1975). *Taenia* was found in 7 of 12 wild black bears in central Alaska (Hatler 1967), in 2 of 30 wild black bears in Montana (Worley *et al.* 1976), in 14 of 66 wild grizzly bears in Montana (Worley *op. cit.*), and in a captive Himalayan bear in India (Stiles and Baker 1935). Other reports of adult cyclophyllidean tapeworms include *Pentorchis arktei* in a sun bear (*Helarctos malayanus*) in Burma (Meggitt 1927), *Taenia ursi-maritimi* in captive polar bears (*Ursus maritimus*) in Europe (Rudolphi 1810; Linstow 1878), and *T. ursina* in a captive brown bear in Copenhagen (Linstow 1893). Wardle and McLeod (1952) listed *T. ursina* and *T. ursi-maritimi* as *nomina dubia*.

Horstman (1949) stated that he found two new species of tapeworms, *Mesocetoides krulli* and *Anacanthotaenia olsenii*, in wild black bears in Colorado. However, as far as we could determine from the *Zoological Record* and from the *Nomenclator Zoologicus* by Edwards and Hopwood (1966), no descriptions of these cestodes have been published.

Bears also can serve as intermediate hosts for certain cyclophyllidean cestodes (Meggitt 1924). Batsch (1786) listed *Ursus* sp. as a host for hydatid cysts of *Echinococcus granulosis*, and Diesing (1851) reported cysticerci (*Cysticercus cellulosae*) from a brown bear, presumably from the Old World. Martin (1950) found numerous unidentified cysticerci in practically every skeletal muscle of a wild black bear in California. The bear weighed 85 kg (188 pounds), had little fat, and had a lusterless pelt when killed on 13 October.

Pseudophyllidean Tapeworms

The only pseudophyllidean tapeworms reported from bears from North America have been from the genus *Diphyllobothrium*. Bears acquire these parasites by eating fish that contain plerocercoids (Rausch 1954).

There has been disagreement concerning the specific identification of several of these cestodes (see review by Rausch 1954). *Diphyllobothrium* from wild black bears from Yellowstone National Park have been identified as *D. latum* (Skinker 1931; Rush 1932), *D. cordatum* (Scott 1932) and *D. cordiceps* (Rausch 1954). Specimens identified as *D. latum* by Rush (1932) later were identified as *D. cordatum* by Scott (1932).

Rausch (1954) provisionally described tapeworms from brown bears (*Ursus arctos middendorffi*) on Kodiak Island, Alaska, as a new species, *D. ursi*. Cestodes tentatively identified as the same species were found in 3 of 21 grizzly bears from northwestern Canada (Choquette *et al.* 1969). Skinker (1931) reported *D. latum* from an unidentified bear from Ketchikan, Alaska. *Diphyllobothrium* was found in 16 of 66 grizzly bears and in 2 of 30 black bears in Montana (Worley *et al.* 1975). *Diphyllobothrium* also was found in unidentified bears from the northwestern United States and Alaska (Ward 1927) and in wild black bears in southern Alaska (Rausch 1961) and Minnesota (Vergeer 1930, unpublished data). *Diphyllobothrium* formerly was found in the droppings of four of ten wild black bears in Minnesota (Vergeer 1930) but more recently has become uncommon (Rogers 1975). Horstman (1949) reported *D. latum* from a captive polar bear in Minnesota.

In the Old World, *Diphyllobothrium latum* and *D. cordatum* were found in wild brown bears from southeastern USSR (Bromlei 1965). Additionally, *Bothriocephalus ursi* was found in a brown bear in a zoo in Germany (Landois 1877), and *Bothriocephalus* sp. was reported from a polar bear from a zoo in Dublin (Foot 1865). In the past the genus *Bothriocephalus* was a general receptacle for unassigned pseudophyllidean forms; more than 200 have been relegated to it at various times (Wardle and McLeod 1952).

Adverse effects upon bears from tapeworms usually are not evident (Rausch 1955). However, in an exceptional case, a captive black bear cub died in Alaska from complications that arose after strobilae of *Diphyllobothrium* sp. (probably *D. ursi*) completely occluded its pancreatic ducts (Rausch *op. cit.*). In Yellowstone National Park, Wyoming, Rush (1932) found that a wild black bear in poor condition contained about 100 tapeworms (*Diphyllobothrium* sp.) and had occlusions and invaginations of the intestine. The bear had been killed because of its nuisance activities.

NEMATODES

Intestinal Nematodes

For the ascaridoid nematodes, we have followed the classification of Sprent (1968) in which the ursine members of the genera *Ascaris* and *Toxascaris* are reclassified in a new genus, *Baylisascaris*. Members of this genus are common in bears and have been reported from all species except *Tremarctos ornatus* (Sprent 1968). *B. transfuga* has been found in wild black bears in Ontario (Sprent 1950; 1951), Wyoming in 1 of 8 bears (Rush 1932), Minnesota in 5 of 7 bears (Rogers 1975), Montana in 24 of 30 bears (Worley *et al.* 1976), and Alaska (Rausch 1961). *B. transfuga* also was found in wild grizzly bears in

northwestern Canada in 16 of 21 bears (Choquette *et al.* 1969) and Montana in 53 of 70 bears (Worley *et al.* 1976).

In the Old World, *Baylisascaris transfuga* was reported from wild brown bears in south-eastern USSR (Oshmarin 1963) and from a wild Yezo brown bear (*Ursus arctos yezoensis*) from Japan (Okoshi *et al.* 1962). Mozgovoi (1953) reported this parasite from *U. a. caucasicus* but did not state whether the bear was wild or captive. Bromlei (1965) stated that in the Old World *B. transfuga* is found in Caucasus, Baikal, Chukotka, Indonesia, Syria and Tibet.

Captive bears from which *Baylisascaris transfuga* were collected include polar bears from Australia (Sprent 1968) and Moscow (Mozgovoi 1953), brown bears from Czechoslovakia (Jaros *et al.* 1966) and Moscow (Mozgovoi 1953), and sloth bears (*Melursus ursinus*) and Himalayan bears (*Selenarctos thibetanus*) from India (Baylis and Daubney 1922). In the Philadelphia Zoo, it was collected from *Ursus americanus*, *U. maritimus*, *U. arctos syriacus*, *U. a. pruinosus*, *U. a. beringianus*, and *Helarctos malayanus* (Canavan 1929; Stiles and Baker 1935).

Three other species of roundworms of the genus *Baylisascaris* have been collected from bears (Sprent 1968). Khera (1951) described a new species, *B. melursus*, from the sloth bear in India. The giant panda (*Ailuropoda melanoleuca*), which some authors (e.g. Sarich 1973) consider to be a bear, was host to another species, *B. schroederi* (McIntosh 1939). *B. multipapillata* was collected from a captive black bear in Germany and described by Kreis (1938). The latter species also was collected in New York from captive black bears and from 20 of 65 wild black bears (King *et al.* 1960). Mozgovoi (1953) stated that *B. multipapillata* and *B. transfuga* may prove to be the same species.

Ascaridoids (species not given) were found in 9 of 12 wild black bears in Alaska (Hatler 1967), in wild black bears in western Washington (Poelker and Hartwell 1973), and in Himalayan bears in southeastern USSR (Bromlei 1965).

Baylisascaris sp. apparently caused the death of an unidentified and presumably captive bear (Mozgovoi 1953). The bear contained 100 specimens in the intestine, which is the usual location for this parasite. In addition, it contained 97 in the stomach, two in the oral cavity, and one in the larynx. Mozgovoi concluded that death in this case was due to the fact that 'the location was an abnormal one that is frequently observed with ascarids and that usually causes death.'

Toxocara canis and *T. mystax* were found in captive brown bears in Bale, Germany (Couturier 1954).

Four species of hookworms, *Ancylostoma brasiliense*, *A. ceylanicum*, *A. malayanum*, and *A. caninum*, were reported from captive sloth bears in India (Baylis and Daubney 1922). *A. ceylanicum* long was considered a synonym of *A. brasiliense*, but Biocca (1951) showed that the two are distinct. *Ancylostoma malayanum* also was reported from Himalayan black bears from India and Ceylon (Lane 1916) and from a captive sun bear from India (Baylis and Daubney 1922).

Female hookworms were collected from the polar bear and deposited in the Vienna Museum under the name *Strongylus ursi-maritimi*; Dujardin (1845) described these specimens and assigned to them the name *Dochmius ursi*. *Dochmius* now is considered a synonym of *Uncinaria* (Levine 1968). The northern carnivore hookworm (*Uncinaria stenocephala*) was found in brown bears (*Ursus arctos caucasicus*) from the vicinity of the Caspian Sea (Rukhliadev and Rukhliadeva 1953, Sadykhov 1962).

In North America, a new species of hookworm, *Uncinaria* (= *Dochmoides*) *yukonensis*, was described by Wolfgang (1956) from specimens collected from one of two wild black bears in Yukon Territory, Canada. Choquette *et al.* (1969) found the same species in 10 of 21 wild grizzly bears from the same area, and Jonkel and Cowan (1971) found it in a wild black bear in Montana. Worley *et al.* (1976), also working in Montana, found *Uncinaria* (species not given) in 1 of 30 wild black bears and in 12 of 69 wild grizzly bears. *U. yukonensis* was reported from both black and brown bears in Alaska (Rausch 1961; 1968). Additionally, Olsen (1968) described a new species of hookworm, *U. rauschi*, which is found in both black and brown bears in Alaska.

In the Philadelphia Zoo, Canavan (1929) found many stomach-worms (*Haemonchus contortus*) in the duodenum and large intestine of a 19-year-old polar bear. Stomach-worms more commonly live in the abomasum of certain ruminants. In the same zoo, *Cyathostoma bronchiale*, which usually is a parasite of the respiratory passages of waterfowl, was found in the small intestine of a brown bear (*Ursus arctos collaris*) (Stiles and Baker 1935).

Extra-intestinal Nematodes

Diesing (1851) listed *Nematoideum ursi*, a parasite of *Ursus arctos*, as *genere penitus dubia* and listed *Taenia ursi* in the synonymy of *N. ursi*. *Taenia ursi* has been reported as a parasite of bears (species not given) by Gmelin (1790).

King *et al.* (1960) found a new species of lungworm of the genus *Crenosoma* in the larger air passages of 3 of 53 wild black bears in New York, but they did not find it in 17 captive black bears. Bromlei (1965) found unidentified nematodes averaging 300 mm long and 1.5 mm thick in the bronchi of a wild Himalayan bear in south-eastern USSR. Hosford *et al.* (1942) noted that black bears are known to have been infected with the eye worm (*Thelazia californiensis*) in California, but they did not provide specifics. Hutyra *et al.* (1946) reported that the kidney worm (*Dioctophyma renale*) was found free in the abdominal cavity of an unidentified bear.

Chandler (1950) found numerous *Gongylonema pulchrum*, which more commonly parasitize the esophagus or rumen of ungulates, in the tongue of an emaciated, moribund, wild black bear in Pennsylvania. Chandler pointed out that there is no way to distinguish *G. pulchrum* from '*Spiroptera ursi*', reported for the European brown bear by Rudolphi (1819), or from *Gongylonema contortum*, reported for the same host by Molin (1860).

Dirofilaria ursi, a filarial worm, first was reported from *Selenarctos thibetanus japonicus* from Japan (Yamaguti 1941). In the Old World, the species also was reported from *Ursus arctos beringianus* from Sakhalin Island, Siberia (Petrov and Krotov 1954) and from a brown bear from south-eastern USSR (Oshmarin 1963). Choquette (1952) obtained filarial worms from the abdominal cavities and the submucosa of the esophagus of wild black bears from Ontario and Quebec. He provisionally described the material as a new species, *Dirofilaria desportesi*; but after Anderson (1952) redescribed *D. ursi* from material obtained in southern Ontario, Choquette *et al.* (1969) placed the name *D. desportesi* in the synonymy of *D. ursi*. Anderson (1952) found *D. ursi* in the subcutaneous tissue of each of 20 wild black bears from Algonquin Park, Ontario. King *et al.* (1960) found adults in 3 of 55 wild black bears and found microfilariae (larvae of *Dirofilaria*) in the blood of 34 of 36 wild black bears in New York. However, this parasite, which is transmitted by mosquitoes, was not found in the blood of 17 black bears from zoos in New York (King *op. cit.*). Rogers (1975) found adult *D. ursi* in wild black bears in Michigan and Minne-

sota. Rogers and Seal (unpublished) found microfilariae in the blood of each of 47 wild black bears 14 months of age or older in Minnesota. Rausch (1961) stated that he collected *D. ursi* only once from a black bear in Alaska, although the same parasite is common there in the brown bear. Similarly, Worley *et al.* (1976) did not find *Dirofilaria* in 30 wild black bears in Montana but did find it in 2 of 13 wild grizzly bears. In the same state, Jonkel and Cowan (1971) found *D. ursi* in two wild black bears. Choquette *et al.* (1969) found *D. ursi* in 3 of 27 wild grizzly bears from north-western Canada.

Trichinella spiralis in bear meat poses a potential public health hazard, and workers have given considerable attention to determining the prevalence of this nematode in various geographic areas. *Trichinella* was found in polar bears in zoos in Germany (Bohm 1913), London (Leiper 1938), and Philadelphia (Canavan 1929, Brown *et al.* 1949). Grjuner (1915) reported trichinosis as the cause of death of a captive European brown bear that was fed trichinous rats. However, documentation that trichinosis was the cause of death was not provided.

Doege *et al.* (1969) reported *Trichinella* in a wild Himalayan black bear in Thailand. Reports of *Trichinella* in wild polar bears, brown bears and black bears are summarized in Tables 1, 2 and 3, respectively. The combined data

TABLE 1. SUMMARY OF REPORTS OF *TRICHINELLA SPIRALIS* IN WILD POLAR BEARS *URSUS MARITIMUS*.

Geographic location	Number examined	Number infected	(Percent infected)	Source
Alaska	17	9	(53)	Rausch <i>et al.</i> 1956
Alaska	104	57	(55)	Fay 1960
Canada*	—	—	—	Cameron 1960
Southampton I., Canada	3	2	—	Brown <i>et al.</i> 1948
Greenland	16	6	(39)	Thorborg <i>et al.</i> 1948
Greenland	112	31	(26)	Roth 1950
Greenland	231	56	(24)	Madsen 1961
Svalbard	7	7	—	Brown <i>et al.</i> 1949
Svalbard	8	7	—	Connell 1949
Norwegian and Barents Seas	278	163	(59)	Thorshaug and Rosted 1956
Rudolph Land I.*	—	—	—	Kozemjakin 1959
Paleartic*	—	—	—	Brusilovskiy 1957
N.E.Siberia	19	1	(5)	Ovsjukova 1965
Holarctic Total	795	339	(42.6)	Average of all reports

* One or more infected bears were found at this location, but the number of bears examined was not reported.

TABLE 2. SUMMARY OF REPORTS OF *TRICHINELLA SPIRALIS* IN WILD BROWN-GRIZZLY BEARS *URSUS ARCTOS*.

Geographic location	Number examined	Number infected	(Percent infected)	Source
Alaska	20	10	(50)	Rausch <i>et al.</i> 1956
N.W. Canada	24	21	(86)	Choquette <i>et al.</i> 1969
Montana	171	103	(60)	Worley <i>et al.</i> 1976
California*	—	—	—	Walker 1932
USSR	1	1	—	Lukashenko <i>et al.</i> 1971
N.E.Siberia	19	11	(58)	Ovsjukova 1965
E.Siberia	14	2	(14)	Toshev 1963
N. Siberia	10	0	(0)	Gubanov 1964
Caucasus mountains	5	0	(0)	Rukhliadev and Rukhliadeva 1953
Azerbaijan*	—	—	—	Sadhykov 1962
Germany*†	—	—	—	von Bockum-Dolffs 1888
Holarctic Total	264	153	(59.8)	Average of all reports

* One or more infected bears were found at this location, but the number of bears examined was not reported.

† Species not given, presumably *Ursus arctos*.

show a higher incidence of *Trichinella* in brown bears (59.8 percent) and polar bears (42.6 percent) than in black bears (3.2 percent). The data do not support the hypothesis advanced by King *et al.* (1960), Brown (1967) and Wand and Lyman (1972) that garbage is the main source of trichinosis in bears. In general, the data suggest that a higher proportion of the bears are infected in remote areas than in areas with a dense human population. Worley *et al.* (1974) also noted that in the United States trends of trichinosis in grizzly bears 'strongly suggest that the availability to bears of infected sources of food was inversely proportional to their degree of association with civilization.' Madsen (1961), Zimmermann and Hubbard (1969), Rausch (1970) and Lukashenko *et al.* (1971) suggested that, for carnivores, carcasses of other carnivores are a major source of *Trichinella*. Madsen (1961), Rausch (1970) and Rogers (1975) suggested that cannibalism of carcasses could be a major source of infection for bears. In fact, 12 of 13 carcasses of black bears in Minnesota were cannibalized, often by more than one bear (Rogers *op. cit.*).

In remote areas of the Far North, hunting increases the number of carcasses available to bears because hunters usually leave carcasses in the field after skinning them (Rausch 1970). Conversely, in areas that are accessible by road, hunters usually use both the meat and hides of bears and leave only gut piles (Dahlen 1959). *Trichinella* larvae usually are not found in visceral organs (Soulsby 1968), so gut piles usually are not infective unless they contain the diaphragm. Hence, intense hunting pressure in accessible areas may reduce the number of carcasses available to bears if hunting deaths tend to replace natural deaths and crippling losses are less than the natural death rate. Hunt-

TABLE 3. SUMMARY OF REPORTS OF *TRICHINELLA SPIRALIS* IN WILD BLACK BEARS *URSUS AMERICANUS*.

Geographic location	Number examined	Number infected	(Percent infected)	Source
New York	49	3	(6)	King et al. 1960
Vermont	35	0	(0)	Babbott & Day 1968
Vermont*	—	—	—	Roselle et al. 1965
New England	372	5	(1.3)	Harbottle et al. 1971
Michigan	23	0	(0)	Zimmermann 1974†
Wisconsin	163	6	(3.8)	Zimmermann 1974†
Minnesota	6	0	—	Zimmermann 1974†
Colorado	66	0	(0)	Zimmermann 1974†
New Mexico	14	0	(0)	Zimmermann 1974†
Arizona	4	0	—	Zimmermann 1974†
Wyoming	15	0	(0)	Zimmermann 1974†
Montana	80	5	(6.3)	Worley et al. 1976
Idaho	44	1	(2.3)	Zimmermann 1974†
Oregon	50	0	(0)	Zimmermann 1974†
California	54	7	(13)	Zimmermann 1974†
Alaska	1	0	—	Zimmermann 1974†
S. Alaska	23	5	(22)	Rausch et al. 1956
United States (Total)	999	32	(3.2)	Average of all reports

* One or more infected bears were found at this location, but the number of bears examined was not reported.

† Personal communication.

ing pressure in the eastern United States is intense (Stickley 1961, Wakefield 1972) and may account in part for the low incidence (1.3 percent) of *Trichinella* in bears there.

ARTHROPODS

Lice

Lice, *Trichodectes pinguis pinguis*, were reported from brown bears in Europe by Burmeister (1838) and Werneck (1948) and from a Himalayan black bear in zoo in Paris by Neumann (1913). Bromlei (1965) found unidentified lice on a wild Himalayan bear in southeastern USSR.

In North America, a new subspecies of louse (*Trichodectes pinguis euarctidos*) was described by Hopkins (1954) from specimens obtained from black bears in Ontario and British Columbia. This subspecies also was found on wild black

bears in Michigan (Rogers 1975), Minnesota (unpublished data), New York on 23 of 306 examined (King *et al.* 1960), and Montana on 2 of 153 examined (Jonkel and Cowan 1971). Worley *et al.* (1976) found *Trichodectes* (species not given) on 1 of 6 wild black bears in Montana. No lice have been reported from grizzly-brown bears from North America.

Fleas

For the fleas, we have followed the classification of Hopkins and Rothschild (1956). Fleas identified as *Chaetopsylla setosa* were reported from wild black bears in southern British Columbia (Rothschild 1906, Hopkins and Rothschild 1956) and Montana (Hubbard 1947) and from wild grizzly bears from British Columbia (Jellison and Good 1942, Ewing and Fox 1943, Holland 1949).

A larger species of flea, *Chaetopsylla (Arctopsylla) tuberculiceps ursi*, was reported from wild grizzly bears in southern Alberta (Rothschild 1902, Hopkins and Rothschild 1956), southern British Columbia (Holland 1949), and Alaska (Rausch 1961). The same subspecies was found on wild black bears in south-central Alaska (Jellison and Kohls 1939) and in Montana (Hubbard 1947). In Montana, Jonkel and Cowan (1971) found it on 4 of 153 live-trapped black bears, and Worley *et al.* (1976) found *Chaetopsylla* spp. on 1 of 3 wild grizzly bears.

Another subspecies, *Chaetopsylla tuberculiceps tuberculiceps*, was reported from brown bears from Norway, Russia and the Italian Alps (Hopkins and Rothschild 1956). The close taxonomic relationship between *C. t. tuberculiceps* of Eurasia and *C. t. ursi* of North America is shown by the fact that fleas with characteristics intermediate between the two subspecies were collected from a wild brown bear (*Ursus arctos yesoensis*) on the island of Hokkaido, Japan (Sakaguti 1960). The specimens from Japan tentatively were classified as *C. t. tuberculiceps* (Sakaguti *op. cit.*).

Another flea, *Thrassis spenceri*, was reported from a grizzly bear from British Columbia (Hubbard 1947). This species of flea usually lives on marmots (*Marmota*) which occasionally may be eaten by grizzly bears. *Pulex irritans* were collected from four wild black bears in northern California by D. Kelley-house and were identified by H. Egoscue (Egoscue 1975, pers. comm.). Worley *et al.* (1976) found fleas tentatively identified as *Pulex* sp. on one of six wild black bears in Montana.

Fleas apparently are less common on bears in eastern North America. King *et al.* (1960) found no fleas on 306 wild black bears in New York. However, unidentified fleas were found on a wild black bear in Michigan (Rogers 1975), and a large population of *Orchopeas caedens*, which usually are associated with red squirrels (*Tamiasciurus*), were found in Minnesota in the den of a young bear a few days after the bear had left the den. The bed in the den was undisturbed, and there was no sign that any animal other than the bear had used the den.

Acarina

In North America, wood ticks (*Dermacentor andersoni*) were found on wild grizzly bears in Montana and on wild black bears in Montana and Colorado (Henshaw and Birdseye 1911, Cooley 1938, Horstman 1949, Worley *et al.* 1975). Jonkel and Cowan (1971) found *D. andersoni* on each of 117 black bears captured in Montana during May and June but found none on 36 black bears captured in late summer. Jonkel and Cowan stated that infestations in spring generally were heaviest on subadult bears, possibly because 'subadults are in poorer

condition than the adults at this time of year, [and] they probably have more difficulty resisting ectoparasites'.

Rogers (1975) collected dog ticks (*Dermacentor variabilis*) from wild black bears in Michigan and Minnesota during late spring and early summer, and Dodds *et al.* (1969) took the same species from a wild black bear in Nova Scotia. Rogers (1975) also reported 30 winter ticks (*D. albipictus*) from one of seven adult bears examined in dens in Minnesota in late March; two 2-month-old cubs in the den with the infested bear were free of ticks. King *et al.* (1960) found soft ticks of the genus *Ixodes* (tentatively identified as *I. cookei*) on 4 of 306 wild black bears in New York.

In the Old World, *Ixodes ricinus* and *Dermacentor cf. venustus* were found on brown bears in the Pyrenees (Couturier 1954). Bromlei (1965) reported that although Himalayan bears and brown bears in south-eastern USSR commonly are infested with large numbers of ticks (*Dermacentor silvarum*, *Haemaphysalis japonica douglasi* and *Ixodes persulcatus*) during late spring and summer, only one of 19 Himalayan bears examined during winter carried ticks (*Ixodes persulcatus*). Again, newborn cubs denning with the infested bear were free of ticks.

Dermacentor auratus and *Haemaphysalis hystricis* were collected from Himalayan black bears in Burma, and *H. formosensis* was taken from the same host in Taiwan (Stiles and Baker 1935). *Haemaphysalis hystricis*, *H. leachi* and *H. semermis* were found on sun bears (*Helarctos malayanus*) in Malaya (Stiles & Baker 1935, Hoogstraal *et al.* 1966). Stiles and Baker (*op. cit.*) reported several additional ticks (*Dermacentor compactus*, *Hyalomma aegyptium*, *H. hussaini*, *H. monstrossum*, *Rhipicephalus haemaphysaloides*, *R. sanguineus*, *Haemaphysalis spinigera* and *H. bispinosa*) from unidentified bears. The locality of *H. bispinosa* was not given, but all others were listed as from India.

Fain and Johnston (1970) described a new species of mite (*Ursicoptes americanus*) from the skin of a captive black bear in Europe. Neumann, in 1892, reported *Sarcoptes scabiei* from a wild brown bear from the Pyrenees (Couturier 1954).

HOST LISTS

No reports of parasites were found for the spectacled bear (*Tremarctos ornatus*) of South America, and only one report was found of a parasite from the giant panda *Ailuropoda melanoleuca*. That parasite, an ascarid worm (*Baylisascaris schroederi*), has been reported only from the giant panda (Sprent 1968).

Parasites of Polar Bears

Seven parasites were reported from polar bears, but only one, *Trichinella spiralis*, was reported as being from a wild host. The remaining six species of parasites include three species of nematodes (*Haemonchus contortus*, *Dochmius ursi* and *Baylisascaris transfuga*) and three cestodes (*Diphyllobothrium latum*, *Bothriocephalus* sp. and *Taenia ursi-maritimi*).

Parasites of Black Bears

Thirty-one parasites have been reported from black bears in North America. These include two protozoa (*Eimeria albertensis* and *E. borealis*), a trematode

(*Nanophyetus salmincola*), the rickettsia-like agent of Elokomin fluke fever transmitted by *N. salmincola*, ten cestodes (*Taenia saginata*, *T. pisiformis*, *T. krabbei*, *T. hydatigena*, *Anacanthotaenia olseni*, *Mesocestoides krulli*, *Diphyllobothrium latum*, *D. cordatum*, *D. cordiceps* and *D. ursi*), nine nematodes (*Baylisascaris transfuga*, *B. multipapillata*, *Uncinaria yukonensis*, *U. rauschi*, *Crenosoma* sp., *Thelazia californiensis*, *Gongylonema pulchrum*, *Dirofilaria ursi* and *Trichinella spiralis*), and eight arthropods (*Trichodectes pinguis euarctidos*, *Chaetopsylla setosa*, *C. tuberculaticeps ursi*, *Pulex irritans*, *Ixodes* sp. (probably *cookei*), *Dermacentor andersoni*, *D. variabilis* and *D. albipictus*). In addition, a mite (*Ursicoptes americanus*) was reported from a captive black bear in Europe, and numerous fleas (*Orchopeas caedens*) were found in the den of a wild black bear in Minnesota a few days after the den was abandoned.

Parasites of Brown-grizzly Bears in North America

Fifteen parasites have been reported from brown-grizzly bears in North America. These include a trematode (*Echinostoma revolutum*), three cestodes (*Taenia krabbei*, *Diphyllobothrium latum* and *D. ursi*), six nematodes (*Baylisascaris transfuga*, *Cyathostoma bronchiole*, *Uncinaria yukonensis*, *U. rauschi*, *Dirofilaria ursi* and *Trichinella spiralis*), and five arthropods (*Chaetopsylla setosa*, *C. tuberculaticeps ursi*, *Thrassis spenceri*, *Pulex* sp. and *Dermacentor andersoni*). Eleven of these species also were reported from wild black bears.

Parasites of Brown Bears in Eurasia

Twenty-eight parasites have been reported from brown bears from the Old World. These include two protozoans (*Eimeria ursi* and *Isoospora fonsecai*), a trematode (*Nanophyetus salmincola*), and presumably the rickettsia-like agent of Elokomin fluke fever carried by *N. salmincola*, five cestodes (*Diphyllobothrium latum*, *D. cordatum*, *Taenia ursina*, *Cysticercus cellulosae* and *Bothriocephalus ursi*, eleven nematodes (*Nematoideum ursi*, *Dochmius ursi*, *Spiroptera ursi*, *G. contortum*, *Baylisascaris transfuga*, *B. multipapillata*, *Toxocara canis*, *T. mystax*, *Uncinaria stenocephala*, *Dirofilaria ursi* and *Trichinella spiralis*), and eight arthropods (*Chaetopsylla t. tuberculaticeps*, *Trichodectes p. pinguis*, *Ixodes persulcatus*, *I. ricinus*, *Dermacentor silvarum*, *D. cf. venustus*, *Haemaphysalis japonicus douglasi* and *Sarcoptes scabiei*).

Parasites of Himalayan Black Bears

Thirteen parasites have been reported from Himalayan black bears in south-east Asia or Japan. These include a trematode (*Dicrocoelium lanceatum*), a cestode (*Taenia* sp.), five nematodes (*Baylisascaris transfuga*, *Ancylostoma malayanum*, *Dirofilaria ursi*, *Trichinella spiralis*, and unidentified nematodes from the bronchi), six ticks (*Ixodes persulcatus*, *Haemaphysalis formosensis*, *H. hystricis*, *H. japonicus douglasi*, *Dermacentor silvarum* and *D. auratus*), and unidentified lice. In addition, a louse (*Trichodectes p. pinguis*) was reported from a Himalayan black bear in the Paris Zoo.

Parasites of Sun Bears

Five parasites have been reported from sun bears in southeast Asia. These include a cestode (*Pentorchis arkteios*), a hookworm (*Ancylostoma malayanum*), and three ticks (*Haemaphysalis semermis*, *H. leachi* and *H. hystricis*).

Parasites of Sloth Bears

Five nematodes (*Baylisascaris transfuga*, *B. melursus*, *Ancylostoma malayanum*, *A. brasiliense* and *A. caninum*) were reported from sloth bears in India.

Parasites of Unidentified Bears

Seven ticks (*Hyalomma aegyptium*, *H. hussaini*, *H. monstrosus*, *Rhipicephalus sanguineus*, *R. haemaphysaloides*, *Haemaphysalis spinigera* and *Dermacentor compactus*) were listed from unidentified bears from India. Five other parasites from unidentified bears include two protozoans (*Babesia* sp. and *Leishmania* sp.), the larval form of a cestode (*Echinococcus granulosus*), a nematode (*Dioctophyma renale*), and a tick (*Haemaphysalis bispinosa*).

PARASITISM OF BEARS DURING HIBERNATION

Bears that live in northern latitudes hibernate during cold seasons when food is scarce (Folk *et al.* 1976). In Alaska and northern Canada, denning begins as early as September and ends as late as mid-May (Rausch 1961, Choquette *et al.* 1969). During hibernation, bears usually do not eat, and the metabolic rate is reduced markedly (Maxwell *et al.* 1972, Folk *et al.* 1976). Several authors (Rush 1932, Rausch 1954, 1961, Bromlei 1965, Choquette *et al.* 1969, Rogers 1975) have presented evidence that intestinal parasites that derive nourishment directly from the ingesta of the host pass out of the alimentary canal before hibernation begins. Rausch (1961) stated 'Ascarids may be found in considerable numbers in bears during the fall, but they are evidently lost prior to denning (unpublished data).'

Choquette *et al.* (1969) found *B. transfuga* in 16 of 21 grizzly bears examined in north-western Canada between mid-May and mid-October but found ascarids in only one of five grizzlies examined during November through early May. The infected bear probably had not begun its winter sleep when killed in December and still may have been feeding on frozen salmon.

Rogers (1975) collected 962 fecal droppings throughout the year from wild black bears in Minnesota. Ascarids (*Baylisascaris transfuga*) were found only in droppings passed on 9 September, 6 October and 16 October. The bear that passed ascarids on 9 September began denning ten days later.

Rush (1932) obtained strobilae of *Diphyllobothrium* from droppings of three of five black bears treated with an anthelmintic medicine in late summer. He obtained no strobilae from five bears treated similarly but from a different area in October. Rausch (1954) reiterated reports from a professional hunter, noting that each of 11 brown bears killed on Kodiak Island in September contained cestodes, but that none was found in six bears killed after 20 October. Five bears killed during June before they could become reinfected by eating salmon also appeared to be free of cestodes. On the other hand, Rausch (1954) also reported that, according to a biologist on Kodiak Island, an old bear killed on 26 December contained approximately 500 cestodes.

Some *Diphyllobothrium* may survive through winter by means of destrobilization (Rausch 1961). *Diphyllobothrium* with only slightly developed strobilae were found in the intestine of a female black bear killed at its den in Alaska on 26 February (Rausch *op. cit.*).

Helminths that do not derive nourishment directly from the ingesta of the host apparently are not lost during denning. Rausch (1961) and Choquette *et al.*

(1969) found hookworms (*Uncinaria yukonensis*) in denning black and grizzly bears, and Rogers (1975) collected winter ticks (*Dermacentor albipictus*) and adult *Dirofilaria ursi* from denning black bears. However, Rogers and Seal (unpublished data) found that microfilariae were much less abundant in blood samples taken from bears during the summer.

Life cycles of fleas (*Chaetopsylla*) that infest bears have yet to be documented but probably are tied to the denning habits of their hosts. Fleas typically leave their host as adults to lay eggs in bedding material. There the eggs hatch, and the young develop and wait for a suitable host. For fleas to build up a high population on a given host, the host must return to beds where fleas have bred. Perhaps one reason that few black bears carry heavy populations of fleas is that the black bear tends to use a different den each winter and a different bed each night during the summer (unpublished data). However, a large population of fleas (*Orchopeas caedens*) was found in the recently abandoned den of a young bear in Minnesota (unpublished data). Presumably if certain fleas reach the den of a bear, they can build large populations during the denning period which is longer than six months in many cases.

SUMMARY

At least 77 species of parasites have been reported from bears, but there is no evidence that parasites are a common cause of mortality. Pathological effects usually are not apparent in parasitized bears (Horstman 1949, Rausch 1955, Jonkel and Cowan 1971, Poelker and Hartwell 1973). However, in two exceptional cases, captive bears died because helminths became located in unusual sites where they occluded passageways (Mozgovoi 1953, Rausch 1955, Poelker and Hartwell 1973). Four heavily parasitized wild bears in poor condition have been reported (Rush 1932, Chandler 1950, Martin 1950, Jonkel and Cowan 1971), but in each case it was impossible to distinguish cause from effects, i.e. whether the poor condition was caused by parasites or whether parasites took over because the bear already was weakened. In the latter situation, parasitism easily could lead to further deterioration of health.

Parasites of bears from northern regions apparently are well adapted to the hibernating and fasting habits of their hosts. Intestinal parasites that derive nourishment directly from materials ingested by the host usually pass out of the alimentary canal before hibernation begins. Further study is needed to determine whether or not the demands of parasites that derive nourishment from blood or other body fluids are reduced while the host is hibernating.

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Paper 43

Succinylcholine Chloride Immobilization of Black Bears

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INTRODUCTION

Succinylcholine chloride is a potent relaxant of voluntary striated muscle but has little direct effect on smooth muscle. It has no anesthetic or pain-obliterating properties; therefore, immobilized animals remain completely conscious although unable to move. The duration of effect is quite brief because succinylcholine is rapidly destroyed by non-specific cholinesterases in the blood plasma and liver. Immobilization lasts five to 12 minutes in man and horses and somewhat longer in other species, with ruminants generally requiring longest recovery periods (Stowe *et al.* 1958).

Since the discovery of its curariform properties in 1949, succinylcholine has been widely used for immobilization of animals and in human surgical procedures. Several workers have used succinylcholine on bears (Black 1958, Knudsen 1959, Craighead *et al.* 1960, Troyer *et al.* 1961, Hornocker 1962, Mundy 1963, Pearson *et al.* 1968, Jonkel and Cowan 1971 and Mundy and Flook 1973).

Despite its common usage, the disadvantages of this drug and the factors that modify its effects are not well known. Certain of these aspects were investigated in the course of population studies of black bears (*Ursus americanus*) in the Upper Peninsula of Michigan during 1966 through 1968 and in northeastern Minnesota during 1969.

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METHODS AND MATERIALS

For preliminary studies, three bears which were to be killed were confined in

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pens and used for comparative study of the effects of injection into different tissues and for evaluation of the dose-effect relationship. One of them, a 194 kg animal, was given nine equal doses (117 mg each) over a period of two weeks by means of projectile syringes equipped with 2.5 cm needles. Each dose was injected into a different area of the body, and the time from injection to collapse was noted. Entry points were marked by shaving the areas around them. After the bear was sacrificed, the entry points were dissected to determine the types of tissue into which each dose had been injected. In this way, the relationship between the type of tissue at the point of injection and time to onset of effects were learned.

To determine how responses varied with dosage, the two other bears were given injections that ranged from ineffective dosages (< 0.10 mg/kg) to lethal dosages (>2.0 mg/kg). These were administered intramuscularly at intervals of 24 hours or longer. Effects of each dose were recorded; following sacrifice of the bears, the entry points of the syringes were examined for subdermal tissue damage.

In field studies in Michigan, 191 immobilizations of black bears were accomplished by several methods. A pole-mounted syringe (Black *et al.* 1959) was used to inject 112 box-trapped and two treed bears. A syringe gun was used to inject 73 free-ranging bears (in garbage dumps or campgrounds) and four animals caught in leg-hold traps. Approximately twenty additional free-ranging bears escaped into heavy cover after being darted. Intramuscular injection was intended in all cases.

Doses generally were prepared from crystalline succinylcholine chloride (Anectine, Burroughs, Wellcome and Company) by dissolving 100 mg amounts into one ml of distilled water just prior to use, making a concentration of approximately 90.0 mg/ml. In a few cases, commercial solutions such as Sucostrin (E.R. Squibb and Sons Company, 20 mg/cc) or Quelicin (Abbott Laboratories, 25 mg/cc) were used. These solutions lose potency at a rate of about 3 percent per month at room temperature, so they were carried afield in an ice chest. A dosage of 0.75 mg of succinylcholine per kilogram of estimated bodyweight generally was given after experience showed that lower dosages often were insufficient. Immobilization was prolonged with sodium pentobarbital (Erickson 1957).

Data routinely recorded included sex, date, weight, dose, manner of delivery of drug, undesirable effects, and latent period. The terms *latency* or *latent period* were used to denote the time between injection and immobilization. Bears were considered to be immobilized when they were unable to stand. All bears were observed for at least an hour and then hidden in the brush. Recoveries were confirmed by examining release sites a day or two later.

The hearts of three bears (one from Michigan and two from Minnesota) that died during immobilization were examined macroscopically and compared with the hearts from six bears that were shot. The only data reported from the Minnesota study are mortality data.

RESULTS

Penned Animals

The effectiveness of succinylcholine injections in the 194 kg bear mentioned above varied with the vascularity of the tissue at the site of the injection (Table 1). Injections into muscle produced immobilization in approximately two

TABLE 1. SUMMARY OF NINE IMMOBILIZATION ATTEMPTS USING EQUIPONDERANT DOSES OF SUCCINYLBCHOLINE INJECTED INTO DIFFERENT AREAS OF A 194 kg BEAR. *

Injection number	Date	Site of Injection	Tissue Type	Response
1	8-18	rump	Entry hole not discernable	Latency 8 minutes
2	8-21	left shoulder	muscle	Latency 2 minutes, duration 38 min.
3	8-23	high on rump on midline	10 cm of fat under skin	No visible effects
4	8-24	high on rump on midline	10 cm of fat under skin	No visible effects
5	8-26	middle of side near last rib	2.4 cm of fat under skin and covering 2 cm of muscle covering 7th rib	Latency 13 minutes, duration 73 min.
6	8-28	high on neck	0.6 cm of skin and 0.9 cm of fat covering muscle	Latency 4 minutes, duration 100 min.
7	8-29	posterior side of upper hind leg	Dart bounced out upon discharging	No visible effects. Blood and drug ran out of entry hole.
8	8-30	side of chest behind shoulder	skin 0.5 cm, fat 1.2 cm, muscle 0.3 cm, fat 3 cm	Latency 8½ minutes, duration 52 min.
9	9-1	upper part of hind leg	5 to 8 cm of fat	No visible effects. Dart bounced out and exact point of entry could not be found.

*All injections were of 117 mg. (0.6 mg/kg) and were given by means of projectile syringes equipped with 2.5 cm needles.

minutes (Injection 2, Table 1), but injections of the same dosage into fat resulted in prolonged latent periods (Injections 5, 6 and 8, Table 1) or no visible effect (Injections 3 and 4, Table 1) depending upon the thickness of the fat. One dose (Injection 7, Table 1) that was injected into vascular tissue was washed out of the entry hole by blood, and no visible effects ensued.

Increasing the dosage in the other two penned bears resulted in only slightly and inconsistently reduced latent periods. The median latent period was two minutes and ranged from one to four minutes in 37 of the 40 successful immobilizations. Six injections failed to produce immobilization because they were injected into fat or were otherwise faulty. Two of these failures resulted when blood and drug ran out of holes that remained in the skin after projectile syringes discharged and fell away. In general, it appeared that latency was affected less by dosage than it was by the vascularity of the tissue into which the drug was injected. Peak immobilization and paralysis occurred within fifteen minutes of collapse at all dosages.

Dissection of punctures from projectile syringes revealed pockets in subcutaneous fat. These pockets, which varied in size according to the amount of solution injected, apparently were created by the explosive entry of drugs expelled from syringes by powder charges.

Wild Bears in the Field

Extensive field studies in Michigan involved 191 immobilizations of 186 wild bears of both sexes representing various age and weight groups. Data from penned bears were not combined with data from wild bears.

General Reactions to Injections

Most free-ranging bears ran for heavy cover after being struck by projectile syringes. They usually collapsed within 2½ minutes but still were able to move their heads and bite for another minute or so. Respiratory muscles were the last to be affected and the first to recover.

Many bears in box traps already were lying down when succinylcholine chloride took effect. In these animals, transient muscle fasciculation, which often appeared as a wave-like rippling under the skin, and drooping of the head were taken as signs of adequate immobilization. Approximately 76 percent (84 of 111) of the trapped bears were immobilized with initial injections.

During peak immobilization, the thoracic component of respiration often was depressed; and respiration appeared to be accomplished mainly by abdominal movements which appeared to be diaphragmatic. In 21 (11 percent) of the 191 immobilizations, respiration was depressed to the point that artificial respiration was required to prevent death. Spontaneous respiration usually resumed within fifteen minutes of collapse; but in one case, artificial respiration was necessary for 55 minutes.

Dosage

Dosage data suitable for analysis were obtained from 177 immobilization attempts. Nine attempts involved cubs and will be considered separately (see below). Data from the remaining 168 bears were divided into the following four response groups:

- I. Bears not immobilized (n = 27; median dosage 0.55 mg/kg)

- II. Bears immobilized and breathing adequately ($n = 118$; median dosage 0.80 mg/kg)
- III. Bears requiring artificial respiration and recovering ($n = 14$; median dosage 1.0 mg/kg)
- IV. Bears that died ($n = 9$; median dosage 1.2 mg/kg).

Data from males (112) and females (56) were subjected to Duncan's Multiple Range Test which indicated no significant differences in response due to sex.

Application of the same test showed that the dosages of groups I, II and III were significantly different from one another ($P < 0.05$), indicating that response was at least partially dependent upon dosage. Dosage differences between bears that required artificial respiration and recovered (Group III) and those that died (Group IV) were not significant after the datum from one bear accidentally given a triple dose (2.4 mg/kg) was deleted from Group IV. Groups II, III and IV include data from both trapped and free-ranging bears, but Group I includes data only from trapped bears.

Data for the 168 bears were used to construct dose-response curves (Marsh 1951) in which dosages were plotted against percentages of animals that were immobilized (Curve A, Fig. 1) or that died or experienced prolonged respiratory paralysis (Curve B, Fig. 1). (Death from apnea was prevented by artificial respiration, and 14 of the 23 animals comprising Curve B were revived.) The 20 free-ranging bears that escaped were not considered in construction of the dose-response curves; hence, the percentages indicated in Curve A should be regarded as maxima and actually could be as much as 9 percent lower if all of the 20 failed to become immobilized. Similarly, Curve B would be too low if

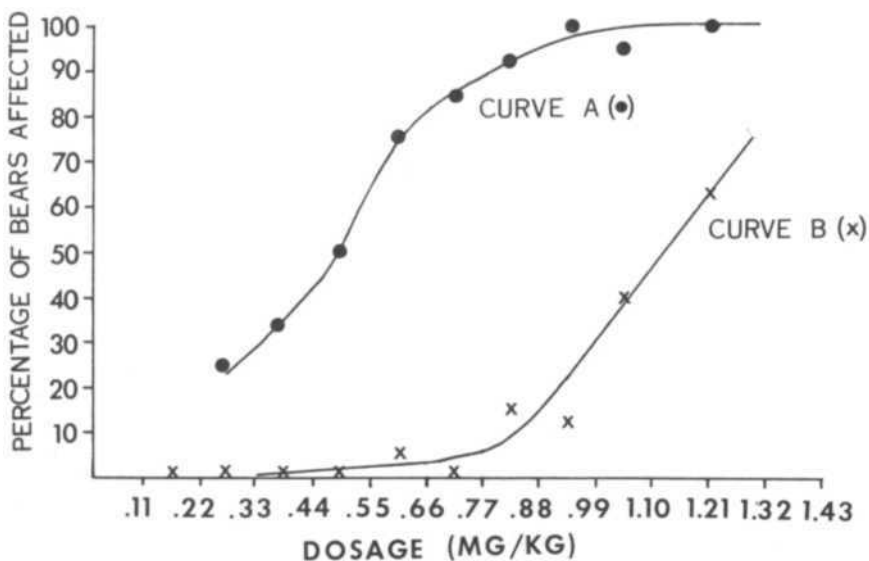


Fig. 1 Dose-response relationship of 168 wild bears to succinylcholine chloride. Curve A shows percentage of animals immobilized at each dosage. Curve B shows percentage that required artificial respiration or died at each dosage. A concentration of 90 mg/cc was used in most cases.

TABLE 2. RELATIONSHIP BETWEEN SUCCINYLCHOLINE DOSAGE AND NUMBER OF SUCCESSFUL IMMOBILIZATIONS WITH LATENCY LESS THAN 1 AND LESS THAN 2.5 MINUTES.

Mg/kg	Number of Immobilizations	Number with latency less than 2.5 minutes	Number with latency less than 1 minute
0.33	10	2 (20%)	1 (10%)
0.50	15	6 (40%)	2 (12%)
0.66	31	18 (60%)	4 (13%)
0.75	32	29 (90%)	14 (45%)
0.9	30	28 (92%)	12 (40%)
1.0	22	17 (80%)	11 (50%)
1.1	9	8 (88%)	6 (67%)
1.2	3	3 (100%)	2 (67%)
1.3	4	4 (100%)	4 (100%)

TABLE 3. RESULTS OF ADMINISTERING SUCCINYLCHOLINE CHLORIDE TO BLACK BEAR CUBS

Date	Sex	Weight in kg	Dose (mg)	Mg/kg	Response
6/29	male	7	18	2.6	slightly ataxic
6/29	female	7	18	2.6	slightly ataxic
7/28	female	9	18	2.0	required artificial respiration for 6 min.
7/28	female	9	14	1.6	no effect
8/9	male	10	10	1.0	immobilized in 3 minutes
8/9	male	11	12	1.1	no effect
8/12	male	14	4	0.3	no effect
8/14	female	11	18	1.6	immobilized in 15 min.—injected into body cavity.
8/14	male	14	18	1.3	immobilized in 85 seconds

any of the 20 bears died. However, bears that were able to run long enough to move beyond the area in which search efforts were concentrated probably did not die because long latent periods generally were associated with an absence of undesirable effects (see below).

Figure 1 indicates that respiratory paralysis and cardiac arrest were uncommon at dosages less than 0.75 mg/kg but were common among bears that received higher dosages. At a dosage of 1.1 mg/kg, approximately half of the animals required artificial respiration or died.

TABLE 4. DEATHS OF BLACK BEARS FROM DRUG(S)

Bear*	Date	Body weight (kg)	Succinyl-choline Chloride (mg/kg)	Latent period in sec.	Sodium Pento-barbital (mg/kg)	Time until death in min.	Sex
1 FR	7-12	114	1.0	90	none	<10	male
2 FR	7-27	31	2.3	30	none	<10	male
3 FR	7-28	48	0.86	30	none	<15	female
4 FR	7-30	34	0.95	60	none	<10	male
5 B	8-21	43	1.0	40	none	<15	male
6 FR	7-17	210	0.86	70	10.0	<15	male
7 B	6-20	88	1.2	60	37.0	15	male
8 B	7-19	34	1.3	45	32.0	40-60	female
9†FR	8-17	130	0.84	55	23.0	<20	male

*B = box-trapped; FR = free-ranging.

† Necropsy showed large fresh hemorrhagic areas in both ventricles of the heart.

Latency

Latent periods tended to become shorter as dosage was increased (Table 2). However, latent periods varied considerably at all dosages suggesting that other factors such as supply of blood to injected tissues also were important, as was observed in the penned bears.

Seventy-one bears became immobilized in less than 75 seconds, and 22 (31 percent) of these suffered undesirable affects. By comparison, only one (2 percent) of 58 bear;? with longer latent periods died or required artificial respiration.

Most (21 of 23) cases of respiratory paralysis or death occurred when dosages greater than 0.75 mg/kg were injected into tissue vascular enough to permit immobilization in less than 75 seconds. Undesirable effects occurred in 40 percent (21 of 54) of the cases in which both high dosage and rapid immobilization occurred.

Age

Nine cubs, which weighed 7 to 14 kg, were less sensitive to succinylcholine than were adults. Several of them were affected little by dosages up to 2.6 mg/kg, which probably would have been lethal for adults. However, one cub required artificial respiration after receiving a high dosage (2.0 mg/kg) (Table 3). The sensitivity of cubs seemed to increase through the summer; and by the time they were a year old, their sensitivity differed little from older bears.

Mortality

Twelve (6 percent) bears died in 191 succinylcholine chloride immobilization

in Michigan. All of the deaths but one occurred within 20 minutes of immobilization. Two bears died as a result of falling from trees while immobilized, one cub died from hemorrhage caused by a projectile syringe, and nine bears (4.5 percent) died from the effects of succinylcholine or pentobarbital (Table 4). For purposes of constructing dose-response curves, the latter nine deaths may have been a factor in two of them (Bears 7 and 8, Table 4).

In the Minnesota study, three of 18 succinylcholine-injected bears died. Terminal symptoms and necropsy data from these suggest that cardiac damage may be responsible for a significant percentage of the deaths from succinylcholine.



Fig. 2 Heart of an old 142 kg black bear that died 5-10 minutes after an intramuscular injection of 0.53 mg/kg of succinylcholine chloride. Note the hemorrhagic area (see arrows) on the left ventricle (below center) and on the right ventricle (upper left).

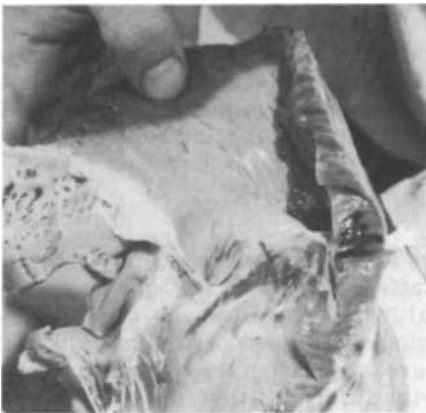


Fig. 3 Same heart as in Fig. 2 showing a cut made through a hemorrhagic area in the right ventricle. Blood draining into the heart from the hemorrhagic area indicates that the lesion was fresh.

Each of the three respired adequately and spontaneously for the first several minutes of immobilization. Then respiration became labored and gasping even though there was no flaccid paralysis of the thoracic muscles, and death ensued in one to three minutes. Palpation of thoraxes prior to death revealed no detectable heartbeat or only a grossly irregular beat. Terminal signs preceding death included jerking and twitching of individual muscles rather than the fasciculation that commonly accompanied immobilization. All three had been given succinylcholine only; one had received a single injection of only 0.53 mg/kg but the other two had received multiple injections. Two of the bears were necropsied immediately, and extensive, fresh endo- and epicardial hemorrhages were found (Figs. 2 and 3). The single bear from Michigan that was necropsied after immobilization (Bear 9, Table 4) also showed extensive, fresh endocardial hemorrhage. No such hemorrhages were found on the hearts of six bears shot by hunters.

DISCUSSION

Factors that influence the effectiveness of succinylcholine chloride were discussed by Rogers (1970). One such factor is the concentration of succinylcholine chloride solution.

Vanderveen *et al.* (1963) found in a controlled study of man that intramuscular doses of 100 mg/cc concentrations were less effective than equiponderant doses of 20 mg/cc concentrations. The differences may be due to an osmotic impediment in the absorption of hypertonic concentrations (a concentration of approximately 38 mg/cc is isotonic). Data in Table 5 suggest a correlation between high concentration and high dosage requirement. Possibly the relatively high concentration (90 mg/cc) used in this study was responsible in part for the relatively large dosages that were necessary to achieve immobilization. However, Harthoorn (1965) did not consider high concentrations to be less effective than equiponderant ones of lower concentration.

The effects of succinylcholine also may be influenced by body temperature. In summer, body temperatures of bears immobilized with succinylcholine range from 36.8 to 41.8°C, depending largely upon amount of exertion prior to immobilization (personal observations, Rogers). Knudsen (1959) reported that bears overheated in traps sometimes required additional doses to achieve immobilization. Similarly, Bigland *et al.* (1958) and Zaimis *et al.* (1958) showed that when body temperature was lowered experimentally, susceptibility to succinylcholine in cats increased. Susceptibility decreased when subjects were rewarmed. These effects of body temperature may be related to increased enzymatic destruction of the drug at higher temperatures (Foldes 1959).

The body temperature of bears during winter denning are from 3 to 7 °C lower than the usual summer body temperature of 38 °C (Hock 1951, Irving and Krog 1954, Hock 1957, Rausch 1961, Erickson and Youatt 1961), so prolonged immobilization would be expected in denned bears. However, to achieve immobilization in three denned bears, Jonkel and Cowan (1971) found that reduced dosages were insufficient.

Craighead *et al.* (1960) may have been the first to consider cardiac disturbance a possible cause of death for bears treated with succinylcholine. It is becoming increasingly clear that succinylcholine is a high risk drug when used under field conditions. There is no antagonist to succinylcholine, and some bears experience cardiac arrest (or apnea, Pearson *et al.* 1968) at dosages lower than those required to achieve immobilization consistently in bears. Cardiac dis-

TABLE 5. SUMMARY OF SUCCINYLBCHOLINE CHLORIDE DOSAGE DATA IN BEARS

Species	Number of Bears	Concentration in mg/cc	Recommended dosage in mg/kg	Range of dosages used successfully	Source
<i>U. americanus</i>	—	20-50	.60	—	Black (1958)
<i>U. americanus</i>	35	20-50	.55	.22 to .88	Black <i>et al.</i> (1959)
<i>U. americanus</i>	30	20	.44	.31 to .53	Knudsen (1958)
<i>U. arctos horribilis</i>	30	'high potency solutions'	.55 to .73*	.48 to 1.1**	Craighead <i>et al.</i> (1960)
<i>U. arctos middendorfi</i>	65	20	.44	.26 to .70	Troyer (1961)
<i>U. americanus</i>	—	not reported.	.44	.20 to .79	Jonkel (1960)
<i>U. arctos horribilis</i>	20	variable	.40	.26 to .55	Pearson <i>et al.</i> (1968)
<i>U. americanus</i>	20	variable	.42	.20 to .55	Pearson <i>et al.</i> (1968)
<i>U. americanus</i>	191	90	.70	.31 to 1.6**	This paper

*based on lean weight

**considering only single initial doses

turbances can occur even though a subject is not fully paralyzed and is respiring spontaneously (see also Bullough 1959). Death from respiratory paralysis can be prevented by artificial respiration, but there is presently no field procedure for preventing death from cardiac arrest. Barbiturates administered before succinylcholine apparently have reduced the incidence of cardiac disturbances in man (Schoenstadt and Whitcher 1963) and horses (Hansson 1956, 1957, Larsen 1958, Hofmeyr 1960, Tavernor 1960), but such premedication is not feasible with wild bears.

The use of multiple doses to achieve or prolong immobilization appears to be particularly dangerous. Choline, produced by the hydrolysis of succinylcholine to succinylmonocholine and choline, can sensitize subjects to subsequent doses of succinylcholine; following sensitization, cardiac disturbances can be produced by the entire succinylcholine molecule (Williams *et al.* 1961, Schoenstadt and Whitcher 1963). Pearson *et al.* (1968) abandoned the practice of prolonging immobilization with additional doses after two of five bears died. Two of the three bears from Minnesota that apparently died from myocardial injury were administered multiple injections to achieve immobilization. Repeated doses of succinylcholine also increase the likelihood of cardiac arrest in man (Bullough 1959, Craythorne *et al.* 1960, Lupprian and Churchill-Davidson 1960, Williams *et al.* 1961, Williams and Crain 1962, Schoenstadt and Whitcher 1963).

Larsen *et al.* (1959) stated that the severity of cardiac damage appears to be related to dosage. They observed endocardial hemorrhages in 10 of 15 horses killed by rifle fire following recovery from succinylcholine immobilization. Damage was found primarily in the right ventricles and was more common in horses treated with higher dosages. No cardiac damage was found in the hearts of seven additional horses which had not been given the muscle relaxant and were killed by shooting. Electrocardiograms recorded for six of the immobilized horses were compatible with a diagnosis of sudden myocardial injury. It is significant that all of the fifteen immobilized horses recovered from the paralytic effects of the drug and were able to stand even though 10 of them had suffered myocardial injury. It seems probable that some bears that recovered and were released in this study had similar injuries.

Cardiac arrests following treatment with succinylcholine have also caused mortalities among horses and zebras with deaths occurring from within ten seconds of intravenous injection to 30 minutes after recovery (Hansson 1957, Tavernor 1959, Larsen *et al.* 1959, Lock and Harthoorn 1959, Hofmeyr 1960). In one case, electrocardiograms showed that ventricular fibrillation began 45 seconds after the intravenous injection of succinylcholine chloride and that death occurred 135 seconds later (Hofmeyr 1960). Postmortem findings, where reported, indicated gross vascular damage to the larger arterial trunks or to the myocardium as we observed in black bears.

Numerous studies have demonstrated a release of potassium from skeletal muscle into plasma following succinylcholine injection (Klupp and Kraupp 1954, Paton 1956, Mazze *et al.* 1969, Weintraub *et al.* 1969, Evers *et al.* 1969); subsequently, much of the potassium is excreted through the kidney (Stevenson 1960). The induced temporary hyperkalemia long has been suspected as a cause of cardiac irregularities and arrest (Stevenson and Hall 1959, Allan *et al.* 1961, Galindo and Davis 1962, Dowdy and Fabian 1963, Belin and Karleen 1966, Surawicz 1967, Weintraub *et al.* 1969). Mazze *et al.* (1969) showed that hyperkalemia in man is more pronounced and cardiac effects are more frequent in traumatized patients, particularly in burned patients. These workers monitored cardiac function and plasma potassium levels in 14 traumatized patients before, during and after succinylcholine administration. In each case, succinyl-

choline injection was followed by a significant rise in plasma potassium and a concomitant appearance of cardiac irregularities. Of the five patients showing the greatest rise in plasma potassium, three experienced ventricular fibrillation. Despite this evidence, however, hyperkalemia does not explain all cardiac disturbances following succinylcholine (Williams *et al.* 1961, Evers *et al.* 1969, Mazze *et al.* 1969).

Succinylcholine can stimulate the vagal nerve and produce bradycardia and arrhythmia (Craythorne *et al.* 1960, Williams *et al.* 1961, Adams and Hall 1962, McCaughey 1962). There is also evidence of catecholamine release from adrenergic tissue capable of producing tachycardia and hypertension (Stevenson and Hall 1959, Williams *et al.* 1961, Galindo and Davis 1962, Katz and Katz 1966, Tavernor and Lees 1970). Furthermore, catecholamine release has been implicated in the pathogenesis of hemorrhagic areas in the heart (Reichenbach and Benditt 1970).

Succinylcholine has other undesirable effects, although none is as serious as its effects upon the respiratory muscles or heart. Muscle fasciculation occurs at the onset of immobilization and (in man) is transiently painful. Muscle pain also is common in man one or two days after recovery (Bennike and Nielson 1964). Several cases of myoglobinuria suggest damage to muscle cells (Airaksinen and Tammisto 1965) and potential toxicity to kidneys.

Drug-related mortality occurred in nine (4.5 percent) of 191 immobilizations in this study. The number of bears that survived but suffered myocardial injury is unknown. Although the high mortality rate may have been due in part to the relatively large dosages, there is a clear need for a more humane, reliable and safer immobilizing agent for bears. There are several possibilities, including the combination of phencyclidine (Sernylan) and promazine (Sparine) that Seal *et al.* (1970) reported to be effective, safe and possibly anesthetic. In our own experience with this combination, no fatalities have occurred in over 500 successful immobilizations of black bears in Minnesota.

SUMMARY

Succinylcholine chloride, a muscle relaxant commonly used in projectile syringes, was employed in 191 immobilizations of black bears in the Upper Peninsula of Michigan during the summers of 1966 through 1968. Dosages of 0.66 to 0.75 mg/kg were required to achieve immobilization consistently. These dosages, which are higher than those used for bears by other workers, may have been necessary because hypertonic solutions (90 mg/cc) were used; hypotonic solutions (less than 38 mg/cc) generally were used by others. There were twenty-three cases of respiratory paralysis or cardiac arrest. Twenty-one (91 percent) of these cases occurred when dosages greater than 0.75 mg/kg were injected into tissue vascular enough to facilitate immobilization in less than 75 seconds. Artificial respiration prevented suffocation, but field procedures were not available to prevent death from cardiac arrest. The latter was produced by dosages as low as 0.53 mg/kg. The administration of multiple injections to achieve or prolong immobilization seems particularly likely to cause myocardial injury and cardiac arrest. The effects of succinylcholine on the heart are discussed. The effectiveness of succinylcholine apparently is influenced by its concentration, the vascularity of the tissue into which it is injected, body temperature, and whether the bear is older or younger than about one year.

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Paper 44

Cranial Variation in Polar Bears

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INTRODUCTION

Various attempts at understanding geographic variation in Polar bears have been made since Knotterus-Meyer (1908) began to confuse the issue by recognizing seven forms of what had previously been considered a monotypic circum-polar species. The most recent and noteworthy contribution was by Manning (1971), who outlined the earlier work.

Briefly summarized, Manning demonstrated a cline of increasing size from East Greenland across Canada to the Bering Strait. He suggested that the population of largest bears, from the Bering Strait area and southward, could be considered subspecifically distinct, but left it unnamed pending further investigation.

The present study was initiated in order to examine more closely the extent and kind of geographic variation in Alaskan polar bears. A variety of multivariate analyses were conducted on Manning's data, and on additional specimens obtained since the completion of Manning's work.

MATERIALS AND METHODS

A total of 295 skulls of Alaskan polar bears was examined. The seventeen skull measurements used and described by Manning (1971) were taken with calipers. The measurements were: (1) Condylbasal length (CBL); (2) Molar-premaxilla length (MPL); (3) Mastoid breadth (MB); (4) Zygomatic breadth (ZB); (5) Supra-orbital breadth (SB); (6) Cranial length (CL); (7) Facial length (FL); (8) Maxilla-supraorbital height (MSH); (9) Least cranial breadth (LCB); (10) Interorbital breadth (IB); (11) Breadth at canines (BC); (12) Palatal breadth (PB); (13) Length P4 to M2 (LP4-M2); (14) Crown length of M2 (LM2); (15) Crown length of M1 (LM1); (16) Coronoid height (CH); (17) Condylopalatal length (CPL).

Basic statistical analyses were performed with a univariate program (D-STST) in use at the Smithsonian Institution Information Systems Division. Ratio diagrams modified from Simpson (1941), as used by Anderson (1972), were used as a graphic method of comparing measurements and proportions between groups of specimens. The data were also analysed with subroutines contained in the Numerical Taxonomy System of Multivariate Statistical Programs (NTSYS), developed by F. J. Rohlf and associates of the State University of New York at Stony Brook.

Although the original analyses utilized individual specimens, many of the results presented here are based on group means generated by the earlier computer runs. Limitations on sample sizes owing to variation in age and sex, as well as incomplete specimen data, necessitated this approach. Only the results of analyses, on adult animals are reported here.

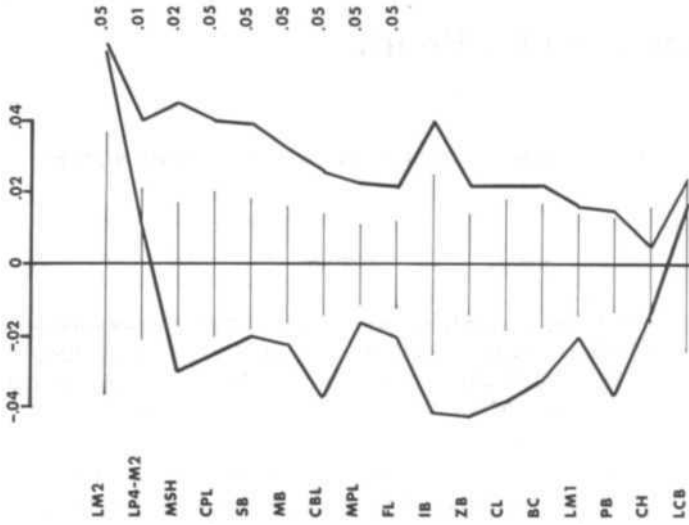


Fig. 2. Ratio diagram for females.

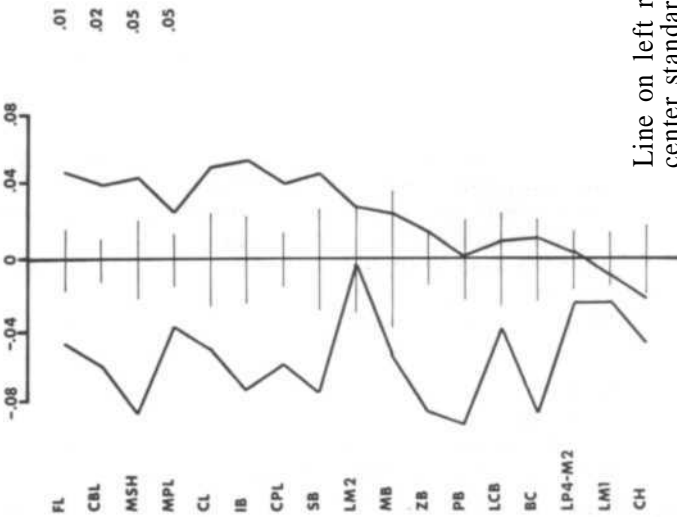


Fig. 1. Ratio diagram for males.

Line on left represents East Greenland; center standard Alaska North; line on right Alaska South. Numbers on right show significance level of T-test differences between the two Alaska populations. Scale across top represents units of difference in common logarithms among the two sample means (East Greenland and Alaska South) and that of the reference sample (Alaska North). Horizontal bars on reference sample represent confidence limits of two standard errors on either side of the reference sample mean.

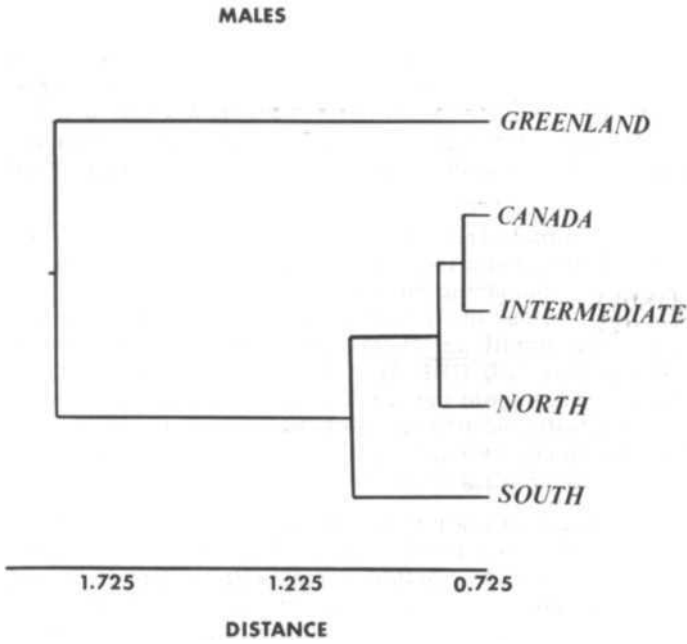


Fig. 3. Distance phenogram for males. The cophenetic correlation coefficient is 0.907.

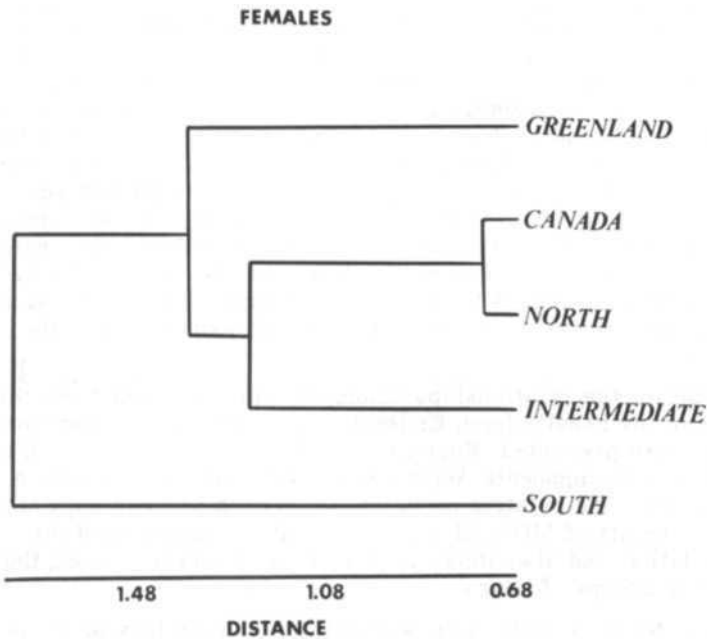


Fig. 4. Distance phenogram for females. The cophenetic correlation coefficient is 0.770.

RESULTS AND DISCUSSION

The Alaskan material was grouped into three samples based on the earlier results of Manning (1971). The Alaska North sample includes animals mainly from areas to the east of Wainwright, especially Pt. Barrow, Colville and Barter Island. The Intermediate sample was drawn from Pt. Lay, Wainwright, Icy Cape and Franklin Point. Animals from Cape Lisburne south were included in the Alaska South sample.

In the ratio diagrams, the animals from the Intermediate sample were allocated to the Alaska North and South populations by using Pt. Lay as the dividing line. Figure 1 is a ratio diagram comparing means of males of the East Greenland and Alaska South samples to those of Alaska North. As can be seen, there are four characters which show significant differences between the two Alaska populations. These characters (FL, CBL, MSH, MPL) reflect the greater skull length and height of male bears from the Alaska South population. Figure 2, for females, shows nine significant differences between the two Alaska populations. That the Alaska South population averages large in all 17 characters in both males and females is obvious from Figures 1 and 2.

Results of a cluster analysis on a matrix of Euclidean distance coefficients support the above results. Phenograms in Figures 3 and 4 illustrate the clinal nature of the variation across North America with the small Greenland animals at the top of the phenograms and larger animals at the bottom. The phenogram for males (Fig. 3) shows the close relationship of the Canada, Alaska North and Alaska Intermediate populations; whereas the phenogram for females (Fig. 4) appears to stress the distinctiveness of the Alaska South population, as in the ratio diagrams.

The results of the principal components analyses on character correlation matrices are shown in Figures 5 and 6. In both cases, component number one accounts for much of the variation (77% in males, 69% in females). For males, the three characters contributing most to component number one are zygomatic breadth, supraorbital breadth and interorbital breadth. For females, the correspondingly important characters are breadth at canines, condylobasal length and supraorbital breadth. The second principal component for males which accounts for an additional 12 percent of the variation, is heavily loaded for the three toothrow measurements: length of M1, length of P4-M2, and length of M2. The second principal component for females, which accounts for 19 percent of the variation, is heavily loaded for interorbital breadth, cranial length and palatal breadth. Not unexpectedly these results indicate the major source of variation in these bears to be size, with more subtle shape variations as shown by Operational Taxonomic Units (OTU) coordinates on the second Principal Component.

To more clearly define the relationships among the various populations three dimensional plots of the results from Kruskal's nonmetric multidimensional scaling (MDSCAL) are presented (Figures 7 and 8). While not greatly different from the Principal Components Analyses, the MDSCAL plots may be a better representation of the relative phenetic differences between populations (Rohlf, 1972). The results of MDSCAL confirm the distinctiveness of the Alaska South population, and also show the phenetic similarities among the northern or interior groups of bears.

The patterns suggested here agree well with current and ice flow patterns in the Arctic region. The East Greenland population occurs mainly in the south flowing Greenland current. The Alaska South population is found mainly in the northward moving currents from the Bering Strait. The interior populations

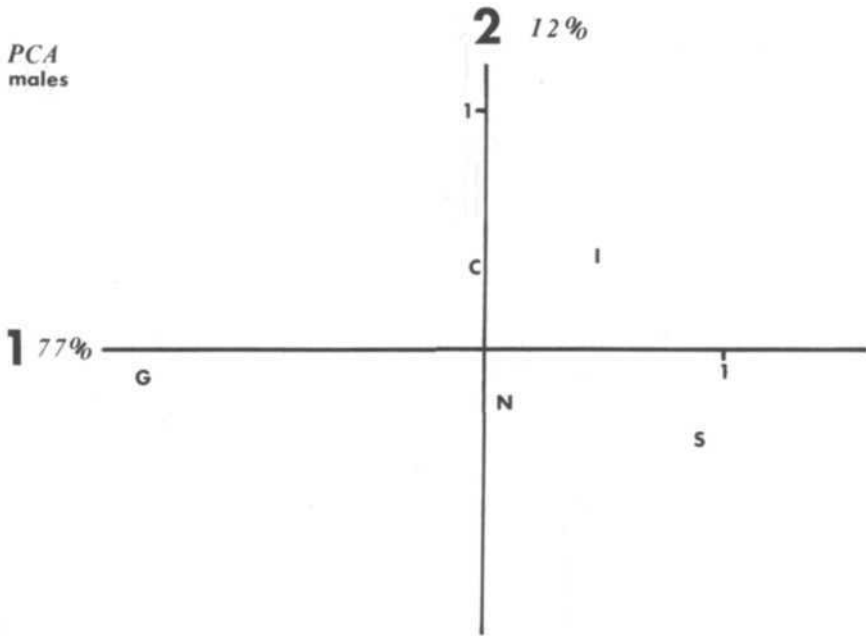


Fig. 5 Principal components analysis for males. G–Greenland; C–Canada; N–Alaska North; I–Intermediate; S–Alaska South.

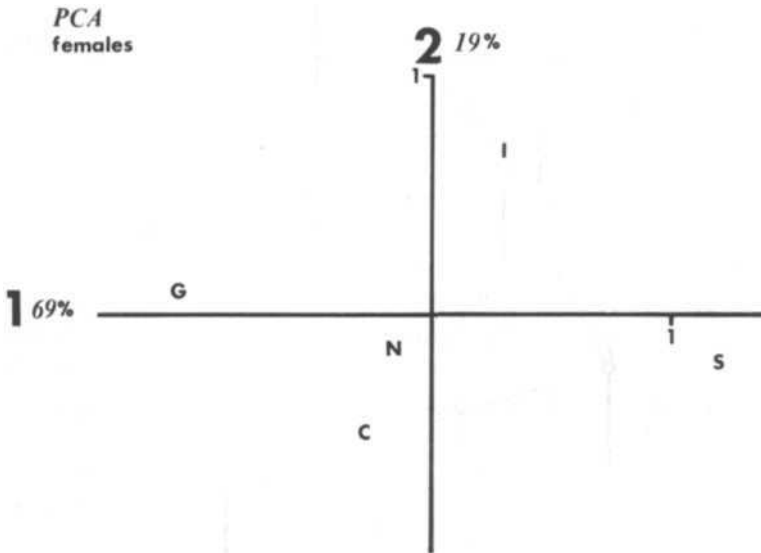


Fig. 6. Principal components analysis for females. Abbreviations as in Fig. 5.

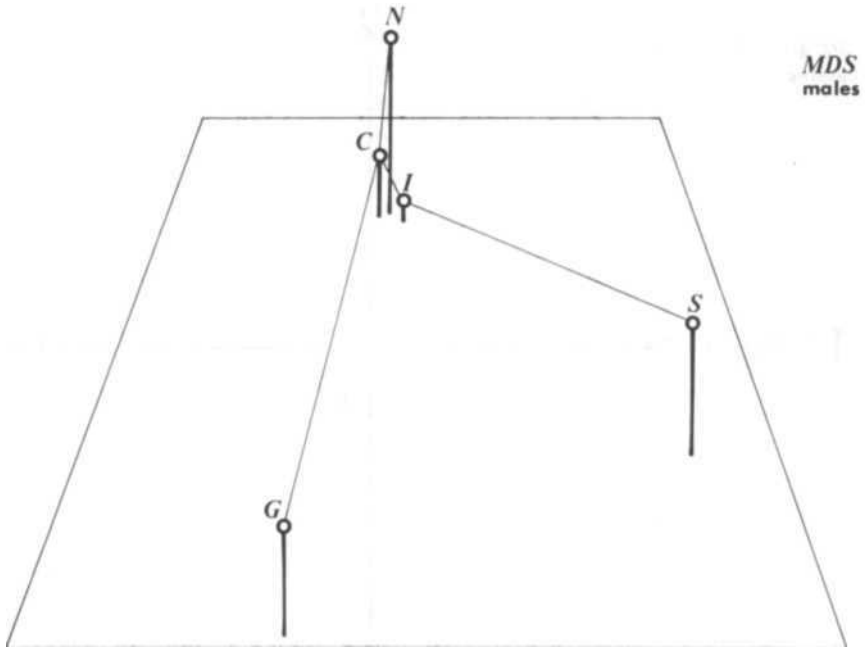


Fig. 7. Three dimensional representation of MDSCAL for males. The stress value is zero.

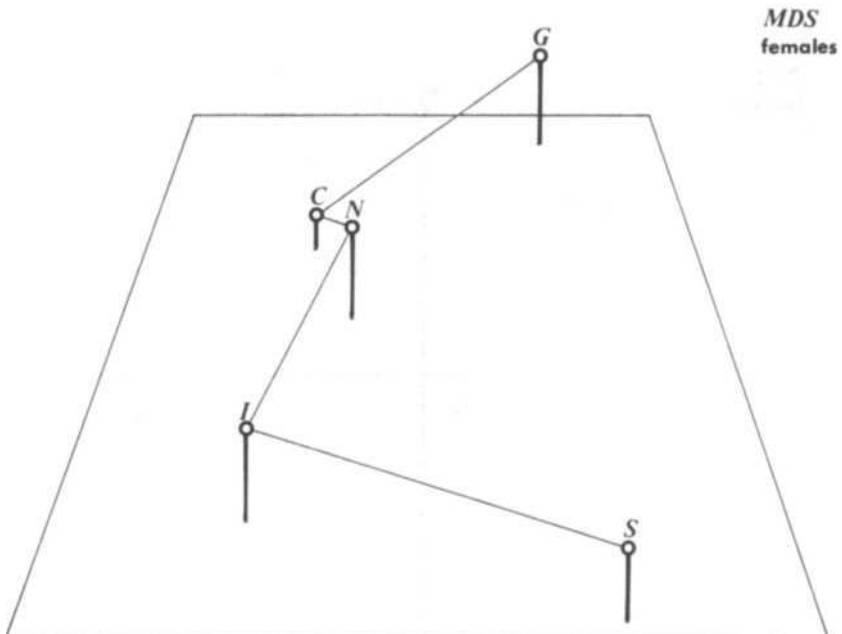


Fig. 8. Three dimensional representation of MDSCAL for females. The stress value is zero.

are affected by a variety of east or west-flowing currents across the top of North America, which may facilitate gene flow among these populations.

If subspecies were to be recognized, the East Greenland bears should be allocated to the nominate race, *Ursus maritimus maritimus* Phipps. The type locality for *U. maritimus* is Spitzbergen (Phipps, 1774). The population extending from West Greenland through Northern Alaska would take the name *U. m. labradorensis* Knotterus-Meyer. As Manning (1971) has pointed out, however, these interior Nearctic bears appear to be quite similar to the Palearctic populations which would assume the name *U. m. marinus* Pallas. In either event, there is no name currently available for the Alaska South population.

Although these results are tentative, pending the examination of a few additional specimens, I think some general conclusions are possible. The generally clinal nature of the variation originally pointed out by Manning (1971) is verified. There are definite steps in the cline at the extremes, such that the East Greenland population and the Alaska South population can be separated readily from an interior group extending from West Greenland to Pt. Lay, Alaska. Although these differences may be of sufficient magnitude to warrant subspecific recognition, I think nomenclature stability will best be served by considering *Ursus maritimus* monotypic, at least until the Old World populations have been similarly analysed.

ACKNOWLEDGEMENTS

Clyde Jones, Sandra Husar and Robert Fisher aided in measuring specimens. Jack Lentfer made available most of the specimens used in this study, and Pat Liba provided valuable help in locating some of the data. Michael Bogan provided computer assistance, and both he and Henry Setzer greatly improved the manuscript with their critical comments.

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Paper 45

Helminth and Arthropod Parasites of Grizzly and Black Bears in Montana and Adjacent Areas

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INTRODUCTION

Parasites of free-ranging grizzly and black bears in North America have been investigated periodically since the early part of the present century. The emphasis in many of these studies was on the role of bears as potential sources of parasites transmissible to man such as the trichina worm, *Trichinella spiralis* (Maynard & Pauls 1962, Harbottle *et al.* 1971, Wand & Lyman 1972) and the broad fish tapeworm (Vergeer 1930, Rush 1932, Skinker 1931, 1932). Other work has been confined primarily to taxonomic surveys or descriptive studies of parasitism in wild bears (Horstman 1949, Olsen 1968, Choquette *et al.* 1969). Little of the literature has been concerned with the potential influences of parasitism on the health of bear populations in the environment. The present study was designed with this objective in mind.

MATERIALS AND METHODS

Entire carcasses or selected organs or tissues from grizzly and black bears were obtained from a variety of sources, including National Park Service personnel in Yellowstone and Glacier National Parks, Fish and Wildlife service predator control agents, Montana Fish and Game Department biologists, and hunters. The area surveyed included approximately the western third of Montana and Yellowstone National Park. Most bears were necropsied within 48 hours after death except for the examination for *T. spiralis* larvae, for which tissues were frozen and stored for periods of 1 to 6 months before processing. Samples of tongue, masseter, diaphragm and femoral muscle were examined routinely for the presence of trichina larvae as described previously (Worley *et al.* 1974). If only the head was available, tongue and masseter were examined. Complete necropsies were performed on 70 grizzly and 30 black bears. 160 grizzly and 80 black bears were checked for *Trichinella* larvae. Ages of 127 grizzly bears were determined according to the techniques listed by Greer (1974). Ages of black bears were not determined.

Other organs which were examined routinely when the entire carcass was submitted were liver, lungs, heart, kidneys, urinary bladder, subcutaneous con-

TABLE 1. PREVALENCE AND INTENSITY OF PARASITES IN GRIZZLY BEARS FROM MONTANA AND WYOMING

Parasite	Mean percent prevalence*	Percent positive by age class						Av. intensity of infection (range)
		sub	1-2	3-5	6-9	10-15	16+	
Nematoda								
<i>Trichinella spiralis</i>	$61.3(\frac{98}{160})$	$11(\frac{1}{9})$	$50(\frac{9}{18})$	$67.9(\frac{19}{28})$	$63.3(\frac{19}{30})$	$38.9(\frac{7}{18})$	$87.5(\frac{21}{24})$	51.1(0.12-708)1
<i>Baylisascaris transfuga</i>	$75.7(\frac{53}{70})$	$40(\frac{2}{5})$	$76.9(\frac{10}{13})$	$80(\frac{4}{5})$	$92.3(\frac{12}{13})$	$90(\frac{9}{10})$	$80(\frac{12}{15})$	33.8(1-480)
<i>Uncinaria</i> sp.	$17.3(\frac{12}{69})$	$0(\frac{0}{5})$	$46.1(\frac{6}{13})$	$40(\frac{2}{5})$	$7.6(\frac{1}{13})$	$0(\frac{0}{10})$	$13.3(\frac{2}{15})$	128.8(1-900)
<i>Dirofilaria ursi</i>	$2.8(\frac{2}{70})$	$0(\frac{0}{5})$	$7.6(\frac{1}{13})$	$0(\frac{0}{5})$	$7.6(\frac{1}{13})$	$0(\frac{0}{10})$	$0(\frac{0}{15})$	3.5(2-5)

Cestoda								
<i>Diphyllobothrium</i> , sp.	$24.2(\frac{16}{66})$	$20(\frac{1}{5})$	$7.6(\frac{1}{13})$	$20(\frac{1}{5})$	$23(\frac{3}{13})$	$70(\frac{7}{10})$	$13.3(\frac{2}{15})$	$49.6(0.1-379)†$
<i>Taenia</i> sp.	$21.2(\frac{14}{66})$	$0(\frac{0}{5})$	$23(\frac{3}{13})$	$0(\frac{0}{5})$	$30.7(\frac{4}{13})$	$10(\frac{1}{10})$	$26.6(\frac{4}{15})$	$71.5(15.5-145)†$
Trematoda								
<i>Echinostoma revolutum</i>	$3.03(\frac{2}{66})$	$0(\frac{0}{5})$	$7.6(\frac{1}{13})$	$20(\frac{1}{5})$	0	0	0	$6.5(6-7)$

Arthropoda

Dermacentor andersoni — 1 infested bears§*Arctopsylla* sp. — 1 infested bear§

*Based on total bears examined including animals whose age was not determined. The fraction indicates the number of positive animals over the total number examined.

†Expressed as larvae/gm. of tongue.

‡Volume of tapeworm biomass in ml.

§Represents ectoparasites observed; routine examinations not performed.

nective tissue and superficial musculature, pleural and peritoneal cavities, mesenteries, and the entire gastrointestinal tract including contents. The external surface of the body was sometimes examined for ectoparasites, but frequently was given only a cursory search due to time limitations.

Standard parasitological procedures were used to recover parasites from the gastrointestinal tract. After the contents of the alimentary canal were washed on 20-, 40-, or 80-mesh screens to separate worms from ingesta, the washed contents were searched with the aid of an illuminated tray (Barber & Lockard 1973). Any parasites recovered were fixed in AFA solution (tapeworms and flukes) or glycerine-alcohol (roundworms). Attempts were made to identify and enumerate all parasites recovered in order to assess quantitatively the total parasite population from each host. Qualitative fecal examinations were performed routinely to detect worm eggs and coccidian oocysts, using saturated sodium chloride solution for flotation.

RESULTS

Nine species of parasites were found in 160 grizzlies examined partially or in detail during the period from 1968 through 1973 (Table 1). The most frequent of these was the intestinal nematode *Baylisascaris transfuga*, followed in order of prevalence by the trichina worm (*T. spiralis*), broad fish tapeworm (*Diphyllobothrium* sp.), taeniid tape worm (*Taenia* sp.), and hookworm (*Uncinaria* sp.).

Other parasites, which occurred infrequently or rarely, were intestinal flukes (*Echinostoma revolutum*), filarial worms (*Dirofilaria ursi*) wood ticks (*Dermacentor andersoni*), and fleas (*Arctopsylla* sp.).

The acquisition of ascarid infections by *U. arctos* was related directly to the age of the host. The percentage of infected animals increased from 40% in cubs to 92% in 6 to 9 year-old bears. Ascarid worm burdens averaged 33.8 worms and ranged from approximately 1 worm per cub to an average of 58 ascarids per bear in the 10-15 year age class. Worm populations in other age groups were: 1 and 2 years old, 20; 3-5 years old, 3; 6-9 years old, 52; and 16+ years of age 8.

Tissue infections with *T. spiralis* larvae were the second most frequent parasitism encountered in the grizzly (Table 1). Based on data from 130 bears collected between 1968 and 1972, the prevalence of this nematode varied from 45.1% in grizzlies originating in Yellowstone or Glacier Parks to 58.4% in grizzlies from wilderness areas in northern or western Montana. The average concentration of trichinae in the tissues of Park bears was 32 larvae/gm. of tissue (LPG) compared with 59 LPG in wilderness bears. A comparison of predilection sites of *Trichinella* larvae in 42 grizzlies from which several tissues were examined indicated that larval density was highest in tongue (46 LPG), followed by femoral muscle (17 LPG), masseter (14 LPG) and diaphragm (10 LPG). Grizzlies older than 15 years had the highest prevalence but the lowest intensity of *T. spiralis* infection, as estimated by larval concentrations in the tongue.

The relative intensity of tissue infections was highest in the 3-5 year age class (104 LPG), followed by 1-2 and 6-9 year-old bears (intensities of 97 and 36 LPG, respectively). Ten to 15 year-old bears, cubs and 16+ age classes had levels of infection ranging from 21 to 9 LPG.

Two genera of tapeworms were recovered from grizzlies: a *Diphyllobothrium* species which occurred only in Yellowstone Park bears, and a *Taenia* species

which was found throughout the survey area. Based on a volumetric method of determining the total tapeworm biomass per host, taeniid infections averaged 71.5 ml of worm material compared with 49.6 ml for diphyllobothriid populations. The largest tapeworm burden noted during the study was 797 *Diphyllobothrium* in a 14 year-old grizzly collected along the west side of Yellowstone Lake in 1970.

Eight species of parasites were recovered from a total of 80 black bears examined partially or completely during the period from 1966 to 1973 (Table 2). Ascarids were the most common parasite in *U. americanus*, with a composite prevalence of 80% and an average worm burden of 22.7 nematodes per infected host. With two exceptions, all helminths which occurred in grizzlies also were found in black bears. However, the prevalence and intensity of these infections were markedly lower in black bears. Since a majority of the animals on which this study was based originated in the Yellowstone ecosystem in northwestern Wyoming and southwestern Montana, the differences in prevalence of the various helminths and arthropods in the two hosts appear to reflect differences in susceptibility and/or exposure rates resulting from variations in food habits and behavior of the two species.

DISCUSSION

Any assessment of the role of parasites as morbidity or mortality factors in wild bear populations is extremely difficult to document. Individual cases of parasitic disease resulting from excessive parasite burdens have occasionally been observed. Rausch (1955) described a fatal case of *Diphyllobothrium* infection in a young black bear which had been experimentally exposed to an unknown number of plerocercoid larvae. The presence of moderate to large numbers of *Diphyllobothrium* specimens in a few bears in the present study was noted in mature or aged grizzlies which apparently foraged predominantly in inlets and bays of Yellowstone Lake. Most bear infections consisted of from 1 to 100 tapeworms ranging in biomass from 2 to 20 ml.

A potentially detrimental effect of broad fish tapeworms is their ability to absorb large quantities of vitamin B₁₂ from the host's intestine. In man, this can result in pernicious anemia due to the inability of the host to synthesize adequate numbers of red blood cells (Von Bonsdorff 1947). The degree of clinical correlation between *Diphyllobothrium* infections in man and bears is not known. However, Cameron (1945) believed that *D. latum* is an indigenous parasite in North America which may have originated in the brown bear. On the other hand, Rausch & Hilliard (1970) found that *D. ursi* was the common pseudophyllidean tapeworm of bears in Alaska. In the present study, the species of *Diphyllobothrium* occurring in Yellowstone Park bears was not determined because morphological criteria were not considered adequate for a definitive identification. Post (1971) reached a similar conclusion after restudying data and specimens from bears collected over a period of many years in the area of Yellowstone Lake.

The high prevalence of ascarids in both grizzly and black bears and their common occurrence in bears of all ages suggest that the functional immune response to this nematode in bears is minimal. This contrasts with the generally accepted concept that ascarid infections are self-limiting and normally are restricted to immature or young adult animals. In human ascariasis, infection rarely persists for more than one year (Faust 1955). The severity of symptoms in human ascarid infection is proportional to the level of larval

TABLE 2. PREVALENCE AND INTENSITY OF PARASITES IN BLACK BEARS FROM MONTANA AND WYOMING

Parasite	Percent positive*	Location	Av. intensity of infection (range)
Nematoda			
<i>Trichinella spiralis</i>	6.3($\frac{5}{80}$)	striated muscle	18.1 (0.02-26.4)†
<i>Baylisascaris transfuga</i>	80($\frac{24}{30}$)	small intestine	22.7 (1.177)
<i>Uncinaria</i> sp.	3.3($\frac{1}{30}$)	small intestine	23 (—)
Cestoda			
<i>Diphyllobothrium</i> Sp.	6.6($\frac{2}{30}$)	small intestine	11.5 (0.2-20)‡
<i>Taenia</i> sp.	6.6($\frac{2}{30}$)	small intestine	—
Arthropoda			
<i>Dermacenter andersoni</i>	6.6($\frac{2}{30}$)	external body surface	—
<i>Trichodectes pinguis euarcidos</i>	3.3($\frac{1}{30}$)	external body surface	—
<i>Pulex</i> sp.	3.3($\frac{1}{30}$)	external body surface	—

*The fraction indicates the number of positive animals over the total number examined.

†Expressed as larvae/gm. of tongue

‡Volume of tapeworm biomass in ml.

exposure and includes liver damage, intestinal obstruction, pneumonia and a variety of intestinal complications (Arean & Crandall 1971). In view of the widespread occurrence of bear ascarids, they must be considered as one of the most important parasites occurring in *Ursus* spp. in the Montana/Wyoming area.

The potential for trichinosis in grizzly bears ranks *T. spiralis* as a significant parasite in this host. Adverse effects produced by the migrating larval stage in man such as toxemia and elevated body temperature suggest that a similar course of events could occur in bears. A marked inflammatory reaction to the invading parasite in the muscles and other tissues coincides with severe muscle pain, edema, destruction of tissue and blood abnormalities in man (Ribas-Mujal 1971). Gould (1945) estimated that an intake of 3 or 4 trichinae per gram of body weight is lethal in humans. Although considerable variation may exist in the ability of various mammalian species to tolerate the various manifestations of trichinosis, the high intensity of grizzly infections (51. 1 larvae per gm. of infected tissue) and the widespread occurrence of the parasite throughout the study area (61. 3% infected) implicate it as a potentially serious pathogen of *U. arctos*. Additionally, its ability to alter the host's behavior due to pain associated with the migration of larvae in the muscles cannot be excluded as a possible contributor to the abnormal behavior which is occasionally observed in grizzlies in parks and elsewhere throughout the range of the species.

Further studies are needed to characterize the infectivity and survival of bear strains of *T. spiralis* in swine and laboratory animals, in view of the ability of larvae of bear origin to survive for extended periods of time in frozen tissues. In the present study, viable trichina larvae were recovered repeatedly from tongue, masseter and other bear tissues which had been stored at approximately -20°C . For periods of up to 6 months. These observations contrast with those of Ransom (1916), who found that none of the trichina larvae originating in swine, rats or rabbits survived for as long as 20 days at -15°C . when stored in meat. Present regulations involving cold storage of pork are based in part on the belief that freezing for short periods of time eliminates the possibility of human infection with trichinae. The need to reevaluate this aspect of the biology of *T. spiralis* from bears and prepare specific recommendations for cold storage of bear meat intended for human consumption is obvious.

Hookworms (*Uncinaria* sp.) were found to be relatively common parasites of the grizzly in the area north of the 47th parallel in Montana. Since this infection apparently does not occur in either host species in the Yellowstone region, the percentage of infected bears in the enzootic area of northern Montana (54. 5%) is a more accurate indication of its regional frequency. The average worm burden of 128. 8 hookworms per infected host suggests that it may constitute a significant drain on northern Montana grizzly populations. Clinical signs of *Uncinaria* infection in other hosts include anemia, hemorrhagic diarrhea and impaired intestinal absorption (Soulsby 1965). Another facet of hookworm infection involves its effect on fetal mortality and survival of newborn animals. Olsen & Lyons (1962, 1965) have shown that death losses occurring in fur seal pups were due to *Uncinaria lucasi* infections acquired shortly after birth via milk-borne larvae transmitted from mother to offspring during nursing. In dogs, hookworms are frequently transmitted across the placenta from the mother to her unborn pups, resulting in abortion or stillbirth (Stone *et al.* 1970). Although none of these problems are known to occur in hookworm-infected bears, the possibility that similar consequences could result deserves serious consideration.

The filarial worm *Dirofilaria ursi* was described from *Ursus torquatus japonicus* in Japan by Yamaguti (1941). In North America, it has been reported in black bears from widely scattered areas, including Ontario (Anderson 1952), New York (King *et al.* 1960), northern Michigan and Minnesota (Rogers 1975), Montana (Jonkel & Cowan 1971) and Idaho (Furniss, pers. comm.). Both infected grizzlies in the present study were collected in northern Montana in mid-summer. Worms were situated in membranous capsules located in connective tissue surrounding the trachea. No information is available on the pathogenesis of this infection in bears.

Infections with the intestinal trematode *Echinostoma revolutum* were noted twice: in a yearling grizzly collected near Slough Creek in Yellowstone Park and in a three-year-old grizzly taken near Augusta in northwestern Montana. This fluke is known to occur in a variety of hosts, including man, dogs, cats, swine, rats, muskrats, rabbits, otters and monkeys (Beaver 1937). The grizzly is apparently an accidental definitive host which acquires the infection by ingestion of various mollusks, tadpoles or fish containing the metacercarial stage.

Although coccidian oocysts were noted occasionally in the feces of both *Ursus* species examined during the study, it was difficult to determine whether they originated in the bears or had been ingested accidentally during the process of scavenging on carcasses of other animals. For this reason, no data are included on the prevalence of coccidia. This aspect of parasitism in bears remains an obscure subject, although Hair & Mahrt (1970) described *Eimeria albertensis* and *E. borealis* from black bears in Alberta. Their work constituted the first report of coccidia from ursids in North America.

The relatively common occurrence in grizzly bears of trichina worms, ascarids and hookworms and the frequency of concurrent infections with two or more species of helminths suggest that internal parasites may have a substantial effect on the health of grizzly populations which are subjected to other environmental stresses. Complications resulting from parasitism superimposed on malnutrition or other problems no doubt contribute to some grizzly mortality in the field. The types and intensities of parasitism occurring in grizzlies throughout the study area probably would not produce recognizable symptoms of acute disease. However, the overall impact of parasitic disease on the well-being of existing populations of grizzly bears in the United States clearly requires further investigation. The clinical effects of parasitism in black bears would be expected to be much less pronounced because of lower rates of infection and less intensive parasite burdens. The ability of both species to act as reservoirs of certain human parasites, particularly *T. spiralis*, indicates that bears may be largely responsible for the maintenance of zoonoses such as trichinosis in the northern Rocky Mountain region.

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Index of Authors

- BACON, Ellis S. 13-25, 27-36
BEEMAN, Larry E. 87-95
BELIKOV, S.E. 37-40,321-326
BERGSTROM, Andrea S. 235-245
BURGHARDT, Gordon M. 13-25, 27-36,
157-167
CRAIGHEAD, Frank C., Jr. 97-109,
337-356,357-371
CRAIGHEAD, John J. 337-356,357-371
CURATOLO, James A. 403-409
DEAN, Frederick C. 111-119
EGBERT, Allan L. 41-56
ELGMORK, Kåre 281-297
ERICKSON, Albert W. 169-175,431-446
FARO, J.B. 381-390
FOLK, G.Edgar, Jr. 373-380
FOLK, Mary A. 373-380
FOX, J. Carl 455-464
GLENN, L. P. 381-390
GRACHEV, Yu. A. 299-300
GREER, Kenneth H. 177-189,455-464
HARGER, Elsworth M. 169-175
HERRERO, Stephen 121-145
JONKEL, Charles 301-302
JORDAN, Robert H. 57-63
KAAL, Mati 303-308
KEMP, Gerald A. 191-197
KORDEK, Walter S. 215-224
KOROTKOV, A.M. 309-311
KUEHN, David W. 169-175
LARSEN, Thor 199-208
LARSON, Anna 373-380
LENTFER, Jack W. 209-213,381-390
LINDZEY, James S. 215-224
LUDLOW, Jeanne C. 65-69
LUQUE, Michael H. 71-78
MARTINKA, C.J. 147-156
MATULA, George J., Jr. 215-224
McCAFFREY, Eugene R. 235-245
MILLER, Robert L. 225-234
MILLER, L.H. 381-390
OZERETSKOVSKAYA, N.N. 391-402
OZOGA, John J. 169-175
PEARSON, A.M. 247-260
PELTON, Michael R. 87-95,157-167
PEREVERZEVA, Ye. V. 391-402
PIEKIELEK, William P. 215-224
PRUITT, Cheryl H. 79-86
QUIMBY, Roland 403-409
REYNOLDS, Harry V. 403-409
ROBERTSON, Richard 301-302
ROGERS, Lynn L. 169-175,411-430,
431-446
ROGERS, Susanne M. 411-430
SCOTT, Charles D. 157-167
SHARAFUTDINOV, I. Yu. 309-311
SLOBODYAN, A. A. 313-319
STIRLING, Ian 301-302
STOKES, Allen W. 41-56,71-78
STOWE, Clarence M. 431-440
SUMNER, Jay S. 337-356, 357-371
USPENSKY, S. M. 321-326
VARNEY, Joel R. 261-273,357-371
VERESCHAGIN, N. K. 327-335
VERME, Louis J. 169-175
WILL, Gary B. 225-234,235-245
WILSON, Don E. 447-453
WINTERS, John B. 455-464
WORLEY, David E. 455-464
ZAVATSKY, B. P. 275-279