
PRZEWALSKI'S HORSE

Equus przewalskii

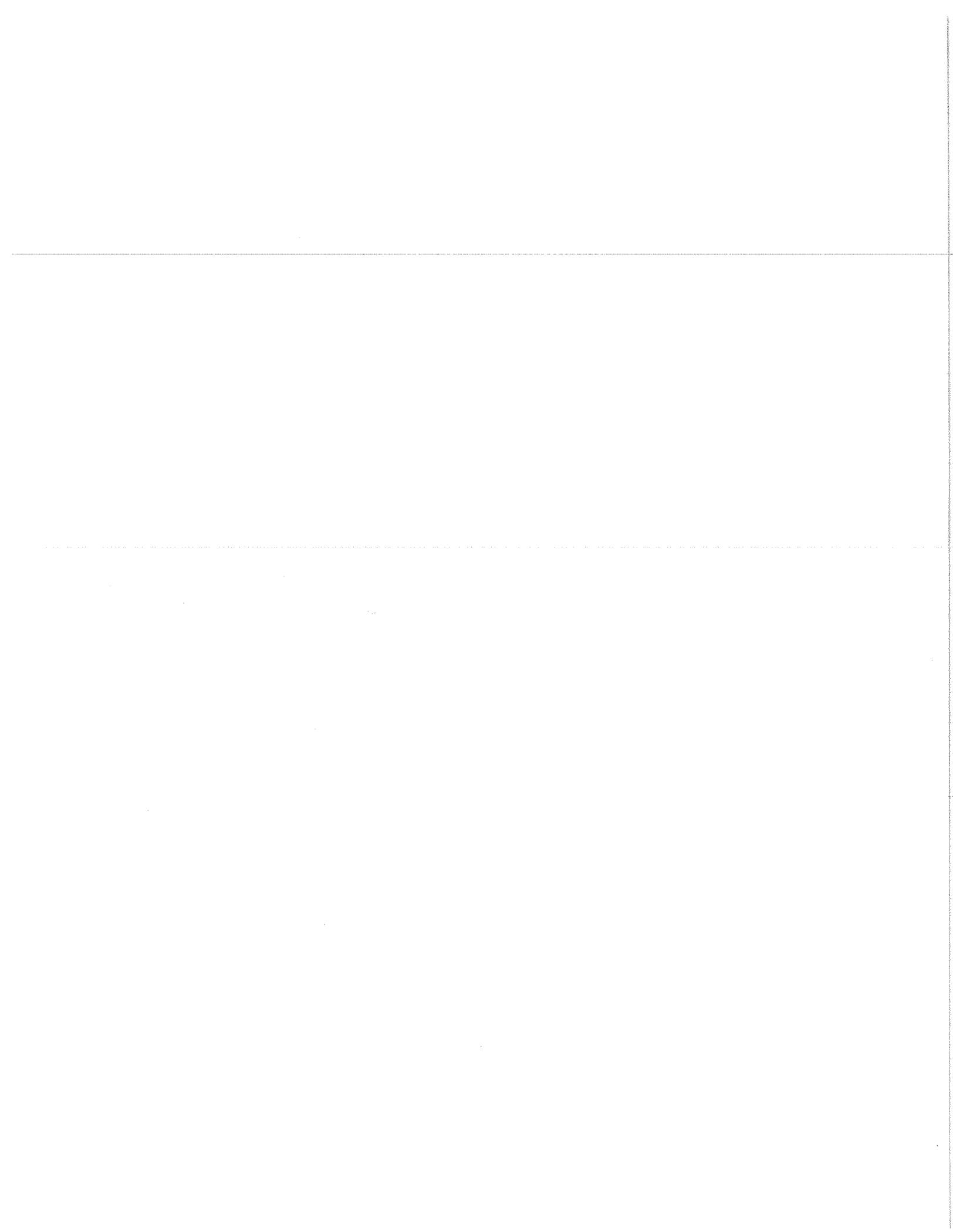
**GLOBAL CONSERVATION PLAN
D R A F T**

Captive Breeding Specialist Group,
Species Survival Commission,
International Union for the Conservation of
Nature and Natural Resources

Prepared by

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10 February 1990



GLOBAL CONSERVATION MASTERPLAN
PRZEWALSKI'S HORSE

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Captive Breeding Specialist Group

Species Survival Commission
International Union for the Conservation of Nature and Natural Resources

U. S. Seal, CBSG Chairman

Date: 23 January 1990

To: Przewalski horse owners

From: CBSG, U.S. Seal

Subject: Working Document for Equus przewalski Global Conservation Plan

1. It has been 5 years since the last convened international meeting of holders of Przewalski's horses. During that time the number of horses in the captive population has grown to near carrying capacity. A primary objective of the captive breeding program has been to achieve reestablishment of the species in secure wild habitat in sufficient numbers to allow continuing evolution of the species by natural selection. A workshop on this topic was held in Moscow June 1985 under the auspices of the Soviet Academy of Sciences, FAO, UNEP, and SSC/CBSG. The proceedings have recently appeared. Several projects to establish wild populations have been initiated in Russia and China and experimental projects have been undertaken in Canada, France, Netherlands, and Australia. The growth of the captive population to near probable carrying capacity, the need to supply animals for release projects, and a concern about the emergence of phenotypic characters diverging from the classical descriptions of the species have made urgent the need for a comprehensive and global conservation plan for the species.

2. An international meeting of holders of the species has been convened, under the auspices of the IUDZG, at Leipzig Zoo, May 18-23, 1990 to consider these issues and to adopt and implement a global conservation plan for the species. In preparation for this meeting of the owners, it was important to have available a thorough analysis of the genetic and demographic status of the captive population and that a draft plan be prepared. A meeting of regional coordinators and population biologists was convened December 9-11, 1989 at the San Diego Zoo under the auspices of the CBSG/SSC to formulate the scientific basis for a global plan, develop population models, review the genetic and phenotypic issues, and to prepare a draft set of goals, objectives, and recommendations for a global plan. The attached document is this draft global conservation plan for your consideration as a basis for discussion, adoption, and initiation of implementation at Leipzig.

3. Past experience suggests that there will be a need for discussion to modify the draft plan after the meeting at Leipzig and to develop further detail for implementation of the plan. I am therefore, scheduling a working group for the Przewalski horse at the CBSG meeting in Copenhagen, August 24-26, 1990.

4. I suggest that, as a goal, we plan to submit a final draft of the plan to the SSC/IUCN for potential endorsement in November 1990 at the meeting in Perth, Australia.

A handwritten signature in cursive script, appearing to read "U. S. Seal".

U. S. Seal, Chairman

PRZEWALSKI'S HORSE

Equus przewalskii

**GLOBAL CONSERVATION PLAN
D R A F T**

SUMMARY AND RECOMMENDATIONS

10 February 1990

PREAMBLE

The Asian wild horse (*Equus przewalski*) is considered extinct in the wild. The last observations are recorded from the 1960's. The Przewalski's horse survives as a captive population and gene pool that is derived largely from Asian wild horse origins but contains appreciable and incompletely documented contribution from domestic horse stock. This captive population and gene pool has been subjected to variable, artificial selection over its 70+ years in captivity. This selection has been oriented mostly toward production of a phenotype that resembles the descriptions and samples of animals from the last wild populations of the species. Thus, this selection has attempted to remove from the population animals possessing phenotypic characteristics considered atypical for the species.

Captive propagation of the Przewalski's horse has become progressively more organized over its history. The International Studbook for Przewalski's horse was one the first efforts of this kind for a species in captivity. Currently, there are formally organized programs in North America (the Species Survival Plan (SSP) of the AAZPA), in Europe (the Europaisches Erhaltungszucht Programm (EEP)), in the U.K. (the Joint Management of Species Group (JMSG)).

Four major objectives have emerged in the programs for propagation of the Przewalski's horse. Perpetuation of the captive population to prevent the complete extinction of this form of equid. Restoration of free-ranging populations to the wild. Preservation of the variation in the gene pool to enhance the success of the perpetuation of the captive population and the restoration to the wild. Selection for a phenotype conforming to the specimens known from the wild and lacking traits that are considered to derive from the domestic influence in the captive gene pool.

Two problems have been perceived with these objectives. Maximizing preservation of genetic variation may be in conflict with selection for a defined phenotype. Providing animals for the restoration projects could detract from the demographic security and genetic variation in the captive population.

Preparatory to the Przewalski's Horse meeting in Leipzig, it has seemed desirable to formulate a proposed global conservation masterplan that will attempt to: (1) better define the objectives for the captive program and reconcile conflicts between them; (2) better coordinate the regional captive programs into an international captive program and (3) better integrate the captive efforts with the restoration projects.

To, this end, a small meeting of the regional coordinators and technical experts was convened at the San Diego Zoo 9-11 December 1989. The draft masterplan they formulated is attached for review by all owners and holders of Przewalski's horse so that this plan can be fully discussed at the Leipzig Symposium. It is hoped that a masterplan accepted by the world's owners and holders of Przewalski's horse will emerge from the meeting in Leipzig.

GOALS AND OBJECTIVES

DEFINITIONS:

1. The Przewalski's Horse (*Equus przewalskii*) population consists of animals registered in the International Studbook.

GOALS:

1. Protect the Przewalski's horse from genetic and demographic extinction.
2. Re-establish the Przewalski's horse in free-ranging populations in wild habitat in sufficient numbers to allow continuing adaptive evolution by natural selection.
3. Manage the captive population to maintain its present genetic variation and to provide horses for reintroduction and release programs.

OBJECTIVES:

1. Establish 5-10 wild populations, each with an N_e of at least 50 or a number of at least 250 adult (3 years of age or older) animals, to achieve a total N_e of at least 1000 and a total number of 5000 adult animals.
2. Monitor the genetic and demographic events in each reintroduced population and review the information each year to guide continuation of the program.
3. Manage these wild and captive populations as a metapopulation by effective exchange of animals among the populations as determined by continuing analysis.

4. Manage the captive population to retain the maximum amount of the available genetic variation surviving from the original wild population. Specific guidelines include, for a period of 200 years: (a) maintenance of 95% of current average individual heterozygosity, (b) avoidance of loss of surviving founder alleles through management of animals diagnosed as genetically important through genealogical analysis, (c) retention of at least current levels of founder allele diversity ($1 - \sum p_i^2$ where p_i 's are the frequencies of individually labelled founder alleles), and (d) preservation of observable rare variant marker alleles.
5. Establish an international management program under auspices of the CBSG by coordinating existing regional programs (EEP, SSP, SMP) and recruiting additional regional programs to manage animals in captivity as a global population.
6. Maintain the managed captive population at 500-750 horses to preserve existing genetic variation at acceptable levels. Conduct adequate exchanges between regional management units to provide representation of the surviving founder alleles in each unit while retaining diversity of this representation among animals. The managed population goal of 500-750 horses will depend upon agreement amongst the regional management units on a common plan with shared demographic and genetic goals. In the event that regional management plans develop differing goals and strategies or are unable to fulfill their contribution to the global plan, the number of horses in the managed captive population may have to be larger.
7. Manage the captive population to provide animals as needed for the reintroduction and release programs while assuring that the genetic variation and demographic security of the captive population are not compromised. Animals would be provided based upon recommendations from the global captive management group in consultation with the managers of the reintroduction and release programs. Requests for animals should be provided 2 years in advance of when animals are required. These animals should be selected to provide each reintroduction site with a full representation of the genetic variation present in the captive population.
8. Develop effective collaboration with the Equid Specialist Group and the Reintroduction Specialist Group to assist in accomplishment of the goals of reintroduction of the Przewalski's horse to the wild.

RECOMMENDATIONS:

Wild Populations:

1. Invite representatives of the Equid Specialist Group and Reintroduction Specialist Group to the Leipzig Przewalski's Horse Meeting in 19-23 May 1990 and the Copenhagen CBSG meeting in 24-26 August 1990 to develop working relationships for the reintroduction program. Also invite representatives from each of the nations in which a reintroduction or experimental release site exists.
2. Establish criteria for reintroduction sites (to be done by the global captive management group working with the Equid Specialist Group, Reintroduction Specialist Group, and national program organizers). The analyses will include maps, climate, year-round forage and water availability, disease, presence of domestic and feral horses, and commitment of governments. Refer to the FAO/UNEP/IUCN Moscow Meeting Proceedings for a working document discussing site selection criteria.
3. Identify at least 5 potential reintroduction sites which might receive animals by 1994. Initiate surveys and determine suitability of each site by 1992. Sites have already been selected in USSR (Ukraine, Kazakstan, Transbaikalia), Mongolia, and China (Xinjing; Gansu). Experimental release sites have also been designated in Canada and Australia.
4. Obtain governmental, organizational, and private support and funding to initiate reintroductions by 1994. UNEP, FAO, WWF and IUCN should be approached as possible participants. Money will be needed to transport animals to release sites, to prepare release sites, and to conduct post-release monitoring programs.

Captive Populations:

1. Create a Przewalski's horse global captive management group, under auspices of the CBSG, consisting of the International Studbook Keeper and the regional program coordinators. The group will guide the management of the captive population on a world-wide basis and identify individual animals for reintroduction and experimental release programs. (First meeting to occur in Leipzig with a follow-up session in Copenhagen 1990 in conjunction with the annual CBSG meeting).
2. Manage the captive population to retain the maximum number of Przewalski's horse founder genes. Formulate guidelines for inclusion of the existing domestic lineage to retain maximum amount of wild founder genes. These guidelines may include provisions for partially genetically isolated subpopulations.

3. Monitor individual heterozygosity, founder allele survival, founder allele diversity, and observable polymorphisms (enzyme, protein, DNA, chromosome, blood group) of the captive population and its subpopulations. Ensure survival of remaining founder alleles through analysis of genetic importance of individuals in various subgroups of the population.

4. Analyze the genetic impact of removal from the captive population of individuals that have been excluded from the EEP for phenotypic reasons. (Attached is a list of these phenotypic reasons and the animals affected.) (Frank Princee will conduct analyses and provide in advance of the Leipzig meeting). Analyze the possibility of genetic linkage between coat color and serum albumin loci (as is established with *Equus caballus*) through examination of segregation patterns for both traits in selected informative families. Demonstration of such a linkage relationship would aid in the identification of carriers. (Ann Bowling will do before Leipzig if possible.)
5. Exchange animals to achieve full founder allele representation in EEP, SSP, UK, USSR, and Australian populations. Maintain diversity of this representation among individual animals.
6. Recommend population objectives for the respective regional programs as:

EEP (Europe)	200-300	SSP (North America)	200-300
U.K.	40- 60	SMP (Australia/N.Z.)	25- 50
USSR	100-500		
7. Individually mark and blood type all animals in the captive population. Freeze branding is recommended for permanent marking using a breeder code and number.
8. Review Studbook for accuracy of all data entries. Animals that are of questionable or uncertain parentage and that cannot be individually identified should be blood typed to establish identity and parentage. Animals that cannot be validated should be removed to a registry.
9. Conduct ongoing research on behavior and investigate the genetic basis of disease syndromes and infertility. Analyze the genetic basis of phenotypic traits which may render animals liable for removal.

COSTS OF PLAN:

1. Maintenance of regional studbooks, routine analyses, and management plans (2 weeks/per regional plan/year).
2. Regional meetings to formulate and implement regional plans (2-3 days).
3. Participation in International Studbook (1-2 days).
4. Marking and blood-typing of animals (sample collection and analyses).
5. Animal movements.
6. Annual meeting of regional coordinators and Specialist Group representatives (3 days).
7. Monitoring of genetic indicators.
8. Establishment, storage, and analysis of frozen tissue samples.
9. Research on problems of the captive horses and their possible genetic bases.
10. Continuing genealogical analyses and population genetic analyses of the Przewalski's horse population.
11. Stabilization of captive population.
12. Participation in reintroduction/release programs.
13. Publication and distribution of plan and supporting documentation.
14. Preparation and distribution of annual reports.
15. Archive photographic records.

GLOBALEN MASTERPLANES FÜR DAS ASIATISCHE WILDPFERD

Definition: Die Przewalskipferd- (*Equus przewalskii*) Population besteht aus Individuen, die im Internationalen Zuchtbuch registriert sind.

Ziele:

1. Schutz des asiatischen Wildpferdes vor genetischem und demographischem Untergang.
2. Wiedereinbürgerung des asiatischen Wildpferdes in die Wildbahn als freilebende Populationen in ausreichend großer Zahl, um eine fortlaufende Anpassung durch natürliche Selektion zuzulassen.
3. Management der Gefangenschaftspopulation, um die jetzige genetische Variabilität zu erhalten und um Pferde für Wiedereinbürgerungs- und Freilassungsprogramme zur Verfügung zu stellen.

Maßnahmen:

1. Aufbau von 5-10 Wildpopulationen, jede mit einer N_e von mindestens 50 oder einer Anzahl von mindestens 250 erwachsenen Tieren (3 Jahre und älter), um eine Gesamt- N_e von mindestens 1000 und eine Gesamtzahl von 5000 erwachsenen Tieren zu erreichen.
2. Überwachung der genetischen und demographischen Ereignisse in jeder wieder ausgebürgerten Population und alljährliche Bearbeitung der erhaltenen Informationen, um die Kontinuität des Programmes zu gewährleisten.
3. Management der Wild- und der Gefangenschafts-Population als Metapopulation durch effektiven Austausch von Tieren zwischen den Populationen, die aufgrund von neuesten Ergebnissen bestimmt wurden.
4. Management der Gefangenschaftspopulation, um das Maximum an vorhandener genetischer Variabilität zu bewahren, die aus der ursprünglichen Wildpopulation übrig geblieben ist. Spezielle Richtlinien für einen Zeitraum von 200 Jahren beinhalten: a) Erhaltung von 95 % der durchschnittlichen, individuellen Heterozygotität, b) Vermeidung von Verlust an Founder-Allelen durch Einsatz von Tieren, die als genetisch wichtig mittels Pedigree-Analysen bestimmt wurden, c) Bewahrung der jetzigen Founder-Allel-Diversität ($1 - \sum p_i^2$, wobei p_i 's die Häufigkeit der individuell bezeichneten Founder-Allele bedeutet, d) Erhaltung von seltenen, verschiedenartigen Marker-Allelen.
5. Erstellung eines internationalen Management Programmes unter der Schirmherrschaft der CBSG durch Koordination der bereits bestehenden Regional-Programme (EEP, SSP, SMP) und Einrichtung zusätzlicher Regionalprogramme, um die Tiere, die sich in Menschenhand befinden, als globale Population zu verwalten.
6. Beibehaltung der z.Zt. verwalteten Gefangenschaftspopulationsgröße von 500 - 750 Pferden, um die vorhandene genetische Variabilität auf akzeptablem Niveau zu halten. Durchführung angemessener Tiertausche zwischen den regionalen Zuchtprogrammen, um eine Präsenz der noch vorhandenen Founder-Allele in jedem Programm zu gewährleisten, wobei gleichzeitig die Diversität dieser Präsenz bei den Tieren erhalten bleiben soll. Ob die in den Zoos angestrebte Populationsgröße von 500 - 750 Tieren ausreichend ist,

hängt von der Zustimmung der einzelnen Erhaltungszuchtprogramme zu den demographischen und genetischen Zielen des globalen Programmes ab. Für den Fall, daß die Regional-Programme abweichende Ziele und Strategien entwickeln oder ihren Beitrag zur Erfüllung des globalen Planes nicht leisten, muß die Zahl der Pferde der betreuten Gefangenschaftspopulation größer sein.

7. Betreuung der Gefangenschaftspopulation, um ausreichend Tiere für Wiederausbürgerungen oder Freilassungen bereitzustellen, bei gleichzeitiger Sicherstellung, daß die genetische Variabilität und demographische Sicherheit nicht gefährdet werden. Die Tiere sollten, basierend auf Vorschlägen der Gruppe, die die Gefangenschaftsherde managed, nach Rücksprache mit den Leitern der Wiederausbürgerungs- und Freilassungsprogramme, zur Verfügung gestellt werden. Anfragen nach Tieren sollten 2 Jahre vor deren Benötigung gestellt werden. Diese Tiere sollten so ausgewählt werden, daß an jedem Wiedereinbürgerungsort die volle Repräsentation der genetischen Variabilität, die es z.Zt. in der Gefangenschaftspopulation gibt, vorhanden ist.
8. Entwicklung einer effektiven Zusammenarbeit mit der Equid Specialist Group und der Reintroduction Specialist Group, die bei der Erreichung des Zieles, das Przewalskipferd wieder auszubürgern, Unterstützung geben können.

EMPFEHLUNGEN

Wildpopulationen

1. Einladung von Repräsentanten der Equid Specialist Group und der Reintroduction Specialist Group zum Leipziger Przewalskipferdtreffen (19.-23.5.90) und zum Copenhagener CBSG-Treffen vom 24.-26. August 1990, um einen Arbeitskreis für das Wiederausbürgerungsprogramm zu bilden. Einladung auch von Vertretern der Nationen, wo wiedereingebürgert, bzw. versuchsweise freigelassen wird.
2. Aufstellung von Kriterien für die Wiedereinbürgerungsplätze (durch die Vertreter des globalen Erhaltungszuchtprogrammes in Zusammenarbeit mit der Equid Specialist Group, der Reintroduction Specialist Group und mit Organisatoren der nationalen Programme). Die Analysen sollen beinhalten: Landkarten, Klimaverhältnisse, Nahrungs- und Wasserangebot über das ganze Jahr, Krankheiten, Vorkommen von Haus- und verwilderten Pferden und Verbindlichkeiten der Regierungen. Bezugnahme auf Proceedings des FAO/UNEP/IUCN-Treffens in Moskau als Arbeitspapier für die Auswahlkriterien des Habitats.
3. Bestimmung von mindestens 5 möglichen Wiedereinbürgerungsgebieten, die im Jahre 1994 Tiere übernehmen könnten. Bis 1992 sollte jedes Gebiet auf seine Eignung hin geprüft und beurteilt werden. Einige Gebiete sind bereits in der UdSSR (Ukraine, Kazakstan, Transbaikalia) Mongolei und China (Xinjing; Gansu) ausgewählt worden. Gebiete zur Freilassung von Pferden als Experiment sind in Canada und Australien bestimmt worden.
4. Beschaffung finanzieller Mittel und Unterstützung aus Staats-, Organisations- oder privaten Quellen, um die Wiedereinbürgerung 1994 zu starten. UNEP, FAO und IUCN sollten als mögliche Teilnehmer angesprochen werden. Geld wird benötigt für die Transporte zu den Wiedereinbürgerungsgebieten, um letztere entsprechend einzurichten und um Überwachungsprogramme nach der Freilassung durchzuführen.

Gefangenschaftspopulation

1. Bildung einer globalen Managementgruppe für das Przewalskipferd in Gefangenschaft unter Schirmherrschaft der CBSG, bestehend aus dem Internationalen Zuchtbuchführer und den Koordinatoren der regionalen Programme. Diese Gruppe soll das Management der Gefangenschaftspopulation weltweit leiten und die einzelnen Tiere für die Wiedereinbürgerung, bzw. experimentellen Freilassung bestimmen. (1. Treffen in Leipzig, ein 2. folgend in Copenhagen 1990 in Zusammenhang mit der jährlichen CBSG-Sitzung).
2. Management der Gefangenschaftspopulation, um das Maximum an Foundergenen zu bewahren. Ausarbeitung von Richtlinien zur Einbeziehung der Linie mit dem Founderanteil der dom. Mongol-Stute, um das Maximum an Foundergenen wilder Vorfahren zu bewahren. Diese Richtlinien können Möglichkeiten für teilweise genetisch getrennte Subpopulationen mit einschließen.
3. Überwachung der individuellen Heterozygotität, des Erhaltens von Founder-Allelen, der Diversität von Founder-Allelen und des zu beobachtenden Polymorphismus (Enzyme, Proteine, DNS, Chromosomen, Blutgruppen) der Gefangenschaftspopulation und deren Subpopulationen. Sicherstellung der Erhaltung verbliebener Founder-Allele mittels Auffindung von genetisch wichtigen Individuen in den verschiedenen Untergruppen der Population.
4. Analyse der genetischen Auswirkung auf die Gefangenschaftsherde bei Ausschluß von Tieren aufgrund von phänotypischen Merkmalen (Frank Princée wird Analysen durchführen und die Ergebnisse vor dem Leipzig-Treffen zur Verfügung stellen). Analyse eines möglichen genetischen Zusammenhanges zwischen Fellfarbe und Serumalbumin-loci (wie bereits für das Hauspferd geschehen) durch Untersuchung von Verteilungsmustern für beide Merkmalsgruppen über ausgewählte und Aufschluß versprechende Familien (Ann Bowling wird dies - wenn möglich - noch vor Leipzig durchführen).
5. Austausch von Tieren, um die gesamte Founder-Allel-Repräsentation in EEP, SSP, UK, UdSSR und australischen Populationen zu erreichen. Aufrechterhaltung der Diversität dieser Repräsentation in den Individuen.
6. Empfohlene Populationsgrößen für folgende Regionalprogramme:
SSP 200 - 300, EEP 200 - 300, SMP 25 - 50, UdSSR 100 - 500,
U.K. 40 - 60
7. Individuelle Markierung und Blutgruppenbestimmung aller Tiere, in der Gefangenschaftspopulation. Ein Kaltbrand wird empfohlen zur dauerhaften Markierung mittels Abkürzung des Zuchtbuchnamens.
8. Überprüfung des Zuchtbuches auf Richtigkeit aller Dateneinträge. Tiere mit fragwürdiger oder unsicherer Abstammung und solche, die individuell nicht identifiziert werden können, sollen mittels Blutgruppenbestimmung Elterntieren zugeordnet werden. Tiere, die nicht identifiziert werden können, sollen in ein gesondertes Register überschrieben werden.
9. Durchführung von Langzeitverhaltensstudien, sowie Abklärung eines möglichen genetischen Ursprungs bei bestimmten Krankheiten und bei Unfruchtbarkeit. Erstellung von genetischen Analysen zur Überprüfung der Tiere, deren Zuchtausschluß aufgrund phänotypischer Merkmale wünschenswert ist.

Aufwand zur Verwirklichung dieses Planes

1. Erstellung der regionalen Zuchtbücher, Analysen und Managementpläne.
2. Regionale Treffen, um regionale Pläne zu formulieren und einzusetzen.
3. Mithilfe bei der Erstellung des Internationalen Zuchtbuches.
4. Kennzeichnung von Tieren und Erstellen ihrer Blutgruppenformeln. (Probenentnahme und Durchführung der Analysen).
5. Tieraustausch
6. Jährliches Zusammentreffen der regionalen Koordinatoren, des Zuchtbuchführers und der Vertreter der Specialist-Gruppen.
7. Überwachung der genetischen Indikatoren.
8. Erforschung von Problemen, die die in Gefangenschaft gehaltenen Pferde betreffen hinsichtlich eines möglichen genetischen Ursprungs.
9. Stabilisierung der Gefangenschaftspopulation.
10. Beteiligung an Wiederausbürgerungs-/Freilassungs-Programmen.
11. Veröffentlichung und Verteilung des Planes und unterstützender Dokumente.
12. Herstellung und Verteilung von Jahresberichten.

ЦЕЛИ И ЗАДАЧИ

ОПРЕДЕЛЕНИЕ:

1. Лошадь Пржевальского (*Equus przewalskii*) как популяция зарегистрирована в международной племенной книге.

ЦЕЛИ:

1. Защита лошади Пржевальского от генетического и демографического вымирания.
2. Восстановление вида в природной среде в достаточном количестве голов, свободно мигрирующих, имея в виду эволюцию естественного отбора.
3. Наблюдение над популяцией животных, разведенных в неволе, с целью сохранения развития генетических вариаций и подготовки лошадей для программы по восстановлению вида и возвращению его в природную среду.

ЗАДАЧИ:

1. Создать 5-10 диких популяций с N_e не меньше, чем 50 голов или не меньше 250 трехлеток и старше. Добиться абсолютно го N_e не меньше 1000 и общего количества взрослых животных не меньше 5000.
2. Наблюдать за генетическим и демографическим результатами в каждой возобновленной популяции и давать обзорную информацию года для ориентации продолжения программы.
3. На основании продолжающегося изучения управлять эффективным обменом животными между популяциями диких и живущими в неволе животных как метапопуляциями.
4. Сохранить в каждой поименованной популяции максимум количества голов, имеющих генетическую структуру, уцелевшую в оригинальных диких популяциях. Программа восстановления вида рассчитана на 200 лет: а/ сохранение 95% среднего существующего гетерозигота, б/ избегание потерь уцелевших

основателей рода на основе генеалогического анализа, в/ сохранение наименьшего уровня генетических вариаций основателей рода / $I - \sum p_i^2$, где p_i ' обозначает частоту повторяемости отдельно отмеченных основателей рода/, г/ сохранение редких отмеченных экземпляров основателей рода.

5. Основать общую международную программу под эгидой CIBSG Группы специалистов по разведению и селекции животных в неволе на базе координации существующих региональных программ Группы по борьбе с загрязнением окружающей среды, Группы по выживанию видов и Специальной группы поддержки, и в дальнейшем предложить сотрудничество региональным группам для управления популяциями животных, разведенных в неволе, как мировой популяцией.
6. Сохранить популяции животных, живущих в неволе, в количестве 500-750 голов для консервации существующих генетических вариантов на приемлемом уровне. Осуществлять соответствующий адекватный обмен лошадьми между региональными руководителями для обеспечения сохранения многообразия основателей родов. В то же время сохранение многообразия этих представителей животных, живущих в неволе, в популяциях из 500 - 750 лошадей будет зависеть от общего плана и единомыслия руководителей популяций. В случае изменения и совершенствования плана, перераспределения генетических и демографических задач или невозможности выполнения своей части общего плана количество животных в каждой популяции по разведению лошадей в неволе должно быть увеличено.
7. Обеспечить руководство популяций по разведению животных в неволе необходимым количеством лошадей для программы по восстановлению вида, гарантировать демографическую и генетическую защиту и безопасность животных. На основании рекомендаций центрального руководства популяциями разведенных в неволе животных и при консультации главных экспертов общей программы по восстановлению вида каждая популяция будет получать необходимое количество животных, о чем нужно сообщать заранее, не менее, чем за два года.

Выбирать животных, которые представляют полную генетическую вариацию популяции животных, разведенных в неволе.

8. Эффективно развивать сотрудничество с Группой специалистов по изучению лошадей и Группой специалистов по восстановлению вида, которые обязуются содействовать в выполнении задач по восстановлению дикой лошади Пржевальского.

РЕКОМЕНДАЦИИ:

Популяции диких лошадей:

1. Провести совместный семинар по теме "Лошадь Пржевальского" Группы специалистов по изучению лошадей и Группы специалистов по восстановлению вида в Лейпциге с 19 по 23 мая 1990 г. и Группы специалистов по разведению и селекции животных в неволе в Копенгагене с 24 по 26 августа 1990 г. для определения работы по восстановительной программе. Пригласить также на эти встречи представителей тех государств, где существуют реальные местонахождения или проводится эксперимент по восстановлению популяций.
2. Определить критерии восстановления мест обитания животных. Экспертами признать вновь образованную головную группу, постоянно контактирующую с Группой специалистов по изучению лошадей и Группой специалистов по восстановлению вида и национальными организаторами программы. При анализе ситуации учитывать географическое местоположение, климат, природный годовой запас воды и питания, возможные заболевания, наличие диких и домашних животных. Заключение экспертов вручить правительствам стран, заинтересованных в решении этой проблемы. Послать Продовольственной и сельскохозяйственной организации ООН, Программе организации ООН по охране окружающей среды и Международному союзу охраны природы и природных ресурсов научные доклады Московской встречи для обсуждения вопроса о создании рабочего документа по выбору мест селекции и его критериях.

3. Установить по крайней мере пять потенциальных мест обитания, которые могли бы принять животных к 1994 г. Начать изучение вопроса об определении каждого местонахождения к 1992 г. Уже теперь можно было бы назвать СССР /Украина, Казахстан, Трансбайкал/, Монголию и Китай /Ксинь-джанг, Гансю/. Для эксперимента определены места обитания в Канаде и Австралии.
4. Получить государственную, организационную и частную поддержку и финансирование для инициатив восстановительной программы к 1994 г. Предложить сотрудничество Продовольственной и сельскохозяйственной организациям ООН, Всемирной Федерации диких лошадей, Программе организации ООН по охране окружающей среды, Международному союзу охраны природы и природных ресурсов как возможным партнерам. Необходимы средства для нахождения мест обитания, транспортировки животных, контрольных программ после восстановления популяций.

Популяции животных, разведенных в неволе

1. Создать группу руководства общей популяцией лошади Пржевальского, разведенной в неволе, под эгидой Группы специалистов по разведению и селекции животных в неволе, состоящей из хранителя Международной племенной книги и координаторов региональных программ. Эта группа будет руководить всемирной базой популяцией животных, разведенных в неволе, и определять характерные оригинальные экземпляры животных для программы по восстановлению и экспериментальному высвобождению животных на волю. /Первая встреча в Лейпциге с последующими сессиями в Копенгагене в 1990 г., а также с ежегодными встречами с Группой специалистов по разведению и селекции животных в неволе./
2. Руководить популяцией разведенных в неволе животных для сохранения максимума лошадей Пржевальского – основателей рода. Определить общий курс включения существующих домашних родословных для сохранения наибольшего количества диких основателей рода. Это направление должно предусмотреть частично генетически изолированные популяции.

3. Наблюдать индивидуально гетерозигот, выживание основателей родов, их многообразии и поддающийся наблюдению полиморфизм /энзим, протеин, ДНК, хромосомы, группу крови/ в популяциях разведенных в неволе животных и в подпопуляциях. Гарантировать выживание основателей родов путем анализа генетически важных характеристик в различных подгруппах популяций.
4. Анализировать генетическое влияние отделения лошадей, разведенных в неволе, от экземпляров животных, исключенных из Программы по борьбе с загрязнением окружающей среды по фенотипическим причинам. /Прилагается список фенотипических причин и животных, пораженных болезнью./ /Фрэнк Прайси будет руководить анализом и обеспечивать успех лейпцигской встречи./ Анализировать генетическую связь между окраской шерсти и serum albumin loci /как известно в Equus caballus / путем контроля выделения обоих свойств в отобранных, содержащих информацию семействах. Демонстрация такой родственной связи в семействах будет поддержкой в определении носителей этих свойств. /Анна Бойлинг, если возможно, сделает этот анализ до встречи в Лейпциге./
5. Обменивать животных до полного достижения восстановления основателей родов в популяциях Программы по борьбе с загрязнением окружающей среды, Группы по выживанию видов, Англии, Советского Союза и Австралии. Сохранять многообразие этих представителей среди индивидуальных животных.
6. Рекомендовать организовать следующие популяции для региональных программ:
- | | |
|---|-----------|
| Программа по борьбе с загрязнением окружающей среды | 200 - 300 |
| Англия | 40 - 60 |
| Советский Союз | 100 - 500 |
| Группа по выживанию вида /Северная Америка/ | 200 - 300 |
| Специальная группа поддержки /Австралия - Новая Зеландия/ | 25 - 50 |

7. Индивидуально маркировать и устанавливать группу крови всех животных в популяциях разведенных в неволе лошадей. Рекомендуется скотоводам использовать замороженное клеймо для перманентной маркировки кода и номера.
8. Сверять с племенной книгой точность вносимых данных. Животных сомнительного или неизвестного происхождения определять по группе крови. Животных, которые не могут быть признаны чистопородными, снять с регистрации.
9. Проводить исследование образа жизни, повадок, манер поведения и изучать генетическую основу синдромов заболеваний и бесплодия. Анализировать генетический базис фенотипических характерных черт, которые могут оказаться причинами для снятия с регистрации.

ПРИМЕРНЫЙ ПЛАН МЕРОПРИЯТИЙ:

1. Заполнение региональных племенных книг, постоянный анализ и составление планов руководства /2 недели для регионального плана на год/.
2. Региональные встречи для формирования и выполнения планов /2 - 3 дня/.
3. Участие в международной племенной книге /1 - 2 дня/.
4. Маркировка и установка группы крови животных /собираание и анализ образцов/.
5. Миграция животных.
6. Ежегодные встречи региональных координаторов и представителей Группы специалистов по восстановлению вида /3 дня/.
7. Наблюдение генетических индикаторов.
8. Собираание, хранение и анализ замороженных образцов биологической ткани.
9. Исследование проблем, связанных с разведением лошадей в неволе, и их возможных генетических основ.

- I0. Постоянный генеалогический и генетический анализ популяции лошади Пржевальского.
- II7 Стабилизация популяций разведенных в неволе животных.
- I2. Участие в программе по восстановлению и высвобождению вида.
- I3. Публикация и распространение плана и сопроводительной документации.
- I4. Подготовка и распространение ежегодных докладов.
- I5. Собираание фотоматериалов для архива.

关于全球范围内普氏野马保护计划及目标的建议方案：

①

定义：

(一) 普氏野马群体是由国际血统记录部所登记在册的动物组成。

宗旨：

(一) 保护普氏野马使之免遭遗传及种群灭绝。

(二) 在野外重建足够大的野马群，使之可以在自然选择的环境下发展。

(三) 管理驯养马群以保持现有的遗传变异，并使之提供马匹供引进及放养计划之用。

目标：

(一) 组建五至十个野外马群。每群的有效群体规模至少有五十至二百五十头成年马（三岁以上），以达到有效群体总数至少一千头至五千头成年马。

(二) 监测再引进群的遗传及群体统计变化，并且每年检查所有资料，做为进一步计划的基础。

(三) 根据持续监测的结果有效地变动种群结构，即有效地把野外群及驯养群的马匹互换。

(四) 管理驯养群使之保持野生群体留下的遗传变

异。具体措施如下(以二百头计):

②

(a). 保持 95% 现有的个体杂合性。

(b). 通过遗传分析手段避免马匹丧失现有的基本等位基因。

(c). 至少保持现有水平上的等位基因之间的变异。

(d). 保存显著稀有变异标记基因。

(五). 由驯养繁殖专家提出一项国际管理计划。应包含现有的地区计划(欧洲物种保护计划(EPP), 物种保护计划(SSP), 澳大利亚物种保护计划(SMP))并增加新的区域性管理驯养计划, 使之成为全球性统一管理计划。

(六). 驯养群的马匹数量应保持在五百至七百五十头左右, 以便保存现存的遗传变异特性。每个地区管理单位都应具有足够的马匹数量以使之保持原种的等位基因。每群驯养的具体数目(五百至七百五十头)将取决于地区管理单位分担的遗传及种群统计工作的具体情况来决定。如果地区管理计划具有不同的目标和策略, 或不能按全球计划运作。驯养数量可能会有所增加。

(七). 管理驯养群使之能够提供足够马匹用以实施再引进和放养计划。同时又能确保该群的遗传变异及种群统计稳定性不至受到损害。提供野马的计划将由全球驯养小组与再引进和放养计划管理代表协商决定。要野马的申请须在两年以前提出并申明需要的日期。被选送到再引进场的马匹须具备现有驯养群的遗传特性。

③

(一). 由马学专家和再引进专家提出协作方案, 帮助完成普氏野马返回大自然的作。

建议:

野外群体:

(一). 邀请马学及再引进专家团的代表参加一九九零年五月十九日至二十三日在东德莱比锡(LEIPZIG)举行的普氏野马研讨会和八月二十四日至二十六日在瑞典哥本哈根(COPENHAGEN)举行的驯养繁殖专家(CBSG)会议共商实施再引进计划的工作。此外还将邀请有再引进或实验放养场的国家派代表参加以上会议。

(二). 规定再引进场地的标准(由全球驯养管理组领导与马学专家, 再引进专家及国立计划组织成员共同商讨定出), 包括地形、气候、全年饲料和饮水供给、疾病、疯马与野马共存及政府负担等等。请参照粮农组织(FAO)/联合国环境计划署(UNEP)/国际自然保护联盟(IUCN)莫斯科会议汇编中的有关场地选择标准的讨论文件。

(三). 选定五个以上可以建立再引进场的地区, 并于一九九四年引进动物。于一九九二年完成对每个场地的初步调查并确定场地的可用性。现已选定的场地有苏联(乌克兰, 哈薩克, TRANSBAIKALIA)、蒙古和中国(新疆, 甘肃)。试验放养场也已在加拿大和澳大利亚送出。

(四). 争取政府、团体及个人的支持(包括资金上的支持), 使初步再引进计划能在一九九四年实施。联合国环境

④

计划署(UNEP), 粮农组织(FAO)、世界野生动物保护基金会(WWF)和国际自然保护联盟(IUCN)应被接纳为可参与对象。所需资金是用于运送动物到放养场地, 放养场的准备及放养后的监测管理工作。

驯养群体:

(一) 由国际血统记录员和地区计划协调员组成并由驯养繁殖专家领导成立世界驯养委员会。该会将指导全世界的驯养群, 并负责鉴定个体动物及再引进和试验放养计划的实施(首次会议将在莱比锡举行, 然后在哥本哈根的驯养繁殖专家-一九九零年年会上继续讨论)

(二) 妥善管理驯养群使之保持最多的普氏野马原种^普基因数量。具体措施包括使现有家养谱系维持最多野生原种基因。这些可用于部分遗传隔离亚群。

(三) 监测驯养群及其亚群中的个体杂合性, 保留原种^普位基因的个体, 原种^普位基因变异及显著多态性^普等(酶, 蛋白质, 脱氧核糖核酸, 染色体, 血型等)。用遗传分析^普方法使各亚群保持现有原种基因的延续。

(四) 分析个体动物移出驯养群的基因影响。这些动物均因表型性状理由而被欧洲~~普~~物种保护计划排除出来的。(附上受影响动物名单及其表型特征)(FRANK PRINEE 会在莱比锡会议之前进行以上分析)。试图在毛色及血清蛋白位点之间进行遗传连锁分析。该项测定是利用被选出的有利族系分离测定以上两种特征。论证

⑤

这种连锁鉴定基因协带个体将会有很大帮助。(如有可能安·鲍玲(ANN BOWLING)将在莱比锡会议之前做该项试验。

(五). 交换动物使在欧洲物种保护计划(BEP), 物种保护计划(SSP) 英国, 苏联和澳大利亚种群中都有原种基因, 并在个体动物中有变异的代表。

(六). 建议各地区计划马匹数量如下:

物种保护计划	二百——三百头
欧洲物种保护计划	二百——三百头
澳大利亚物种保护计划	十五——五十头
苏联	一百——五百头
英国	四十——六十头

(七). 所有驯养群的马匹都需要做个别标记和血型鉴定。建议采用冷冻烙印法, 利用繁殖密码和数字来进行永久标记。

(八). 复查所有血统记录部所存资料的准确性。如有问题或血统不清而不能识别的动物应做血型鉴定, 辨别身份及来源。不能确证来源的动物应移交登记处。

(九). 继续进行行为研究和探讨基因引起的疾病症状及不育症。分析基因表型特征可能影响到迁移的动物。

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計劃所需費用 (COSTS OF PLAN)

- (一) 維持地區性血統記錄部, 例行分析及管理計劃費用 (每個地區計劃每年約需時間為兩週左右)。
- (二) 地區性會議。宗旨: 陳述和履行地區計劃。
(二至三天左右)
- (三) 參與國際血統記錄部工作 (一至二天左右)。
- (四) 動物作記號和血型鑒定 (收集和分折樣本)。
- (五) 動物遷移費用。
- (六) 地區協調員和專家團代表每年一次的年會 (約三天)。
- (七) 監察遺傳指示器費用。
- (八) 冷藏組織樣本的制定, 貯藏和分折。
- (九) 對有問題的圈養野馬及其遺傳基的可能性的研究。
- (十) 系譜和種群遺傳分析。
- (十一) 穩定圈養群體費用。

(十二) 參與再引進或放養計劃。

(十三) 發行和分配起支持作用的文件和計劃所需費用。

(十四) 年報的準備和分配。

(十五) 攝影記錄檔案所需費用。

PRZEWALSKI'S HORSE

Equus przewalskii

**GLOBAL CONSERVATION PLAN
D R A F T**

ANALYSES OF WORLD AND REGIONAL POPULATIONS

10 February 1990

SUMMARY OF DEMOGRAPHIC AND GENETIC ANALYSES
OF CAPTIVE POPULATIONS OF
PRZEWALSKI'S HORSE

DEMOGRAPHY

The captive population of Przewalski's horse increased from 34 in 1950 to over 900 in 1989 (Table 1 and Figure 1). This increase translates into an annual growth rate of 9-10% (i.e. a lambda of 1.09 to 1.10) for this period (Tables 1 & 3). Over the last 5 years, the growth rate has been slightly higher.

With an annual growth rate of 10%, a formally managed population of 500-700 (as recommended by this draft masterplan) could sustain this size and still produce approximately 50-70 horses per year for reintroduction.

The captive population census by region is summarized in Table 4. There have been 3.7 surviving foals produced in the Chinese population at Xinjiang (Jimsar county).

The age distributions for both sexes in the global population while not strictly achieving demographic stability yet certainly are approaching a stable (i.e. pyramidal) configuration (Figure 2). The sex ratio of the world population deviates significantly from unity with fewer males born (472 vs 564) and more dying (17% vs 13%) in the first year (Table 2). The higher death rate in males continues until about age 8. This disparity in sex ratio is greatest in the EEP population but is present in the SSP and USSR populations. The sex ratio of breeders since 1974 (70:205 or about 1:3) also is significantly different from unity and this bias will have an effect on effective population size.

The age of first reproduction for males is about 4 and for females is about 3 although both sexes are occasionally bred one year younger (Table 2). Females (gestation period 11 months and a foal estrus) can breed every year but the typical interbirth interval appears to be 3-4 years. The oldest age of reproduction for males was about 26 years and 25 years for females. Generation time for males is 13.3 years and for females 10.9 years.

A glossary of demographic terms and concepts is provided on page to assist interpretation of the graphs and tables.

Table 1**Census Report**

Restricted to: PRZEWALSKIS HORSE Studbook

Dates: 31/12/1950 <= date .and. date <= 31/12/1988

=====
Taxon Name: **EQUUS PRZEWALSKII**
=====

Year	Specimen Counts	Lambda
1988	381.530.0 (911)	1.14 .
1987	332.464.0 (796)	1.12 .
1986	304.420.0 (724)	1.12 .
1985	282.374.0 (656)	1.11 .
1984	259.342.0 (601)	1.11 5 yr ave.
1983	237.308.0 (545)	1.11 .
1982	214.286.0 (500)	1.10 .
1981	190.267.0 (457)	1.10 .
1980	173.243.0 (416)	1.10 .
1979	152.228.0 (380)	1.11 10 yr ave.
1978	132.204.0 (336)	1.11 .
1977	117.181.0 (298)	1.11 .
1976	113.157.0 (270)	1.10 .
1975	106.144.0 (250)	1.10 .
1974	102.136.0 (238)	1.10 15 yr ave.
1973	91.122.0 (213)	1.10 .
1972	85.120.0 (205)	1.10 .
1971	84.109.0 (193)	1.09 .
1970	82.100.0 (182)	1.10 .
1969	67.94.0 (161)	1.09 20 yr ave.
1968	68.90.0 (158)	1.09 .
1967	65.86.0 (151)	1.09 .
1966	64.81.0 (145)	1.09 .
1965	58.74.0 (132)	1.09 .
1964	56.68.0 (124)	1.09 25 yr ave.
1963	46.62.0 (108)	1.09 .
1962	37.51.0 (88)	1.09 .
1961	37.47.0 (84)	1.10 .
1960	30.42.0 (72)	1.10 .
1959	23.35.0 (58)	1.10 30 yr ave.
1958	23.33.0 (56)	1.10 .
1957	22.28.0 (50)	1.10 .
1956	21.25.0 (46)	1.10 .
1955	20.20.0 (40)	1.10 .
1954	21.20.0 (41)	1.10 35 yr ave.
1953	19.15.0 (34)	1.10 .
1952	19.16.0 (35)	1.09 .
1951	18.16.0 (34)	1.09 .
1950	16.18.0 (34)	1.09 .

Figure 1

PRZEWALSKI'S HORSE
CENSUS OF CAPTIVE POPULATION

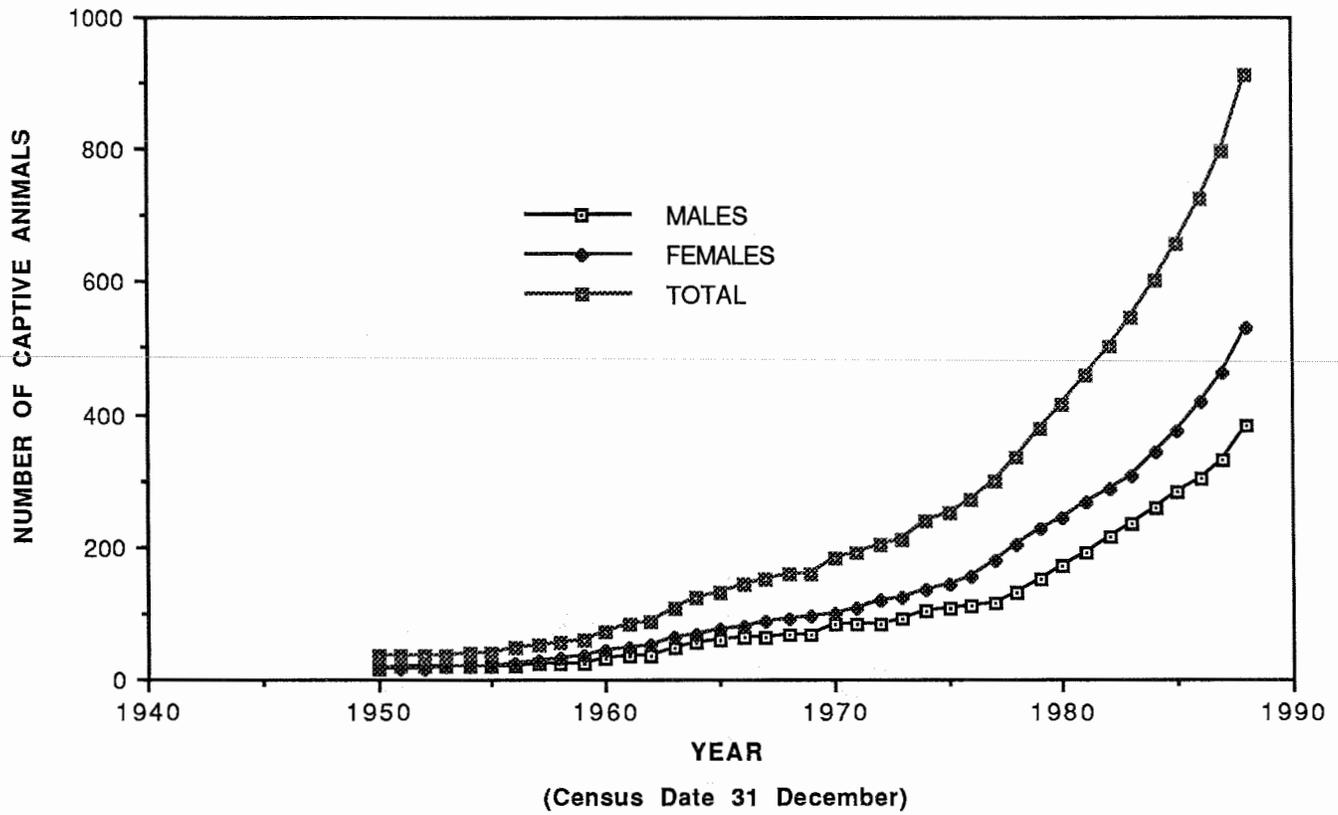


Table 2

Fecundity & Mortality Report

Report End Date:

30 Restricted to:

ASIAN WILD HORSE Studbook

21 Dec 1989

Dates: 01/12/1974 <= date

=====
Taxon Name: **EQUUS PRZEWALSKII**
=====

Age Class	Fecundity [Mx]...				Mortality [Qx]...			
	Male	N	Female	N	Male	N	Female	N
0- 1	0.000	472.4	0.000	563.9	0.170	451.8	0.130	551.2
1- 2	0.000	411.3	0.000	514.4	0.100	395.6	0.060	505.6
2- 3	0.000	340.4	0.050	437.1	0.050	333.1	0.030	431.0
3- 4	0.070	290.2	0.180	381.8	0.040	284.4	0.020	378.3
4- 5	0.190	252.0	0.210	334.9	0.040	247.8	0.030	330.4
5- 6	0.250	217.5	0.240	285.6	0.040	214.0	0.020	283.8
6- 7	0.370	184.0	0.250	252.4	0.040	179.4	0.030	247.4
7- 8	0.390	157.9	0.270	227.6	0.040	154.4	0.030	224.7
8- 9	0.410	137.5	0.310	196.3	0.040	134.9	0.040	193.3
9-10	0.480	120.1	0.270	174.0	0.020	118.6	0.020	172.5
10-11	0.550	99.9	0.300	156.1	0.040	98.2	0.010	155.9
11-12	0.600	87.7	0.290	133.3	0.100	83.6	0.040	130.5
12-13	0.580	77.7	0.340	114.6	0.090	74.2	0.010	113.9
13-14	0.550	68.0	0.270	102.8	0.030	68.0	0.040	101.5
14-15	0.480	59.1	0.290	95.3	0.120	57.0	0.020	94.3
15-16	0.610	49.3	0.290	87.2	0.130	46.7	0.050	85.3
16-17	0.540	38.9	0.240	75.9	0.110	37.6	0.070	73.4
17-18	0.600	35.1	0.210	65.9	0.000	35.1	0.020	65.0
18-19	0.560	32.2	0.250	55.0	0.060	31.7	0.070	53.4
19-20	0.420	26.1	0.180	48.1	0.120	25.5	0.060	47.5
20-21	0.580	20.7	0.130	41.7	0.000	20.7	0.050	41.4
21-22	0.540	17.8	0.140	34.7	0.120	16.8	0.190	31.5
22-23	0.570	15.0	0.140	27.8	0.000	15.0	0.080	26.6
23-24	0.360	15.4	0.060	26.4	0.000	15.4	0.000	26.4
24-25	0.610	14.8	0.020	22.5	0.230	13.0	0.200	20.3
25-26	0.320	9.5	0.030	16.7	0.490	8.1	0.360	14.1
26-27	0.390	6.5	0.000	11.2	0.170	6.0	0.300	9.9
27-28	0.000	3.2	0.000	8.2	0.330	3.0	0.130	7.5
28-29	0.000	2.5	0.000	6.4	0.000	2.5	0.440	4.6
29-30	0.000	1.5	0.000	3.6	0.000	1.5	0.000	3.6
30-31	2.950	0.2	0.000	2.6	0.000	0.0	0.500	2.0
31-32	0.000	0.0	0.000	2.0	0.000	0.0	0.000	2.0
32-33	0.000	0.0	0.000	2.0	0.000	0.0	0.000	2.0
33-34	0.000	0.0	0.000	1.1	0.000	0.0	1.000	1.0
34-35	0.000	0.0	0.000	0.5	0.000	0.0	0.000	0.5
35-36	0.000	0.0	0.000	0.0	0.000	0.0	0.000	0.0
36-37	0.000	0.0	0.000	0.0	0.000	0.0	0.000	0.0

T = 13.257 T = 10.895
 Ro = 3.972 Ro = 2.934
 lambda=1.11 lambda=1.10
 r = 0.104 r = 0.099

30 day mortality: 8%
 (90 out of 1137)

Effective Population Size		Male Female
based on 15 years of data:	Newborns that bred:	70 205
Ne = 71 [Reed, et al. (1986)]	Births/year:	34.7 40.9
	% newborns that bred:	5% 21%

1465 birth events to known age parents tabulated for Mx...plus...
 1 births to dams of unknown age...
 1 births to sires of unknown age...
 2 births to UNK or MULT sires...

Table 3

**DEMOGRAPHIC PARAMETERS
WORLD POPULATION PRZEWALSKI'S HORSE**

OVER ENTIRE HISTORY IN CAPTIVITY

<u>MALES</u>		<u>FEMALES</u>		
G	= 12.259	G	= 10.773	30 DAY MORTALITY = 7%
R ₀	= 2.511	R ₀	= 2.086	(121 out of 1687)
LAMBDA	= 1.08	LAMBDA	= 1.07	
r	= 0.075	r	= 0.068	

	<u>MALES</u>	<u>FEMALES</u>
CAPTIVE-BORN ANIMALS THAT BRED:	171	378
AVERAGE BIRTHS PER YEAR:	8.69	10.0
% CAPTIVE-BORN ANIMALS THAT BRED:	9%	25%

1749 birth events to known age parents tabulated.

883 death events of known age tabulated

= = = = =

FROM 01 DEC 1974 TO 01 JAN 1990

<u>MALES</u>		<u>FEMALES</u>		
G	= 13.257	G	= 10.895	30 DAY MORTALITY = 8%
R ₀	= 3.972	R ₀	= 2.934	(90 out of 1137)
LAMBDA	= 1.11	LAMBDA	= 1.10	
r	= 0.104	r	= 0.099	

	<u>MALES</u>	<u>FEMALES</u>
CAPTIVE-BORN ANIMALS THAT BRED:	70	205
AVERAGE BIRTHS PER YEAR:	34.7	40.9
% CAPTIVE-BORN ANIMALS THAT BRED:	5%	21%

1465 birth events to known age parents tabulated.

537 death events of known age tabulated

Table 4**REGIONAL POPULATIONS OF
PRZEWALSKI'S HORSE**

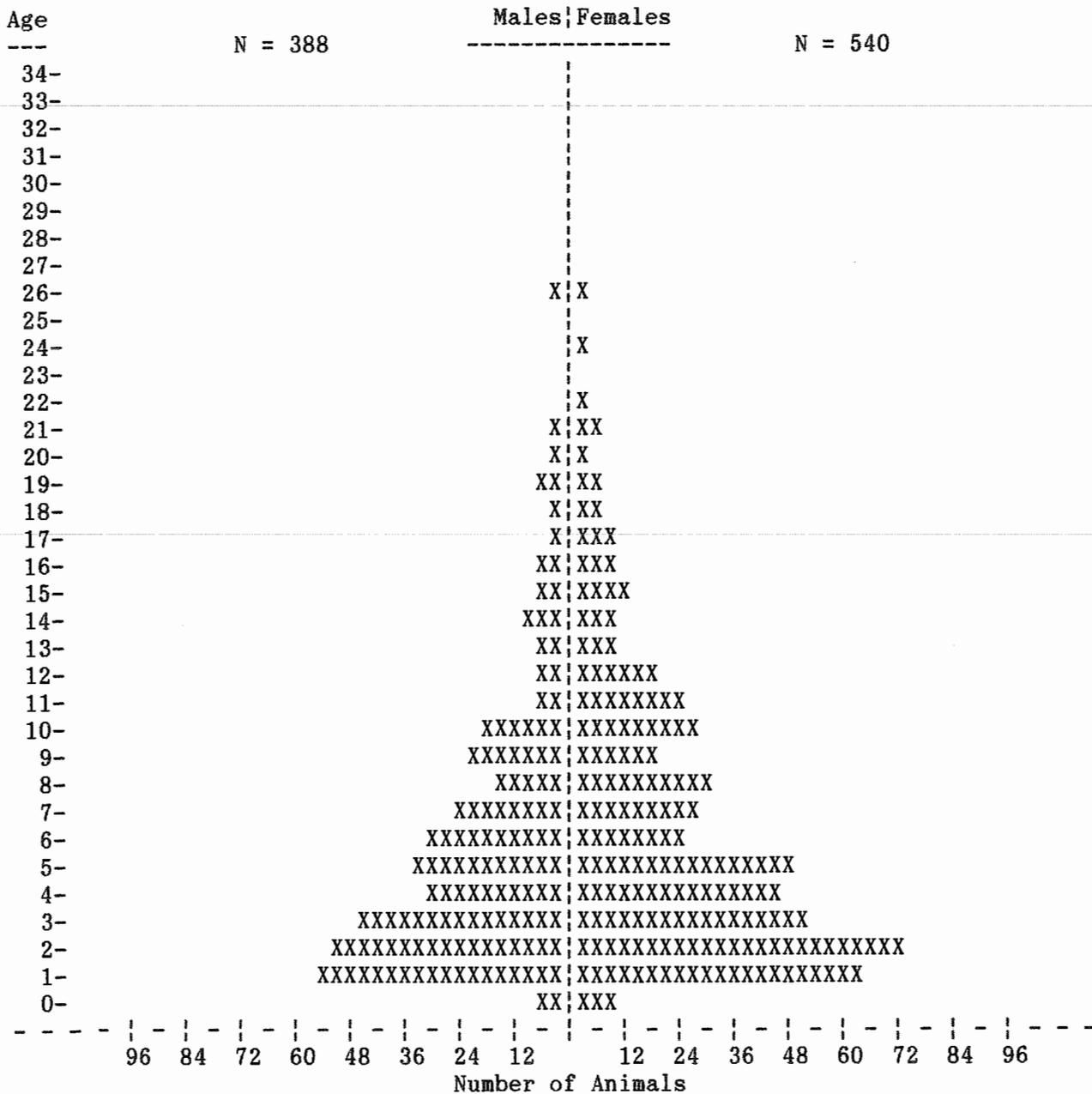
<u>REGION</u>	<u>POPULATION</u>		
	<u>Males</u>	<u>Females</u>	<u>Total</u>
SSP	76	94	170
EEP	100	161	261
UK	20	28	48
USSR	65	76	141
AUSTRALIA	10	17	27
CHINA	13	20	33
OTHER	<u>104</u>	<u>144</u>	<u>248</u>
TOTAL	388	+ 540	= 928

Figure 2

Age Pyramid Report
PRZEWALSKI'S HORSE Studbook

Report Date:
12 Jan 1990

=====
Taxon Name: EQUUS PRZEWALSKII
=====



X >>> Specimens of known sex...
 ? >>> Specimens of unknown sex...

R_0 Net reproductive rate, the rate of change per generation.

If $R_0 < 1$ Population is declining

$R_0 = 1$ Population is stationary
(Does not change in number)

$R_0 > 1$ Population is increasing

G Generation Time

Average length of time between the birth of a parent and the birth of its offspring. Equivalently, the average age at which an animal produces its offspring)

GENETICS

Genetic diversity is important for species for both fitness (i.e., the ability to survive and reproduce under existing environmental conditions) and adaptability (i.e., the ability to survive and reproduce under changed environmental conditions in the future). Small populations lose genetic diversity at both the population level due to random drift and at the individual level due to inbreeding.

The amount of genetic diversity that is contained in the current captive population of Przewalski's horse can be estimated by analytical and simulation models. These models and metrics measure the genetic diversity in the current captive population relative to the original wild population and the sample of founders from the wild population, that established the captive population. The surviving population of Przewalski's horse contains genetic material from a total of 13 founders: 12 "wild" individuals (questions have been raised about the purity of some of these founders considered wild) and 1 domestic mare.

Each of these founders contained a set of genes, its genome. Together the 13 founders of the current population of Przewalski's horse contained 13 genomes. Each genome consisted of many thousands of genes. Each gene occupies a locus on a chromosome. Every diploid animal, hence each founder horse, carried two copies of each gene at each locus. For purposes of genetic analysis, each of these copies of the genes in the founders are considered distinct alleles. Thus the founders of the current population of Przewalski's horse carried a total of 26 alleles at each locus.

Because of genetic drift and bottlenecks in the pedigree of the captive population over its history, some of the diversity as measured in terms either of original founder genomes or alleles has been lost. Two different models have been used to estimate the amount of this original genetic diversity that is still retained in the surviving population of Przewalski's horse. Their results are in close agreement.

One model (gene drop analysis) simulates the survival or loss of alleles through the actual pedigree of the Przewalski's horse. This model has been developed by a number of researchers including Dr. Jean McCluer, Dr. Georgina Mace, and Dr. Robert Lacy. Dr. Lacy's version has been used for this analysis of the Przewalski's horse.

For each animal born in the pedigree, the gene drop program randomly selects one of the two alleles carried at a locus by each of the animals's parents (one from the father and one from the mother) to form the animal's genotype. This process is repeated a large number of times or runs (e.g. 1000) for the entire pedigree and averages are calculated for these 1000 runs.

The averages are an estimate of the percentage of all genes in the current population that descend from each of the different founders. This percentage is known as the existing founder representation. The existing representation of each of the 13 founders is presented in Figures 3-9 for the various regional populations of Przewalski's horse.

It is also possible to estimate the fraction of each founders' genome that is still present in the current population. Some of the alleles and hence a portion of the genome from each founder have been irretrievably lost due to random drift and pedigree bottlenecks. Hence it is possible and informative to also measure the fraction of each founder's genome and number of alleles that have survived (been retained). The percentage representation and the fraction of the genome that have survived varies for each of the founders.

Table 5A presents a summary of the genome survival in each of the regional populations of Przewalski's horse. Of the 13 original founder genomes, about 4 to 5 founder genomes still survive in the captive population (founder genomes surviving). There are inequalities in the representation of the alleles and genomes that have survived from each of the founders. Hence, representation of some founders is more secure (occurs in more copies or animals) than others. The metric 'founder genome equivalents' considers not only loss of alleles and parts of genomes due to bottlenecks but also this uneven distribution. It will be observed that this uneven distribution of founder representation reduces the actual diversity in the population. (Compare actual (act.) founder genome equivalents to actual founder genomes surviving). By reducing the disparity in the representation of founders, the actual diversity securely present in the population can be increased (toward the potential (pot.) values).

If all, or at least an equal fraction, of each founder's genome and alleles were still present in the population, maximizing preservation of genetic diversity would be equivalent to equalizing the representation of each of the founders. However, since unequal fractions of each founders alleles are still survive in the population, maximizing preservation of diversity requires that founder representation goals be proportional to the fraction of the genome and alleles of each founder that are still present. As an example, suppose one founder still has all of its genome and alleles surviving in the population while another has only half of its genome and alleles surviving. An ideal distribution of representation of these founders should accord twice as much representation to the founder with all of its genome and alleles surviving as it does to the founder with only half of its genome and alleles surviving.

A metric known as 'target founder representation' is intended to provide a measure of this desired founder representation that is proportional to the fraction of each founder's genome and alleles that actually survive in the population. Arranging matings that produce offspring that will move the existing representation for each founder closer to the target value will maximize preservation of genetic diversity in the population.

The existing and target representation of the 13 founders are presented for the various regional populations in Figures 3-9. In each case, the target representations are proportional to the fraction of each founder genome that survived in the population. These graphs illustrate that both the existing and target founder distribution is disparate for the 13 founders, that the existing distribution diverges significantly from the target values, and that the regions differ in the patterns of these founder distributions.

The other model used is analytical rather than a simulation. This model has been developed by Dr. Elizabeth Thompson and colleagues (c.f. papers in Appendix II).

This model also presumes that for each gene or locus, each founder carried two distinct alleles. Thus the 13 founders of the Przewalski's horse population carried a maximum of 26 alleles: 24 from the "wild" individuals and 2 from the domestic mare. This model then estimates the number of these founder alleles that still survive in the population. The results of these analyses are presented in Table 5B. There are about 10.5 original founder alleles still surviving in the captive population. This result agrees with the gene drop analyses that indicated about 5 founder genomes surviving. The number of original founder alleles is twice the number of original founder genomes.

There has been much concern about the presence of domestic horse genes in the captive population of Przewalski's horse. Thompson's analyses permit an evaluation of the genetic diversity contained in the portions of the captive population that are and that are not descended from the domestic mare.

Of the 10.48 founder alleles still surviving in the captive population, 9.91 are believed to descend from the "wild" founders; .57 from the domestic mare. Of the 9.91 alleles of non-domestic origin, only 7.30 are present in the population of animals that lack the domestic mare in their ancestry. Hence, these analyses indicate that there are appreciable non-domestic alleles (2.61) carried only by horses descended from the domestic mare. Of these 2.61 non-domestic alleles carried only by horses with the domestic mare in their pedigree, 1.55 are from founders 11 and 12; 1.06 from other "wild" founders. Consequently, eliminating representatives of the domestic mare could incur loss of a significant fraction of the non-domestic founder alleles that survive in the population.

Table 5B also compares the amounts of "wild" and "domestic" alleles in the North American versus the World population, again with respect to the parts of each population that do and that do not have the domestic mare in their ancestry. Thus, there are 1.24 non-domestic alleles present in the world population that do not currently occur in the North American population. If just the part of the population without the domestic mare in its ancestry is considered, there are .076 non-domestic alleles in the World that do not currently occur in North America.

Further explanation of the concepts and terms used in these analyses are provided in the Genetics Glossary.

Table 5A

**SUMMARY OF GENETIC STATUS
OF REGIONAL CAPTIVE POPULATIONS
OF PRZEWALSKI'S HORSE**

(ANALYSIS BY ROBERT LACY)

	<u>SSP</u>		<u>EEP</u>		<u>UK</u>		<u>USSR</u>	
	<u>Act.</u>	<u>Pot.</u>	<u>Act.</u>	<u>Pot.</u>	<u>Act.</u>	<u>Pot.</u>	<u>Act.</u>	<u>Pot.</u>
FOUNDER GENOMES SURVIVING	4.61	4.61	5.14	5.14	3.71	3.71	4.28	4.28
FOUNDER GENOME EQUIVALENTS	2.84	4.61	4.57	4.57	3.56	3.71	3.50	4.28
FOUNDER EQUIVALENTS	5.85	10.49	9.54	10.18	10.15	11.17	5.60	9.33
FNDR. ALLELE DIVERSITY RETAINED (= WILD HETEROZYGOSITY RETAINED)	.749	.892	.841	.903	.805	.865	.754	.883

Table 5B

FOUNDER ALLELES SURVIVING

(ANALYSIS BY ELIZABETH THOMPSON ET AL.)

	<u>TOTAL WORLD POPULATION</u>	<u>TOTAL WORLD WITHOUT DOMESTIC</u>	<u>NORTH AMERICA POPULATION</u>	<u>NORTH AMERICA WITHOUT DOMESTIC</u>
ALL ALLELES	10.48	7.30	9.13	6.64
NON-DOMESTIC ALLELES	9.91	7.30	8.67	6.64
NON-DOM. ALLELES IN POP. WITH DOM. INFLUENCE	2.61 (i.e., 9.91 - 7.30)		2.03 (i.e., 8.68 - 6.64)	
<u>ORIGINS OF THESE ALLELES</u>				
FROM FOUNDERS 11 & 12	1.55		1.27	
FROM OTHER FOUNDERS	1.06		0.76	
NON-DOM. ALLELES IN WORLD POP. NOT IN N.A.		1.24 (9.91 - 8.67)		
NON-DOM. ALLELES IN WORLD NON-DOM. POP. THAT ARE NOT IN N.A. NON-DOM.			0.76 (7.30 - 6.64)	

Figure 3

PRZEWALSKI'S HORSE

SSP POPULATION

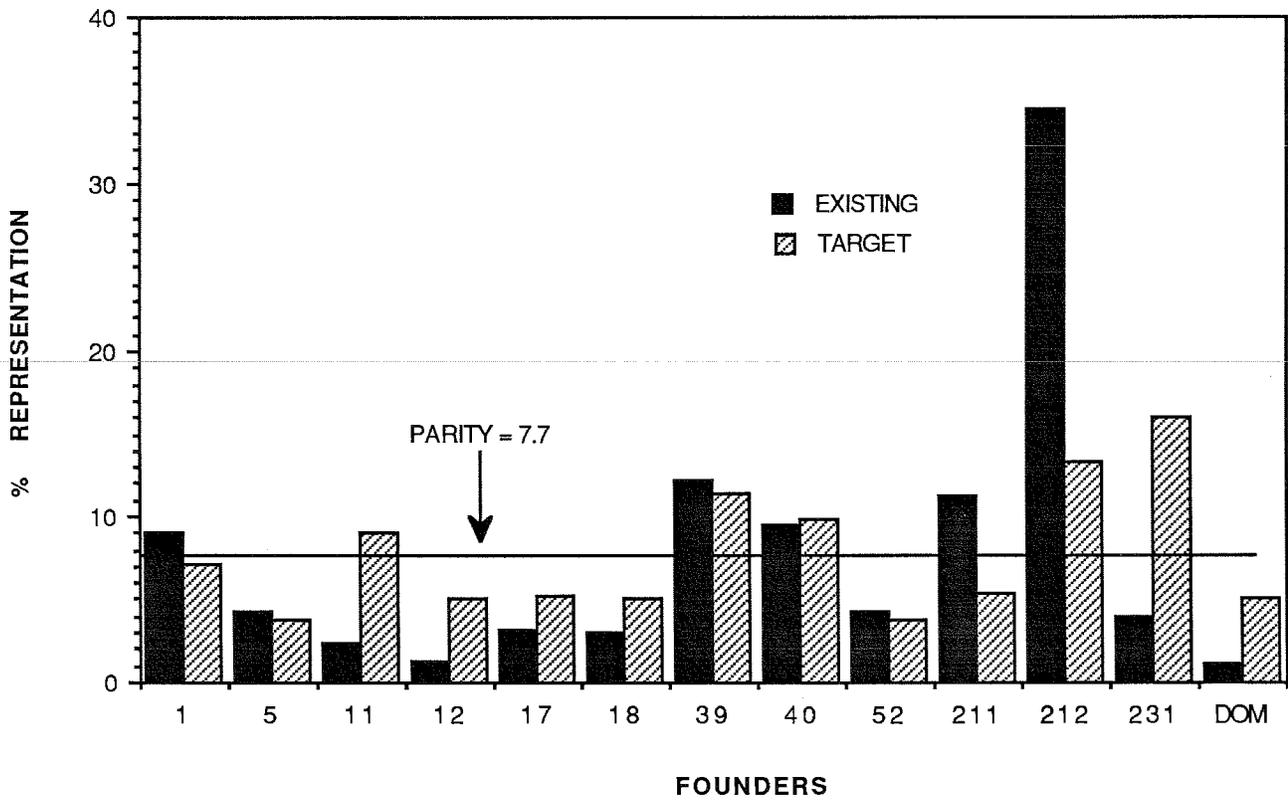


Figure 4

PRZEWALSKI'S HORSE

EPP POPULATION

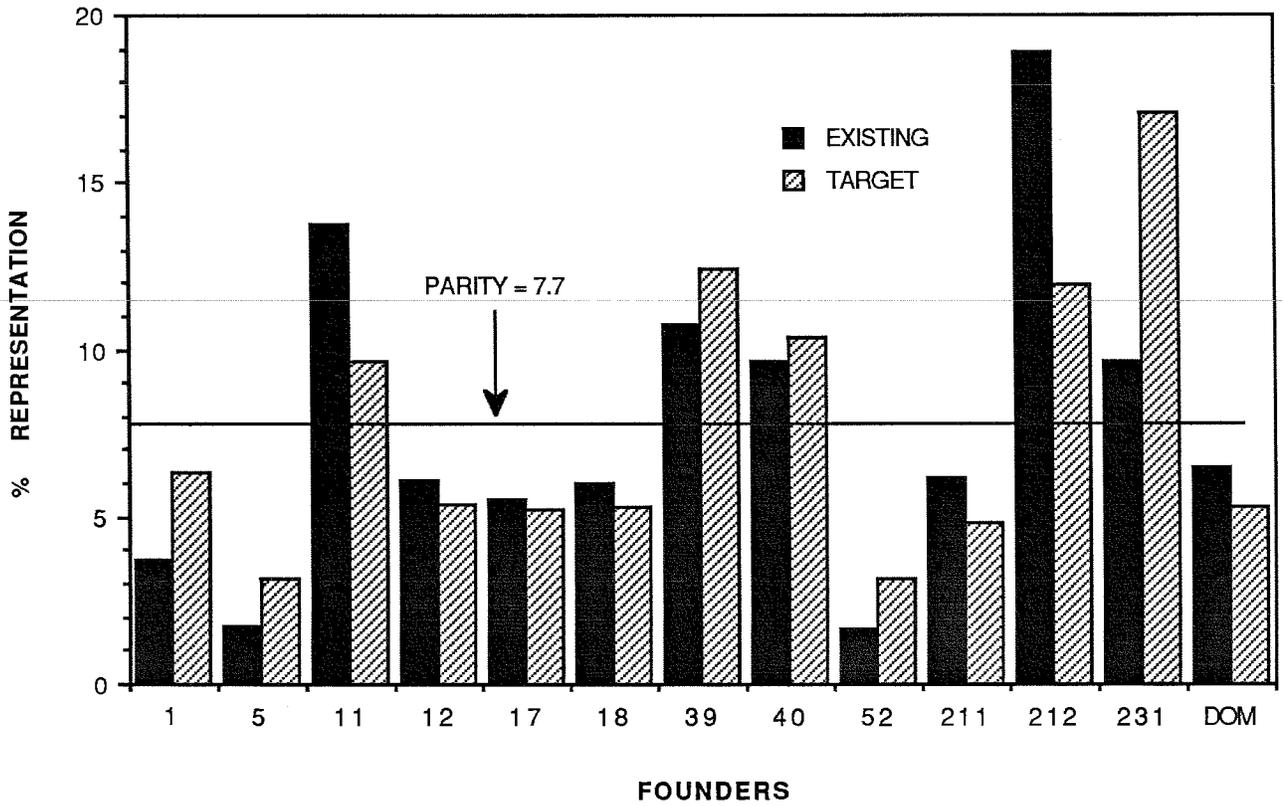


Figure 5

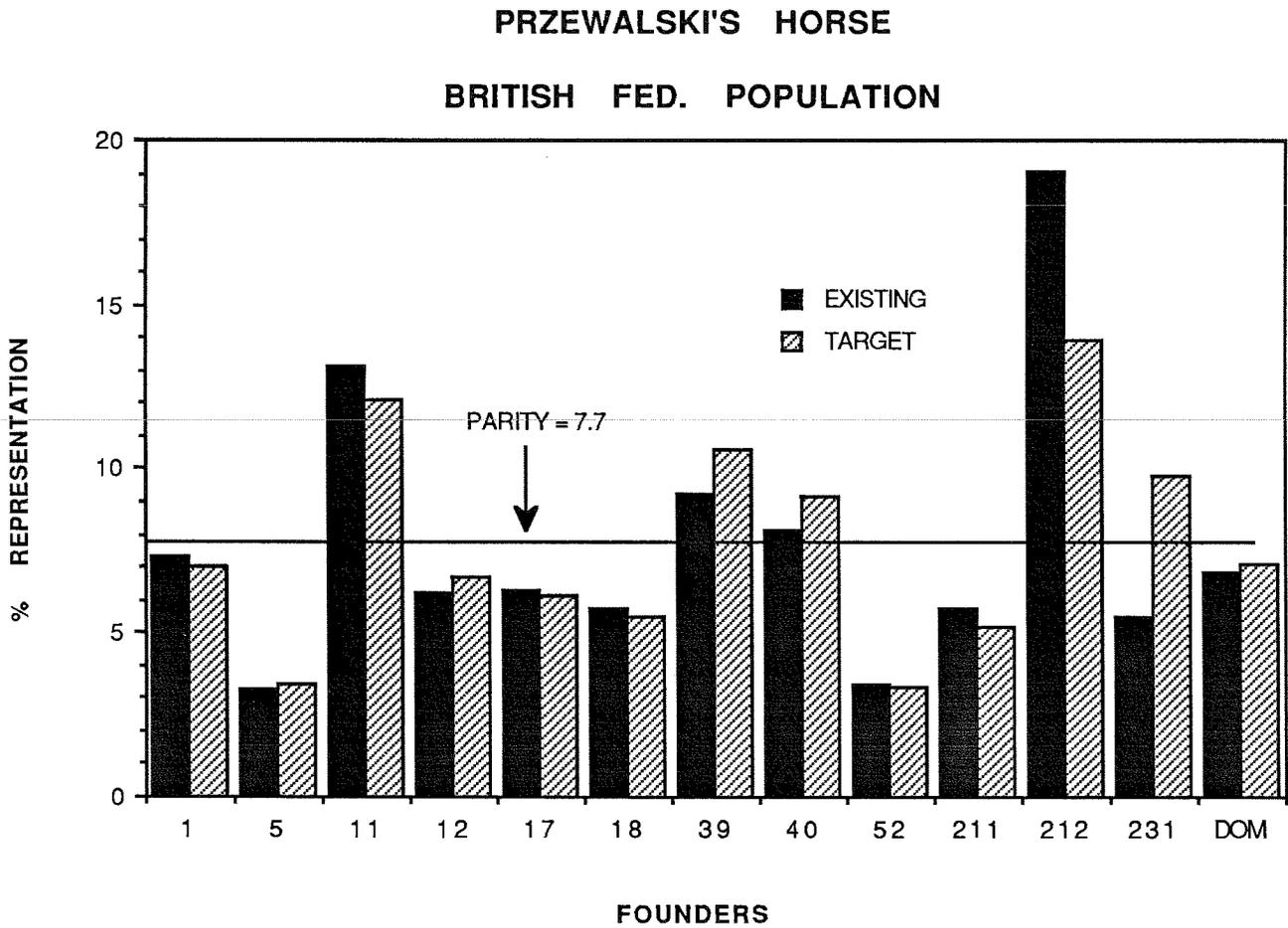


Figure 6

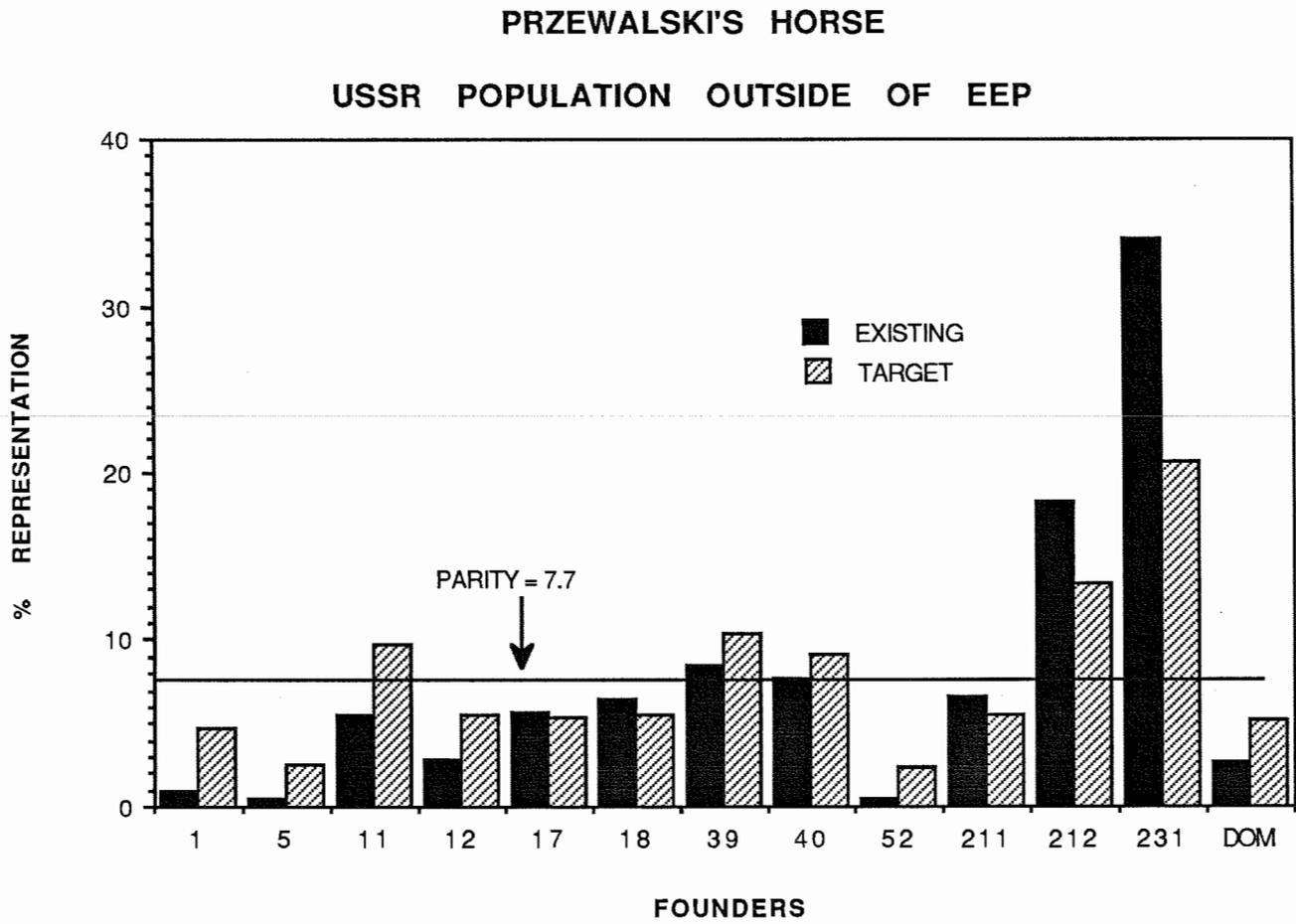


Figure 7

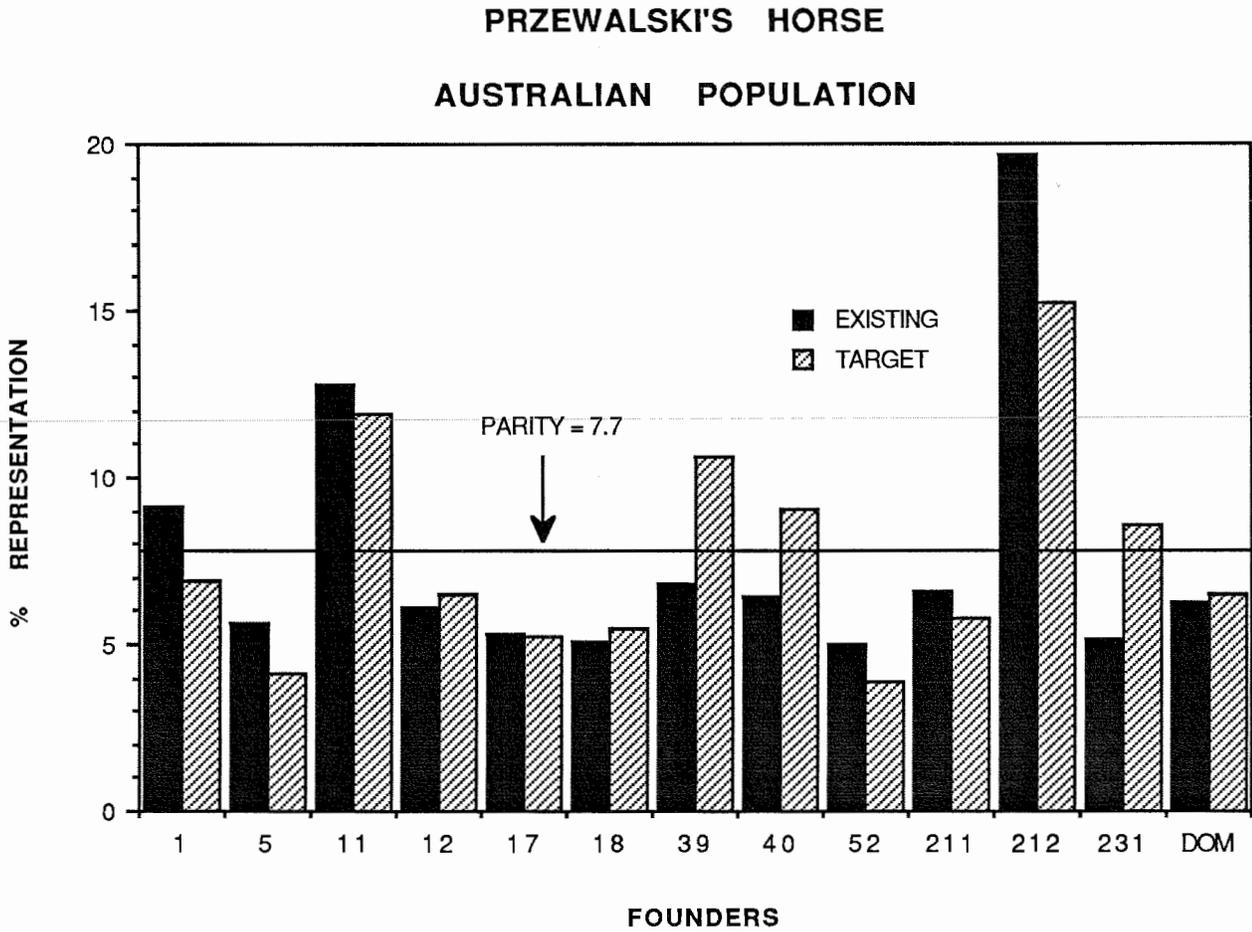


Figure 8

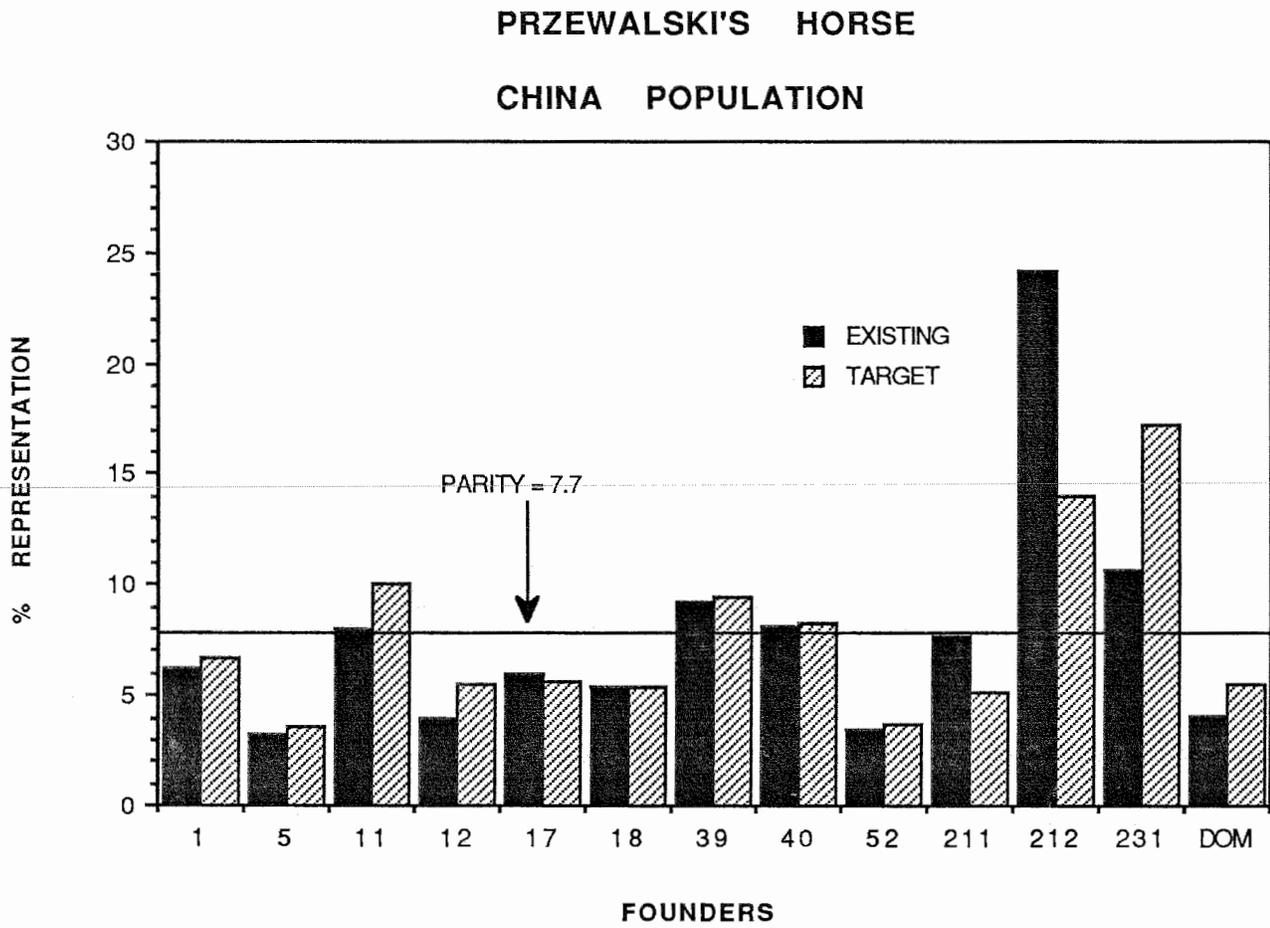
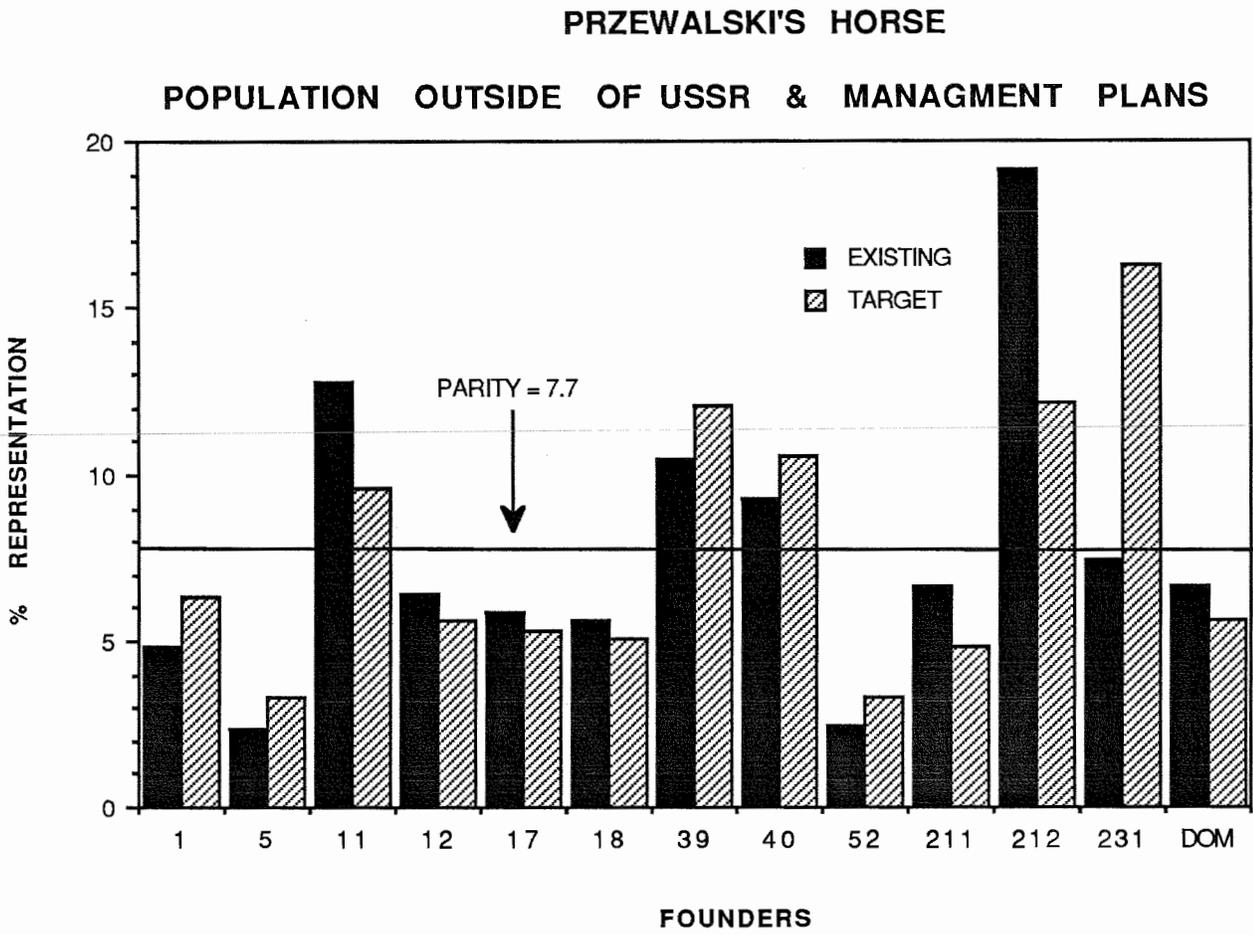


Figure 9



GENETICS GLOSSARY

DNA

Deoxyribonucleic Acid; a chain of molecules contain units known as nucleotides. The material that stores and transmits information inherited from one cell or organisms to the next. The principle DNA is located on the chromosomes in the nucleus of cells. Lesser but still significant DNA is located in the mitochondria.

GENE

The segment of DNA that constitutes a functional unit of inheritance.

LOCUS

The section of the DNA occupied by the gene. Gene and locus (plural: loci) are often used interchangeably.

ALLELE

Alternative forms of a gene. Most strictly, allele refers to different forms of a gene that determine alternative characteristics. However, allele is used more broadly to refer to different copies of a gene, i.e. the 2 copies of each gene that every diploid organism carries for each locus.

ALLELE OR GENE FREQUENCY

The proportion of all copies of a gene in the population that represent a particular allele.

GENOTYPE

The kinds of alleles that an individual carries as its two copies of a gene. As an example, if there are two alleles (A, a) possible at a locus, there are then three genotypes possible: AA, Aa, and aa.

GENOTYPIC FREQUENCY

The proportion of individuals in the population that are of a particular genotype.

HETEROZYGOSITY

The proportion of individuals in the population that are heterozygous (i.e., carry functionally different alleles) at a locus.

HARDY-WEINBERG EQUILIBRIUM

A principle in population genetics that predicts frequencies of genotypes based on the frequencies of the alleles, assuming that the population has been randomly mating for at least one generation. In the simplest case, where there are two alleles (A, a) at a locus and these alleles occur in the frequency p_A and p_a , the Hardy-Weinberg law predicts that after one generation of random mating the frequencies of the genotypes will be: $AA = p_A^2$; $Aa = 2p_Ap_a$; $aa = p_a^2$.

EXPECTED HETEROZYGOSITY = FOUNDER ALLELE DIVERSITY = GENE DIVERSITY

The heterozygosity expected in a population if the population were in Hardy-Weinberg equilibrium. Expected heterozygosity is calculated from allele frequencies, and is the heterozygosity expected in progeny produced by random mating. $1 - \sum p_i^2$, where p_i = the frequency of allele i .

GENE DIVERSITY

Same as expected heterozygosity.

GENOME

The complete set of genes (alleles) carried by an individual.

GENETIC DRIFT

The change in allelic frequencies from one generation to the next due to the randomness (chance) by which alleles are actually transmitted from parents to offspring. This random variation becomes greater as the population, and hence sample of genes, transmitted from one generation to the next, becomes smaller.

BOTTLENECK

A generation in the lineage from a founder when only one or a few offspring are produced so that not all of the founder's alleles may be transmitted onto the next generation.

FOUNDER

An animal from a source (e.g., wild) population that actually produce offspring and has descendants in the living derived (e.g., captive) population. The surviving population of Przewalski's horse contains genetic material from a total of 13 founders: 12 putative "wild" individuals and 1 domestic mare.

FOUNDER REPRESENTATION

The percentage or fraction of all the genes in the population at any given time that have derived from a particular founder.

EXISTING REPRESENTATION

The existing percentage representation of founders in the population.

TARGET REPRESENTATION

The desired or target percentage representation of founders. These target figures are proportional to the fraction of each founder genome that survived in the population. Achieving these target representation values will maximize preservation of genetic diversity.

ORIGINAL FOUNDER ALLELES

The total number of alleles (copies) of each gene carried at each locus by the founders. The 13 founders of the Przewalski's horse population carried a maximum of 26 alleles: 24 from the "wild" individuals and 2 from the domestic mare. The number of original founder alleles is twice the number of original founder genomes.

ORIGINAL FOUNDER GENOMES

The set of all genes in a founder. The sum of all such sets are the founder genomes. The 13 founders of the surviving population of Przewalski's horse contained 13 founder genomes. The number of original founder genomes is half the number of original founder alleles.

FOUNDER ALLELES SURVIVING

The number of alleles still surviving at each locus in the population assuming that each founder carried two distinct alleles at each locus into the derived (captive) population.

FOUNDER GENOMES SURVIVING

The number of original founder genomes still surviving in the population. This metric measures loss of original diversity due to bottlenecks in the pedigree of the population.

FOUNDER GENOME EQUIVALENTS

The number of newly wild caught animals required to obtain the genetic diversity in the present captive population. This metric reflects loss due to both bottlenecks and disparities in founder representation.

FOUNDER EQUIVALENTS

The number of equally represented founders that would produce the same gene diversity as that observed in the surviving population, acknowledging the founder alleles that have already been lost due to bottlenecks. Founder equivalents measures the loss of genetic diversity due to the uneven representation of founder lineages in the surviving population.

EFFECTIVE POPULATION SIZE

A concept developed to reflect the fact that not all individuals in a population will contribute equally or at all to the transmission of genetic material to the next generation. Effective population size is usually denoted by N_e and is defined as the size of an ideal population that would have the same rate of genetic drift and of inbreeding as is observed in the real population under consideration. An ideal population is defined by: sexual reproduction; random mating; equal sex ratio; Poisson distribution of family sizes, i.e. total lifetime production of offspring; stable age distribution and constant size, i.e. demographically stationary.

CARRYING CAPACITY CALCULATIONS

For captive populations being managed for conservation purposes, the carrying capacity represents an analytically determined number that is a compromise between:

- (1) Some minimum that is considered adequate for genetic and demographic viability and
- (2) Some maximum that will not significantly limit utilization of captive space and resources for other taxa.

Concerning the lower boundary for carrying capacities, there is no single magic number that represents a minimum viable population for all taxa. Indeed there is no single number that represents a minimum viable population for any one taxa all the time. Rather viable population size depends on several sets of factors:

- (1) Genetic and demographic objectives of the program;
 - (a) The probability of survival of the population;
 - (b) The kinds and amounts of genetic diversity to be preserved;
 - (c) The period of time over which this genetic diversity and survival probability are to be preserved.
- (2) Biological characteristics of the population;
 - (a) The generation time (average age during life at which animals produce their offspring) in the population.
 - (b) Growth rate of the population;
 - (c) Number of founders;
 - (d) Ratio of genetically effective size N_e to the total size N .
- (3) The kinds and levels of stochasticity operating.

Because, captive husbandry is frequently able to moderate the demographic and environmental stochastic problems that can endanger small populations, carrying capacity determination for captive taxa has concentrated largely on genetic considerations.

On the next two pages are examples of a model and computer software that permits estimation of carrying capacities once certain genetic objectives and biological characteristics are specified. The model is only awkwardly applicable to the Przewalski's horse. The model basically presumes that a captive population is established with some number of founders and then grows from this initial number to the carrying capacity. The percentage heterozygosity retained is calculated relative to the original wild population and the founders. A frequent set of objectives selected for captive populations has been to preserve 90% of original average heterozygosity for 200 years. In the case of the Przewalski's horse much genetic diversity was lost before the inception of programs to preserve it. As a consequence, the more logical objective for the captive population of Przewalski's horse is to attempt to preserve 90% or more of the genetic diversity currently present in the population now.

An approximation of this scenario can be achieved in the model on the next two pages by assuming that some fraction of the living individuals represent the founders. Calculation of what fraction is appropriate should be based on the number and relative distribution of founder alleles in the population. For purposes of this analysis, this fraction has been calculated as an estimate of the genetically effective size of the total population being managed by the formally organized programs in North America, Europe, and Australia/New Zealand. It was estimated that about 550 horses were in these programs at the time of analysis and that the N_e/N ratio was about .3. Hence the number of effective founders employed is 165.

**PRZEWALSKI'S HORSE
CALCULATIONS FOR CARRYING CAPACITY**

Capacity 2.11

=====

Effective Size and Carrying Capacity Necessary for Maintaining the
Specified Amount of Genetic Diveristy for the Specified Amount of Time

Number of Years per Generation: 14.0	# Generations during 200 Years: 14
Yearly Growth Rate (lambda): 1.100	Exponential Growth Rate (r): 0.095
Effective Number of Founders: 165	Growth rate per Generation: 3.798
Estimated Ne/N Ratio: 0.30	Exponential Growth/Gener: 1.334
Desired % Hetero. Retain: 90.0	
Length of Time Period (Years): 200	

Effective Size Required to Maintain 90.0% of the
Original Founder's Heterozygosity for 200 Years: 67

Actual Carrying Capacity Required (Based on Ne/N Ratio): 223

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Capacity 2.11

=====

Actual Carrying Capacities Required to Maintain Various Levels of
Heterozygosity for Various Ne/N Ratios for 200 Years

		PERCENT HETEROZYGOSITY TO RETAIN					
		75.0	80.0	85.0	90.0	95.0	
	0.30	83	107	143	223	457	
Ne/N	0.40	63	80	108	168	343	
Ratio	0.50	50	64	86	134	274	
	0.60	42	53	72	112	228	
	0.70	36	46	61	96	196	
							Table Parameters
							Lambda: 1.100
							Gen. Length: 14.0
							No. Fndrs: 165

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PRZEWALSKI'S HORSE CALCULATIONS FOR CARRYING CAPACITY

Capacity 2.11

=====

Effective Size and Carrying Capacity Necessary for Maintaining the
Specified Amount of Genetic Diveristy for the Specified Amount of Time

Number of Years per Generation: 12.0	# Generations during 200 Years: 16
Yearly Growth Rate (lambda): 1.100	Exponential Growth Rate (r): 0.095
Effective Number of Founders: 165	Growth rate per Generation: 3.138
Estimated Ne/N Ratio: 0.30	Exponential Growth/Gener: 1.144
Desired % Hetero. Retain: 90.0	
Length of Time Period (Years): 200	

Effective Size Required to Maintain 90.0% of the
Original Founder's Heterozygosity for 200 Years: 76

Actual Carrying Capacity Required (Based on Ne/N Ratio): 253

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Capacity 2.11

=====

Actual Carrying Capacities Required to Maintain Various Levels of
Heterozygosity for Various Ne/N Ratios for 200 Years

		PERCENT HETEROZYGOSITY TO RETAIN					Table Parameters
		75.0	80.0	85.0	90.0	95.0	
Ne/N Ratio	0.30	93	120	163	253	520	----- Lambda: 1.100 Gen. Length: 12.0 No. Fndrs: 165
	0.40	70	90	123	190	390	
	0.50	56	72	98	152	312	
	0.60	47	60	82	127	260	
	0.70	40	51	70	109	223	

== 01/11/90 ===== j.ballou-NZP Mar 89 =

PRZEWALSKI'S HORSE

Equus przewalskii

**GLOBAL CONSERVATION PLAN
D R A F T**

OVERVIEW OF REGIONAL CAPTIVE PROGRAMS

10 February 1990

Fifth meeting of the EEP Przewalski Horse Committee (EEPPC)

Date : 29 September 1989

Place: Nieborov - Warsawa in Poland

Committee members

Dr. W. Zimmermann - Cologne (Coordinator)
 Dr. J. Volf - Prague (Studbookkeeper)
 Dr. C. Struyf - Antwerp
 Mr. J. Hennig - Springe
 Ing. M.C.K. Bleijenberg - Rotterdam (Secretary)
 Dr. J.M. Rembiszewski - Warsawa (Host)
 Dr. J.-L. Berthier - Paris
 Dipl. Biol. G. Nötzold - Leipzig (instead of Dr. G. Krische)

and

Dr. L. Kolter - Cologne (EEP contributor)
 Dr. J. Skotnicki - Krakow (guest by the host)
 Dr. A. Sosnowski - Lodz (guest by the host)

Absent with prior notification

Dr. P. Mühling - Nürnberg
 Dr. R. Revers - Salzburg
 Prof. H. Sägeser - Bern

1. The host, Dr. J.M. Rembiszewski, opened the first EEPPC meeting held in Eastern Europe.
2. Suggestion for the distribution of Przewalski Horses born in 1989. It was emphasised that suggestions are based on logical, functional arguments, discussion over these is always possible.
 - From Antwerp to Arnhem : Quatta (4313 F)
 - From Antwerp to stallion reservate Han-sur-Lesse: Quinten (4312 M)
 - A replacement will be sought for the stallion Halamid, with 10 foals this animal is adequately represented in the genepool.
 - From Rotterdam to Arnhem: Riaan (4173 F)
 - From Springe to Arnhem Spring ins Feld (1589 M) not before 1992. With this suggestion Arnhem is assured of a good breeding group in the future. They also should keep Arnh. 27 (4316 F)
 - Committee member Berthier has been asked to check that horses in Azay le Ferron are not used for breeding: these horses are proven*chestnut-gene carriers and ataxic.

* chestnut = sorrel = Fuchs

- The horses in Berlin-West might have a herpes virus. Berlin is willing to lend 2.1 out, before this is done a good veterinary advice is required. It must be noted that Vanessa (1530 F) and Vitus (4160 M) both have more or less conspicuous white stars. The young stallions (1545 and 4160) can be sent to the stallion group in Neumünster if veterinary approval is given.
- Bern must look for a place for Beno (4320 M), son of Donna (540 F). It was advised not to breed with Donna any longer, as she is a proven chestnut-gene carrier.
- It was suggested that Duisburg be asked to place Ulania (4322 F) in the new EEP semi-reserve. This reserve was discussed later. Also Dunja (1337 F) should go to another breeding place, as the pairing with Bolat (738 M) results in a too high inbreeding coefficient (0.4) and is therefore not recommended.
- Helsinki will be asked to stop breeding from Anulka (847 F), as she is a proven chestnut-gene carrier. Volcok (1318 M) should be transferred from Askania Nova to Helsinki as breeding stallion. Transport and vet. requirements are a problem, the same applies to Leipzig, which also gets a stallion from Askania Nova. Solutions have to be found. Zimmermann contacts L. Blomqvist about this.
- The director of the new park in Sweden, the Nordik Ark, located in Hunnebostrand, has contacted Zimmermann with a request for Przewalski Horses, after an antecedent and location research and with the certainty that the EEP rules are accepted, it was decided to supply this zoo with Przewalski Horses. There is even room to place surplus stallions there. The Nordic Ark is also noted as new EEP member.
- The animals, belonging to Karl-Marx-Stadt can now form part of the breeding program. The EEP has been assured that the offspring of the cross-breeding with a Tarpan-female will be kept separately. The EEP did not ask for stopping this hybridisation because of scientific interest.
- Karlsruhe: Caruso (4326 M) and Tatyana (1266 F) will be sent to a neighbouring park if Duisburg agrees. Caruso has to be castrated. Due to aggression Stani (820 M) cannot longer be used as breeding stallion. Karlsruhe agreed to send him to the TiHo Hannover if they get a new stallion. In 1991, when the females are old enough, they will get one, probably from Neuwied (1575 M, 1610 M or 1634 M).
- Kiev asks for females. If the breeding program continues well, they will be offered a mare next year.
- Krakow: Lawenda (672 F) and Step (1026 M) have been identified as chestnut-gene carrier by their chestnut-son 4352 Koral. Suggestion: castrate Step and leave him with Lawenda. Novina (4182 F) from Nieborow goes to Krakow.
- Cologne: Noes (780 F) is a carrier for the chestnut-colour; she will be removed from the breeding programme. Alice (4329 F) will be sent to the new EEP semi reserve, Hubert (728 M) will be sent to Münster, Gino (1495 M) will be used as breeding stallion, Bochin (1429 M) will be sent to Rotterdam, Lord (4327 M) and Ares (4328 M) will be placed in the outer station of Cologne.

- Leipzig will receive a new stallion from Askania Nova, called Moroz (1048 M). Due to sub-, or infertility, Sikkim (1037 M) will be placed in an outer station.
 - Münster: the stallion Victor (1025 M) must be removed from the breeding programme (66 % Wf); see also the minutes of 1987 in Wuppertal and 1988 in Cologne. It is recommended to send him also to the TiHo Hannover or as soon as possible to Weilburg.
 - Springe: stallion Spitzbube (4342 M) will be sent to the stallion station in Neumünster. The mare Spritta (4344 F) is offered to the new semi reserve of the EEP.
 - Nürnberg: The stallion David (558 M) will soon be put together with the mares, so that they can breed after a 4-year pause.
 - Pretoria can get a stallion from America: Rogmar (879 M). As it is not sure that he is fertile also Bosco from Denver will be sent there.
 - Sababurg: 5 stallions (1469 M, 1606 M, 4337 M, 4339 M and 4240 M) will go to the stallion station Edertal in Hessen. Sababurg is asked to improve the horse area that is highly infected by worms. Also the animals have to be treated thoroughly. The EEP also asks Sababurg for 1 or 2 females for the new semi-reserve. A new breeding stallion will be searched for Sababurg.
 - Stuttgart: stallion Priam (1304 M) has not yet arrived from Weilburg due to transport problems.
 - Tallinn: Stallion Bedal (571 M) and the mare Milly (953) got a chestnut-foal (reported by visitors, no answer from Tallin). A solution must be found for this zoo. Before sending animals to Tallinn, the EEP-members would like to see the situation there improved: the horses are still housed in provisional enclosures.
3. By the end of 1989 there will be a total of more than 900 Przewalski Horses in the world, and, if breeding continues at the current rate, the EEP will be unable to place animals over 3 years. Even with selective breeding (see later) it will still be difficult to place animals, in particular stallions. It must be realised that animals surplus to breeding requirements will have to be placed by the zoos themselves after being individually marked (freeze branding). In the future, the EEP will give a non-binding advice regarding breeding. The coordinator would like to reduce the breeding, as she sees the problems with enough spare-place. This subject has to be discussed again one or two years later; the EEP-members should be aware that such a problem can arise soon or later. In order to temporarily remove mares from the breeding programme, information will be sought over an American product which makes mares temporarily infertile. Expansion of the semi reserves will be stimulated and researched by the EEP. In this context and with an eye to future, responsible reintroduction of Przewalski Horses in semi-wild situation, the EEP will seek contact with the following institutions: IUCN, CBSG and WWF.

4. The studbook keeper J. Volf requests that questionnaires be correctly completed and return on time. Only then can the studbook keeper do his work correctly. Some EEP members have not been doing this.
5. In the future, when establishing new pairs, it will be attempted to keep the inbreeding coefficient below 0.2, in exceptional circumstances this can rise to 0.3. In some instances this will now not be achieved as it would involve the transport of too many animals.
6. Herpes virus. By some ponies or donkeys in Bern, herpes virus has been identified. The Berlin Przewalski Horses have been diagnosed as having the virus and have been vaccinated with a live vaccine. In this context, everyone was requested to ask for advice about this virus from their vets, and on this advice to vaccinate their animals if necessary with for example Resequin F. Konz. from the firm Behring. In particular, receiving zoos which do not vaccinate their own animals must enquire as to the vaccination status and possible infection risks for any horses, coming into their collections. In the next meeting Berthier will provide more information on this problem. It will be asked whether vaccinated animals can be transported over borders.
7. Semi-reserve. Just before the beginning of the meeting a written confirmation was received, that the EEP has been offered a semi-reserve. The province of Niedersachsen has offered an area of land, 25 ha grassland and appr. 3 ha woodlands - very suitable for Przewalski Horses. On the financial side it has been decided, that sowing grass and placing fencing will be paid by the province. The husbandry of the horses will be undertaken by a local stud in Hunnesrück (Solling). The Cologne zoo pays the costs that will follow (vet./winter feeding, etc.) On the initiative of Springe and Cologne this work has been realized. It is important that the EEP starts this first external project with a good group of horses.
8. With the new membership of the Nordik Ark it is desirable to accept a member for Scandinavia into the committee. Everyone agrees that L. Blomqvist is the most suitable person and he will be approached. Eventual objections to this proposal must be indicated before the 1st of January, 1990.
9. The problem of infertility or reduced fertility occurs particular in some stallions of the Hellabrunn line. The breeding stallions of Nürnberg, Munich, Leipzig, Rotterdam and some in the USA have low fertility or are infertile. Research on this problem is required and will be undertaken by Dr. Bader, from the Veterinary Faculty in Hannover. The results will be presented in the next meeting. Uptodate we know that sperm concentration is very low with a high amount of morphological deformed sperms.

10. The phenotype. This subject is very topical due to the following:

- In a stock of appr. 900 individuals some selection may occur.
- When selecting, its effect of founder representation has to be taken into account.
- If no selection on external characteristics is made, the external appearance of the P-horse population will change. For example: the number of chestnut-coloured animals will increase further more.

The former crossing of domestic horses and P-horses might have led to the expression of this phenotype of the p-horses and the so called abnormality in the phenotype. As it is not possible to show scientifically what effect of these abnormalities of the phenotype will be on the P-horse population in the future, the EEPPC has decided (and in some instances already has done) to reduce these abnormalities in the population so long as there is no loss of founder representation.

The committee realizes, that the recommendations do not rest on a scientific basis and never scientifically can be proved. The EEPPC has allowed herself to use the knowledge and experience of domestic horse-breeding and previous experience with P-horse breeding.

The undesirable abnormalities have been defined on the basis of literature studies and eye-witness-reports of Dr. Erna Mohr. The EEP-Committee considers the following phenotypical characteristics as abnormal:

- chestnut colour
- black nose
- white star
- white markings on the body
- light coloured iris
- permanent hanging manes (if horses are in good condition)

The EEPPC gives the following recommendations regarding phenotype which should be taken into consideration when establishing or changing groups of P-horses (see also minutes dated 24/10/1986 and 26/11/1988).

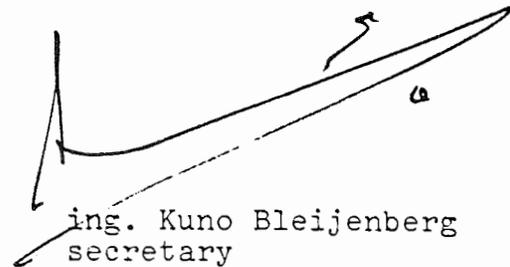
From breeding should be excluded:

- chestnut coloured horses
- the parents of a chestnut
- stallions with a black nose
- horses with a light iris
- stallions with a conspicuous white star or other white patches (if a star occurs in the offspring of a particular combination of stallion and mare, another combination should be sought).
- horses in good conditions which never shed their manes
- stallions with a tail without light coloured hairs near the tailroot

In addition it was decided in former meetings not to breed with cryptorchid stallions and in the case of ataxic horses, the EEPPC should be asked for advise.

Enclosed you find fotoprints of the typical phenotype and of the aberations in the phenotype of a Przewalski Horse.

11. Dr. Jiri Volf, studbookkeeper and committee-member would like to indicate that he is very pleased with the working of the EEPP and the initiatives it has taken.



ing. Kuno Bleijenberg
secretary

Rotterdam, 16 October 1989

Mohr, E. 1967: in Equus, 1 (2), p. 394-395. Bemerkungen zum Erscheinungsbild von Equus przewalskii, Poljakov 1881

Remarks on the phenotype of Equus przewalskii, Poljakov 1881

Summary

The facts and considerations I mentionend in this paper have shown that probably not a single Pzrewalski horse living in captivity today can be considered as pure-bred. The same can be said for Przewalski horses who eventually live still in the wilderness. So it makes no sense to give an appreciation of the different lines.

Under these circumstances I think that the first 3 points of the resolution of the 2 nd Przewalskhi horse Symposium are totally justified. They say:

1. The Symposium has shown that the phenotype of the Przewalski horse has a high variability, which extent should be studied in the future; this work should be supported.
2. It is too early to determine an obligatory standard, because the breeding base is too small. We should wait until the stock has at least doubled, so that at the next Symposium binding proposals can be made. In the meantime the breeders should work on this problem and keep in contact.
3. Up to this day we should breed with all mares.

25 years have passed and two further international symposia. 1965 there existed 58,75 = 133 Przewalski horses. Today we will have appr. 900, 3 times as much as Dr. E. Mohr has asked for. It is now high time to make our decisions.

Asian Wild Horse Species Survival Plan

**Masterplan
1989**

Masterplan Working Group:

O. Ryder
J. Ballou
J. Dolan
T. Foose
N. Reindl
E. Thompson
C. Wemmer

Acknowledgements

Without the support of the zoos that committed their staff and animal resources to the Asian Wild Horse Species Survival Plan, neither an SSP or a masterplan for management would be possible for *Equus przewalskii*.

A particular debt is owed to Charles J. Geyer of the Department of Statistics, University of Washington, for his calculation of gene survival in population subsets.

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Asian Wild Horse Propagation Group

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Introduction

Following the meeting of the Asian Wild Horse SSP propagation group in Portland in 1987, a working group was identified to consider the demographic status and the results of gene extinction studies of the SSP sub-populations and produce a draft masterplan for the management of the SSP population. On 1.1.88, the Przewalski's horse census for the SSP population stood at 55.85. The working group met in San Diego March 7-8, 1988, and produced an outline of this draft masterplan for consideration of the Asian Wild Horse SSP Propagation group. In formulating the recommendations for the future management presented here in draft form, consideration was given to the unique aspects of this species in captivity, including the presence of genes from domestic horses in the population and the recent availability of new methodologies for analysis of gene extinction in complex pedigrees.

Genetic Analyses

Pedigrees have been constructed based on the original studbook (Mohr, 1961) and subsequent work of studbook keeper Dr. Jiri Volf at the Prague Zoo (Volf, 1961 *et seq.*). Przewalski's horses have been bred in captivity for twelve generations. Although there were 70 potential founders only thirteen animals left descendants that contribute to the pedigrees of the living animals. As *Equus przewalskiis* thought to be extinct in the wild (Sokolov and Orlov, 1985; Ryder, 1988), there seems to be no possibility to incorporate new founders.

The pedigree of Przewalski's horses in captivity reveals a number of complex features, including bottlenecks, a founder of alleged hybrid ancestry, genetic contributions of a Mongolian domestic mare (in approximately two thirds of living horses worldwide), and a new founder entering the pedigree 54 years after the initiation of captive breeding (Ryder and Wedemeyer, 1982; Dolan, 1982; Volf, 1959 *et seq.*; MacClure, et al., 1986; Geyer and Thompson, 1988). These complexities have resulted in several suggestions for managing the captive population (Heck, 1980; Ryder and Wedemeyer, 1982; Bouman, 1980), but the genetic sequelae of these various plans has been difficult to assess due to the pedigree complexities.

Founder contribution has been calculated by the traditional methods based on data included in the 1987 studbook reflecting the status of the captive population on 1.I.1987 (Figure 1).

Target Founder contributions, calculated to reflect the adjustments necessary when considering that founder genes have already been lost due to bottleneck effects was calculated by the formula:

$$TFC_x = \frac{S_x}{\sum_{i=1}^{13} S_i} \tag{1}$$

TFC_x — Target Founder Contribution of Founder x
S_x — proportion of Founder x's genome surviving to SSP population

Table 1 presents the founder contributions for the SSP populations and the target founder contributions, which is affected by the proportion of the genome surviving, (determined in this instance from gene drop simulations). These values are depicted graphically in Figure 1. The identification of genetically important animals (individuals possessing unique genes from under represented founders) can be made based on differing computational approaches to the determination of gene extinction probabilities (Geyer et al., 1989). Table 2 contains a listing of individuals that contain founder genes especially useful for achieving the target founder contribution goals. Individuals listed in Table 2 may be useful for either the sub-population possessing genes from #11, #12, and the Mongolian domestic mare, the sub-population lacking genes from

#11, #12, and the Mongolian domestic mare, or both sub-populations. Individuals with founder coefficients greater than the overall sub-population's target founder contribution would, by the production of offspring tend to move the sub-population founder contributions toward the target founder contribution. The distribution of founder coefficients within the SSP population is depicted in Figure 2.

The distribution of genes not identical by descent has been calculated for the entire studbook population and a variety of populations subsets according to the peeling procedure of Cannings and Thompson (1982) which allows the determination of probabilities that 0, 1, or 2 genes not identical by descent from each founder have been transmitted to any individual or set of individuals within the pedigree. These data are presented in Table 3.

Both the gene drop and peeling approaches for examination of gene extinction within pedigree address an issue that founder effect calculations alone cannot, viz., the likelihood that an individual possesses a distinct gene descended from one founder may diminish (or increase) the likelihood of that individual possessing a distinct gene from another founder.

The contributions of some of the founders are inextricably linked. This correlation can be observed qualitatively by an examination of the pedigree. Quantitative estimates of founder contribution concordance can be displayed by the construction of a matrix depicting the numbers of animals with contributions from pairs of founders, and the proportions those animals represent of all living individuals that include contributions from each of the pair of founders (Table 4). This same phenomenon is also apparent in the results of pedigree peeling (Table 5).

A matrix of the coefficients of inbreeding of potential offspring produced as a result of matings between living males and females within the SSP population were calculated (Appendix 1). A matrix of inbreeding coefficients for all possible matings within the world population has also been produced (Canyon Colorado Equid Sanctuary, 1987) but is not reproduced here.

Demographic Analyses

The age structure by sex was determined for the world population (Table 6 and Figure 3), for the SSP population (Table 7 and Figure 4), for the subset of the SSP population possessing genetic contributions from the Mongolian domestic mare as depicted in the International Studbook (Table 8 and Figure 5), and for the SSP population lacking genetic contributions from the Mongolian domestic mare as depicted in the International Studbook (Table 9 and Figure 6).

Age specific survivorships and fertilities were determined for the world Przewalski's horses (Table 10 and Figure 7), for the SSP population (Table 11 and Figure 8), for the subset of the SSP population possessing genetic contributions from the Mongolian domestic mare as depicted in the International Studbook (Table 12 and Figure 9), and for the SSP population lacking genetic contributions from the Mongolian domestic mare as depicted in the International Studbook (Table 12 and Figure 10).

In order to meet demographic and genetic objectives for the SSP, the number of individuals to be managed as a population with a stable age distribution must be defined. This number, referred to as the carrying capacity, is larger than the minimum estimate for a viable population but has an upper limit that incorporates consideration of the facilities and resources available for all taxa in zoological parks. The establishment of the number of individuals for the population at carrying capacity requires delineation of the objectives for genetic management of the population.

Objectives and Their Derivation

Genetic Objectives

Identification of Sub-Populations for Management

The SSP populations of *Equus przewalskii* currently contains two sub-populations that differ in their genetic contributions from founder individuals, their apparent growth rates (Tables 3, 8, 9), and the proportion of their residual genetic variation derived from the Mongolian domestic horse. The extent to which the two sub-groups differ in the number of surviving genes from wild type Przewalski's horse founders (Geyer and Thompson, 1988; Geyer et al., 1989) is presented in Table 10. Although the two population sub-groups identified in the current management plan contain 97.7% (8.997 genes) of the total number of surviving genes in the current SSP population (9.219 genes), the selection against the Mongolian domestic mare results in the selection against wild type genes carried by founders #11 and #12 and would, over time, reduce the number of surviving genes in the SSP population. There are additional unique founder genes surviving in the entire International Studbook pedigree that are not present in the North American SSP population subset. These include genes derived from #11, #12 and the Mongolian domestic mare, but also include genes from other founders (Table 5b). Currently incorporating a mean of 9.129 surviving genes, the North American population (excluding Edmonton) includes 87.1% of the surviving genes from the thirteen founders (Table 3). The proportion of wild type *E. przewalskii* genes surviving worldwide represented within the North American population is 87.5% (Table 5b).

A management plan that strives to preserve the maximum number of genes from the founders in a single population requires introduction of genes from the Mongolian domestic mare into horses whose ancestral contributions lack genetic input from the Mongolian domestic mare. There is reluctance to adopt such an approach, particularly from breeders whose collections consist of Przewalski's horses that lack genetic input from the Mongolian domestic mare as depicted in the International Studbook. The largest single collectively managed population of Przewalski's horses lacking genetic contribution from the Mongolian domestic mare as depicted in the International Studbook resides within North America and is part of the Asian Wild Horse SSP.

However, if two population sub-groups are maintained and separately managed from retention of different combinations of founder genes (e.g., with and without #11, #12 and Mongolian domestic mare), a larger number of genes surviving from the founders could be managed while preserving future options involving the introduction of the genes from the Mongolian domestic mare into the populations lacking genes from the Mongolian domestic mare. Gene flow from the population lacking #11, #12, and the Mongolian domestic mare to the population with genetic contributions from #11, #12 and the Mongolian domestic mare could occur through horses of either sex for the purposes of increasing the number of genes surviving from founders under represented in the subpopulation. Gene flow of wild type founder genes into the SSP sub-population lacking

genetic input from the Mongolian domestic mare may be accomplished by the transfer of selected individuals from outside North America who lack genetic input from #11, #12 and the domestic Mongolian mare.

This later strategy emerged as the consensus plan because it meets the objectives of managing for the survival of the largest possible number of genes possible while still preserving a sub-group of Przewalski's horses lacking genetic contribution from the Mongolian domestic mare as depicted in the International Studbook and thereby preserving options for future management.

The revised management plan now stipulates that stallions as well as mares possessing genetic contributions from #11, #12 and the Mongolian domestic mare be utilized for breeding as is reflected in the breeding recommendations for each institution (see Appendix 1). This reflects a change from earlier strategies.

Managing Genetic Diversity

In the process of producing this masterplan the working group established average heterozygosity as the currency of genetic variability. In addition, the numbers of unique genes from founder individuals (genes not identical by descent) was also utilized as an appropriate measure of surviving genetic variation in the entire captive population and its sub populations.

Temporal Goals for Retention of Genetic Diversity

The Asian wild horse SSP will attempt to preserve 90% of current average heterozygosity for a period of 200 years.

Carrying Capacities

By comparison to extensive work performed by other SSPs, the size of the genetically effective population necessary for achieving the stated genetic objectives of retention of 90% of residual heterozygosity over 200 years is:

$$N_e = \frac{1}{(1 - e^{-(\ln \Delta H/T)})} \quad (2)$$

The census population sizes necessary for retention of average heterozygosity as a function of three different ratios of effective to census population size (N_e/N) have been calculated according to formula (2) and are presented in Table 11. A generation time of 14 years, resulting in a total of 14 generations of management were used in the calculations for estimation of census population size necessary for meeting genetic goals for a population at carrying capacity.

Consideration of these results led to the following consensus suggestions for the carrying capacity of the two sub populations. For the sub-population lacking genetic input from the Mongolian domestic mare, a carrying capacity of 222 animals will meet the above stated goals for the retention of average heterozygosity. For the population with genetic representation from the Mongolian domestic mare and including the wild type genes of founders #11 and #12, a carrying capacity of 111 will be established. The smaller carrying capacity of the sub population with genes from #11, #12 and the Mongolian domestic mare was judged appropriate because: 1) a carrying capacity for the total North American Asian wild horse SSP population of 333 animals represents a realistic goal (Table 13), 2) other regional programs are managing the genetic contributions of #11, #12 and the Mongolian domestic mare in larger populations, i.e., the EEP, 3) the genetic contributions of #11, #12 and the Mongolian domestic mare are at little risk of extinction in the world population (MacClure et al., 1986; Geyer et al., 1989) and 4) gene flow from the sub-population lacking Mongolian domestic mare genes is planned.

Demographic Objectives

Both sub-populations are currently below the designated carrying capacity. The sub-population lacking genes from #11, #12 and the Mongolian domestic mare is currently at an approximate size of 108 animals (49% of carrying capacity). The sub-population possessing genetic contributions from #11, #12 and the Mongolian domestic mare is currently at approximately 48 animals (43% of carrying capacity). Thus, both populations need to continue to grow.

Rates of population growth could be at the rates achieved by the current SSP population since 1975 (Tables 7, 8 and 9). Female demographic parameters are judged to be less artificial than those for males and were chosen for consideration in the population projections. During the period of population expansion a generation time of 10 years has been used for the demographic calculations necessary to manage the population growth to the designated carrying capacities for individuals descended from over represented founders, under represented founders, and for individuals whose founder contributions are at parity. While recognizing that some error is potentially introduced through this method, the working group felt that 1) it was appropriate to distinguish the generation time of the population in its growth phase from the generation time when the population was at carrying capacity and 2) there was concern that a generation time of 14 years, as was recommended for the population at carrying capacity, would not allow for population growth of 10% per year for the total SSP population (16%/year for the sub-population possessing genetic contributions from #11, #12 and the Mongolian domestic mare and 7%/year for the sub-population lacking genetic contributions from #11, #12 and the Mongolian domestic mare).

The number of female offspring required on the average from each individual over its lifetime to sustain the observed rates of population growth are the R_0 's (2.933 for the sub-population possessing genetic contributions from #11, #12 and the Mongolian domestic mare, 2.01 for the sub-population lacking genetic contributions from #11, #12 and the

Mongolian domestic mare and 2.44 for the total SSP population). If we assume or adopt an average growth rate of 10%/year and a generation time of 10 years, the R_0 prescribed would be 2.6, i.e., this value is the number of female offspring required to sustain this rate of population growth. Double this number, i.e., 5 offspring, would represent the total number of offspring that would be required.

However, this required number of offspring really refers to the number of progeny that will themselves survive to reproduce. To determine the number of individuals that must be born in order to produce an average of 5 offspring that survive to themselves reproduce, the survivorship for the total SSP population to age 10 (the generation time chosen for this phase of the population growth curve), $L_x = 0.689$, was divided into 5 (desired offspring). Thus 7.26 ($5 \div 0.689$) represents the total number of offspring that must be born to each animal to insure that 5 will, on the average, survive to reproduce.

Since it was also decided to adopt a 1:2 male:female sex ratio (that is, each reproductive male produces, on average, twice the number of offspring an average reproductive female produces) the best sex distribution of the offspring would be 2/5. This is the average to be sought after and represents the number of offspring indicated in Table 12 for females approximately at parity for their founder contributions.

In order to meet genetic goals, females descended from under-represented founders should on average produce more surviving offspring while females descended from over-represented founder should on average produce fewer surviving offspring. Nonetheless, the average number of offspring surviving to reproduce from all reproductive females should be 2 males and 5 females. These values are presented in Table 12.

Current census populations and estimated carrying capacities for SSP participant institutions are presented in Table 13.

PRZEWALSKI'S HORSE

Equus przewalskii

**GLOBAL CONSERVATION PLAN
D R A F T**

PHENOTYPIC CHARACTERS AND SELECTION

10 February 1990

PRJEVALSKY'S HORSE

(*Equus Przewalskii* Pol.)

BY

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LONDON

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1907



THE PRJEVALSKY HORSE.

(*EQUUS PRJEVALSKII*).

IN the year 1881, I. S. Poliakov founded the species, *Equus prjevalskii*, upon the characters revealed by the examination of the skin and skull of a single specimen which had been presented to the Zoological Museum, St. Petersburg, by N. M. Prjevalsky. Poliakov was of opinion that the animal from which the material has been obtained was three years old at the time of death; but we are compelled to regard it as having been considerably younger if the age be judged by the condition of the teeth, as would be done in the case of the domestic horse. Moreover, seeing that the skin carries the winter coat, it cannot be taken as showing the typical external characteristics of the species; and, consequently, it can be easily understood that some of the features described by Poliakov as specific have been proved not to have this value; with the result that alterations have been found necessary in the list of specific characters as given by him. Thanks to numerous expeditions into Mongolia, the collection of material representing *Equus prjevalskii* is now considerable. The Zoological Museum of the Imperial Academy of Science now possesses thirteen skins, nine skulls of different ages, and an incomplete skeleton. A stuffed specimen is in the Zoological Museum of the University of Moscow, and another is in the Museum at Paris (Jardin des Plantes). Recently, living Prjevalsky horses have been imported into Russia.

F. A. Falz-Fein, as the fruit of assiduous toil, was the first to succeed in obtaining living specimens. Three of his five young thorough-bred mares are still living, as well as two half-bred mares captured by him in 1898. A description of these, with illustrations, will be given later in this communication. In the spring of 1901, Prince A. A. Ochtomsky obtained two young specimens, a mare and a stallion, which he presented, in the same year, to His Majesty the Czar, and which are now in the Imperial stables at Tsarskoe-Selo. The Zoological Garden of Moscow also obtained two young males in 1901, and a mare later.

As I have determined to give a new description of *E. prjevalskii*,

it is not necessary that I should limit myself to the consideration of the single specimen captured by N. M. Prjevalsky, especially seeing that I can extend my investigations by the examination of the material accumulated, as the result of further expeditions, in the Zoological Museum of the Imperial Academy of Science. I have also been able to examine those living representatives of this interesting equine species which are in the Imperial stables at Tsarskoe-Selo.*

The material in the Zoological Museum consists of the following :

Holotypus

(1). A young animal, from 18 to 20 months old, killed in the Steppes of East Dzungaria by Kirgiz hunters, and sent by Tichonov to N. M. Prjevalsky, who presented it to the Zoological Museum. (Skin, No. 1,523; skull, No. 514). This is the specimen upon which the first description of *E. prjevalskii* was based.

(2). An adult stallion, obtained by G. and M. Grum-Grjimaïlo from Goschan. (Skin, No. 3,092; skull, No. 5,214.) Belonging thereto is a skeleton (skull, vertebral column, and the bones of the left limbs).

(3). A female foal obtained by G. and M. Grum-Grjimaïlo, in Goschan. (Skin, No. 3,093; skull, No. 5,217.)

(4). Stallion obtained by G. and M. Grum-Grjimaïlo, in Goschan. (Skin, No. 3,074; skull, No. 5,216.)

(5). A young animal obtained by G. and M. Grum-Grjimaïlo, in Goschan. (Skin, No. 3,091.)

(6). An adult mare obtained by the Consul Schischmareff, in the district of Kobdo, West Mongolia. This was sent to the Museum labelled "Onager." (Skin, No. 3,090; skull, No. 5,213.)

(7). Young filly, from eighteen to twenty months old, in her winter coat. She was obtained by D. Clemenz, from the Dzungarian Gobi, behind the Baityg-Bogdo Mountains, on the frontier of Charamelecetai. (Skin, No. 3,089; skull, No. 5,215.)

(8). An adult mare, obtained by D. Clemenz from the Dzungarian Gobi, between the boundary of Nursu and Simigondse. (Skin, No. 3,087; skull, No. 5,212.)

(9). An adult animal obtained from the same place by D. Clemenz. (Skin, No. 3,088.)

(10). A foal, ten months old, obtained by D. Clemenz from the Gobi Desert, at the Ebi Well, near the road from Kobdo to Barkul. (Skin, No. 3,072; skull, No. 5,211.)

(11). A young foal, of the same age as the last mentioned, and obtained from the same locality by D. Clemenz. (Skin, No. 3,073.)

(12). An adult stallion, killed in January, 1895, near Lake

* One of these animals, the mare, died in December, 1901.

Gutschena, and obtained during the expedition of Roborovsky and Kozlov. (Skin, No. 3,094; skull, No. 5,218.) *Para lypus*

(13). An adult stallion, obtained by D. Clemenz out of the herd of the Van's of Torgoutsk, on the River Bulunga. (Skin, No. 3,071.)

I have had two opportunities of inspecting the living specimens which Prince A. A. Oochitonsky, through the instrumentality of Vaisshainay, obtained in May, 1901, in Kobdo, from the pasture lands of the Van's of Torgoutsk in West Mongolia. In 1901, the Prince very kindly granted me permission to examine these animals then in his stables. At the present time, they are in the Imperial stables at Tsarskoe-Selo, and, thanks to the kindness of the Minister of the Imperial Court, I have again had an opportunity of inspecting them. These horses have been photographed, and Professor P. O. Kovalevsky has produced a water-colour sketch of them, of which I give a photo-zinc copy (Frontispiece).

Up to the present, I have had no opportunity of seeing the horses which are the property of F. A. Falz-Fein. Thanks, however, to the kindness of Mr. Falz-Fein, I am able to give reproductions of photographs of his horses (Fig. 3). I am also indebted to the courtesy of G. A. Koshevnikoff for a short description of the animals written after special observations.

External Characters of *Equus Prjevalskii*.

CONFORMATION.—The external characters of *E. prjevalskii* have been repeatedly described. Poliakov* gave the first description, which was followed by a fuller one by N. M. Prjevalsky.† Grun-Grijmailo‡ described living examples which he had seen in a state of liberty, and skins which he presented to the Zoological Museum. Tichonov§ supplemented Poliakov's description by an account of specimens in the Zoological Museum of the University of Moscow (Expedition of Roborovsky and

* Поляковъ, Лошадь Пржевальскаго (*Equus Przewalskii* n. sp.) 1881. Издание Императорскаго Русскаго Географическаго Общества. p. 10.

† Н. М. Пржевальскій. Третье путешествие въ центральную Азію, Въ Зайсанъ черезъ Хами въ Тибетъ и верховья Желтой рѣки. pp. 40-42.

‡ Гр. В. Грунъ-Гржимайло. Описание путешествія въ западный Китай. Издание Императорскаго Русскаго Географическаго Общества, 1898. pp. 118-211.

§ А. А. Тихомировъ. Дикая лошадь Монголіи. (Естествознание и Географія 1898. No. 4.)

Kozlov, 1896), and specimens which he placed in the Zoological Museum of the Imperial Academy of Science. He referred to the dorsal stripe and to the stripes on the limbs: features which had already been mentioned by Poliakov.

The Prjevalsky horse has attracted the attention of a large number of zoologists interested in the classification of mammals. Consequently, the literature dealing with this species of *Equus* is very rich. In addition to the treatises already quoted, there are statements relating to *E. prjevalskii* in the works of Noack,* Böhm,† Kobelt,‡ Landsell,§ Morgan,|| and Trouessart.¶ And, quite recently, short communications by Grevé** and Matschie †† have been published.

Langkavel, in his interesting work on the Asiatic wild horses, gives an account of the external characters of *E. prjevalskii*, according to Noack, Grun-Grjimaïlo and Prjevalsky.

In many cases the extant descriptions are wanting in accuracy; and some of them are surprising on account of their rather considerable subjectivity. The chief point with which fault may be found in the many systematic descriptions is that they are not based upon measurements of particular parts of the body. For instance, according to Noack, the ears of *E. prjevalskii* are shorter than those of the wild ass and *E. hemionus*; according to Prjevalsky, they are smaller than those of the ass; and, according to Grun-Grjimaïlo, they are remarkably short. Characteristics of such great importance as the length of the ears, by which a distinction is made between the horse and the ass, should be

- √ * Noack (a) *Zoologischer Garten*, 1884, p. 331.
 .. (b) *Natur*, 1892, p. 362.
 .. (c) *Natur*, 1896, p. 264.
 .. (d) *Deutsche Rundschau für Geographie und Statistik*, V. 6, p. 145; VII. 311.
- † Böhm (a) *Geographische Jahrbücher*, V. 11, p. 182.
 .. (b) *Russische Revue*, V. 13, p. 99.
 .. (c) *Schweizerisches Centralblatt für Jagd- und Hundliebhaber*, 1892, p. 76.
 .. (d) *Deutsche Jägerzeitung*, V. p. 295.
 .. (e) *Petermann's Mittheilungen*, 1896, p. 78.
 .. (f) *Verhandlungen der Gesellschaft für Erdkunde*, Berlin, 1883, p. 498.
- √ † Kobelt. *Zoologischer Garten*, 1887.
- § Landsell. *Chinese Central Asia*, V. 2, p. 28.
- || Morgan. *Annals and Magazine of Natural History*, VIII., 1881, p. 16.
- ¶ Trouessart. *La Nature*, XVIII., 1890, p. 869.
- √ ** Grevé. *Equus Przewalskii* Poljakow im Moskauer Zoologischen Garten und einige Bemerkungen über das wilde Pferd überhaupt. *Zoologischer Garten*, XLII., 1901, pp. 275-282.
- †† P. Matschie. *Sitzungsber. d. Gesell. Naturforsch. Freunde, Berlin*, 1893.

described with exactness if they are to possess systematic value. In other words, that such characteristics may be employed in classification, it is necessary, not only to know the absolute size of the ears, but also the proportion which their size bears to that of other parts of the body, and more especially to the size of the head. Only when this is known can we say with certainty that the ears of *E. prjevalskii* are smaller than those of the ass, or that they are remarkably small. On this account I have tried to obtain exact data of the dimensions of individual parts of the body of the Prjevalsky horse, and of the Asiatic ass. With this object, I have availed myself of the excellent plan of measurements given by Nathusius*; as, by it, may be stated a complete and lucid account of the shape of the horse described, and of the characteristics by which its classification is determined. Unfortunately the measurements were beset by certain technical difficulties. It would undoubtedly have been best to have taken them from living horses; but the animals which were at my disposal were so wild that it was not possible to measure them. In default of living material, I first took measurements of a stuffed skin of an adult *E. prjevalskii*, and of the young stuffed specimen upon which Poliakov's description was based. Subsequently, I measured the fresh body of an animal which had died in the Imperial stables. I have also compared the proportions which certain parts of the body bear to each other by means of photographs of living animals. It seems fair to presume that results so obtained are sufficiently correct. A possible error can only be very slight, since the relative proportions—*as*, for instance, the length of the head *as* compared with the length of the body—showed very little difference when the measurements taken from the photographs of living animals were compared with those of the skin. For the sake of brevity, I give an outline drawing (Fig. 2), after Nathusius, in which the various measurements are shown. The drawing is self-explanatory.

As will be seen from the table herewith given, the Prjevalsky horse is about the same size as a small domestic horse. The adult stallion stands about 124 cm. (48.8 inches) at the croup†; and the length of his trunk is 127 cm. (49.9 inches). By his general conformation and in the respective proportions of certain parts of the body, he reminds one very much of the wild ass

* Simon von Nathusius. *Unterschiede zwischen der morgen- und abend-ländischen Pferdegruppe am Skelett und am lebenden Pferde.*—Inaug. diss. Langensalza, 1891.

† According to Grun-Grjivailo, the height at the croup in a ten-year old animal amounted to about 147 cm.

(*E. hemionus* Pall.) and of its variety, the kiang (*E. hemionus* Pall. var. *kiang*, Moorkroft): but the Prjevalsky horse has a relatively larger head than the wild ass. The proportion of the length of the head to that of the body is as 1:2.21. In the onager the proportion is as 1:2.29; and in the kiang as 1:2.25. As regards the shape of the head, the Prjevalsky horse closely resembles the onager and the kiang: a fact already referred to by Poliakov, who added, however, that the head "is not so high and is more slender at the end of the muzzle and in the region of the bones of the nose." I can confirm the statement that the head of the Prjevalsky horse is very like that of the onager and the kiang; but I can obtain no proof that the end of the muzzle and the region of the nasal bones are more slender than in the Asiatic ass. The craniometrical observations which I made revealed no difference.

MEASUREMENTS OF PARTS OF THE BODY OF EQUUS PRJEVALSKII (FIG. 2).

Young mare which died at Tsarskoe-Selo.

The skin of an adult stallion (No. 3,004)-

$a-\beta$	= 508 mm.	$a-\beta$	= 500 mm.
$\gamma-\delta$	= 141 "	—	—
$\alpha\gamma$	= 430 "	$\alpha\gamma$	= 470 "
Circumference of neck	= 900 "	—	—
Length of mane	= 150 "	—	—
ab	= 1,200 "	ab	= 1,200 "
$\alpha\gamma$	= 880 "	$\alpha\gamma$	= 950 "
gx	= 800 "	gx	= 400 "
gy	= 680 "	—	—
mnm	= 1,300 "	—	—
cd	= 1,180 "	cd	= 1,180 "
ef	= 1,160 "	ef	= 1,240 "
ik	= 680 "	ik	= 720 "
gh	= 1,010 "	gh	= 1,210 "
ls	= 330 "	—	—
s	= 175 "	—	—
lm	= 480 "	—	—
nn	= 240 "	—	—
r	= 150 "	—	—
Length of the whole tail	= 930 "	xw	= 1,270 "
Length of the caudal region of the vertebral column	= 350 "	pq	= 720 "
Length of the proximal (short-haired) part of the tail	= 250 "	vs	= 670 "
Circumference of the tail in its proximal part	= 160 "		

The average length of the ear was 140 mm. (5.5 inches) in five specimens (out of eight skins used for making measurements).

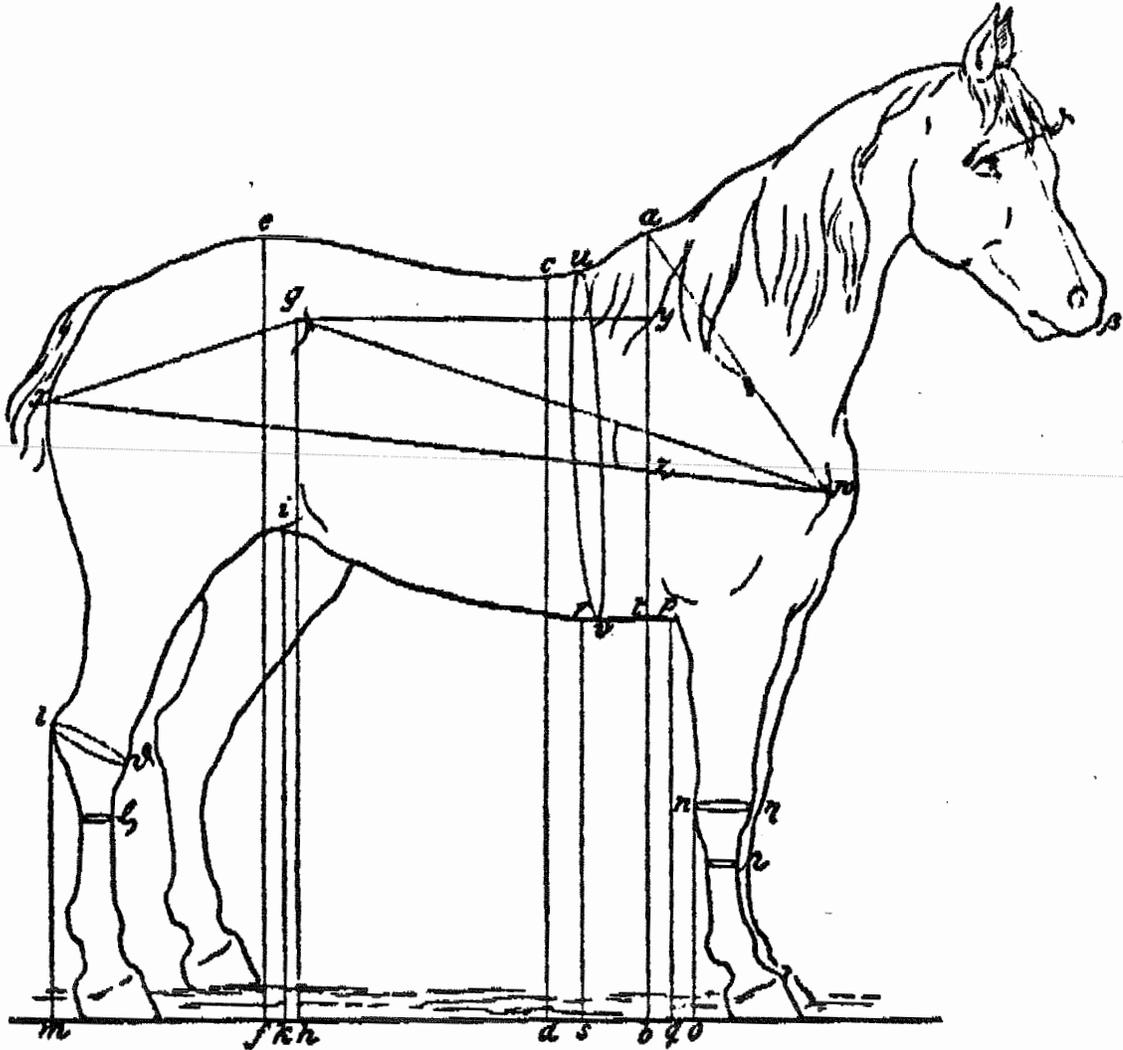


Fig. 2.

This is undoubtedly less than in the onager, the average length of whose ears I found to be 170 mm. (6.6 inches) in four stuffed specimens. The shortest pair of ears measured 165 mm. (6.4 inches), which is much longer than occurred in the Prjevalsky horse. The ears of the kiang are still longer than those of the onager, and averaged 200 mm. (7.8 inches) in three specimens. If the measurements obtained by Langkavel from the kiang in the Hamburg Museum are included, it is found that the length of the ear of the kiang varies from 180 mm. (7 inches) to 200 mm.; that is, the minimum length is greater than the maximum for the onager. In a specimen of the Prjevalsky horse (No. 3,094), the length of the ear is 170 mm.; and this is the greatest length of the ears of any specimen in the Zoological Museum of the Academy of Science. It should be borne in mind that the average length of the head of *E. prjevalskii* is greater than that of the onager or the kiang; and, therefore, the comparative length of the ear of the wild horse is much less than in the wild asses. Thus, in this particular, Prjevalsky's horse resembles more closely the domestic horse (*E. caballus*) than the Asiatic or African wild ass. As stated by the earlier investigators (Poliakof, Prjevalsky and Grum-Grjimailo,* the upper lip of *E. prjevalskii* overhangs the lower lip to a certain extent.

The neck is short and broad. It is shorter than the head, to which it bears the proportion of 1:1.12. Measurements show that the proportion of the length of the neck (from the occipital crest to the withers) to its breadth, at the widest part, is as 1:1.06. The mane, by its length, reminds one of the Asiatic wild ass. As previously stated by Poliakof, it is not very long; begins between the ears, and extends to the withers. Its anterior and posterior portions are short; but about the middle it has a length of from 16 to 20 cm. (6.2 to 7.8 inches). In his description of a dead Prjevalsky stallion, Grum-Grjimailo states that the mane hangs down on the left side of the neck; but Poliakof describes it as being erect. This apparent contradiction can be explained by the difference in the age of the specimens examined by the two writers. Poliakof's description applies to an animal eighteen months' old; whereas Grum-Grjimailo described a ten-year-old stallion. The mane stands erect in all the specimens of different ages in the Zoological Museum; and in no single case does it hang down. In the photograph of an animal described by Grum-Grjimailo—an eighteen months' old male—the mane is erect. The forelock of the Prjevalsky horse is about as little developed as it is in the onager and the kiang.

* Op. cit.

THE PRJEVALSKY HORSE.

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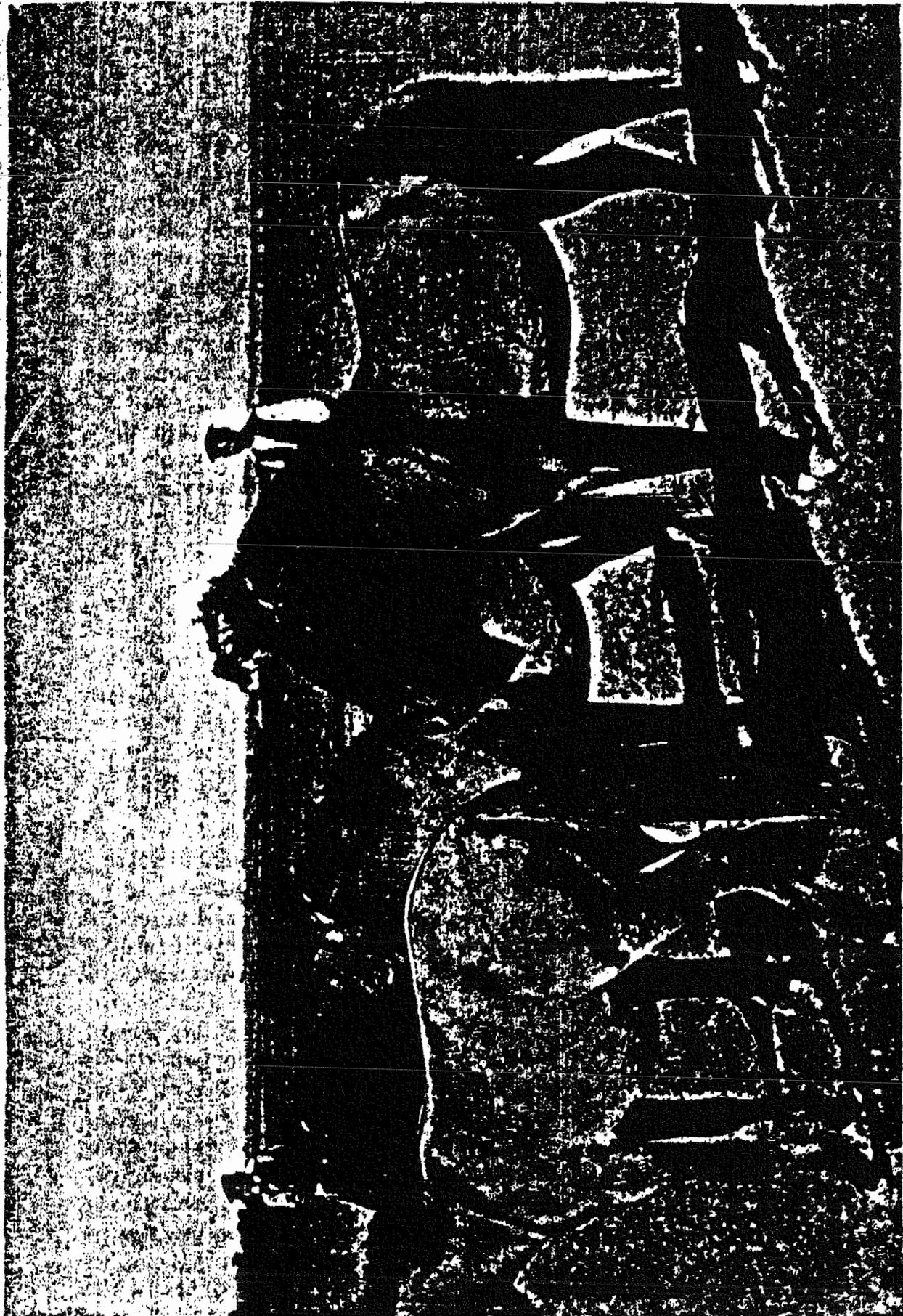


Fig. 3.—Prjevalsky horses in the possession of F. A. Fialz-Fein, among them a bastard Zebra (to the left in the background).

The degree of curvature of the back varies greatly. In two living examples, in which this character can be best observed, the curvature is well marked in one (a mare) and only slightly so in the other (a stallion).

The tail is an extremely interesting feature of the Prjevalsky horse. It is quite peculiar, and resembles neither the tail of the onager nor that of the domestic horse, but is intermediate in form. It differs from that of the onager in that it is not sharply divided into two portions—a proximal part provided with tufts of short hair, and a distal portion covered with long hairs. It differs from the tail of the domestic horse, in that, for a certain distance from the root, its dorsal surface is covered with short hairs. Long hairs also occur on the root, but they are present on the sides only, and therefore are below the short hairs. The tail is very long. In a foal at Tsarskoe-Selo it reached almost to the hoofs. The short stiff hairs on the dorsal aspect of the root are arranged in the form of two converging streaks enclosing a less prominent area, along the centre of which is a darker line forming a continuation of the dorsal stripe of the trunk. The hairs of the dorsal surface differ from the long hairs of the tail not only by their coarseness, but also in their colour. Poliakov states that the short hairs are of the same colour as those forming the dorsal stripe, and that, when the winter coat is concerned, they differ conspicuously from those of the body in their colour, and so resemble the light hairs of the mane and tail.

Poliakov refers to the remarkable thickness of the legs of *E. prjevalskii*. In the living specimens which I have had an opportunity of examining, the legs were by no means thick. On the contrary, they might be described as slight, and looked rather long in comparison with the height of the animal.

The shape of the hoof forms an extremely important difference between the horse and the wild ass. In the ass it is somewhat long, and in the horse it is rounder. Measurements of twenty-two kiangs, five onagers and eight Prjevalsky horses, showed that in the last named the hoof is rounder than in the others—a difference of some importance. In the onager the width of the hoof is to its length as 100:140; in the kiang, as 100:149; and in *E. prjevalskii*, as 100:124. But the maximum and minimum length of the hoof is somewhat variable. In some specimens of the Prjevalsky horse the breadth of the hoof was to its length as 100:144; that is to say, the hoof was relatively longer than that of the average kiang. In the kiang the hoof is occasionally longer than in the onager, and, in extreme cases, a proportion of 100:168

may be attained, thus approaching the maximum for the onager (100:172.5). In general terms it may be said that the hoof has different average proportions in each of the three species of *Equus*; but different individuals reveal considerable variation.

As Poliakov has already pointed out, the Prjevalsky horse has callosities ("chestnuts") on both the anterior and posterior limbs. Their size is variable, but in general, as appears from the following table, the anterior callosities are much better developed than those of the posterior limbs, as is usually the case in the domestic horse. As a rule, the callosities are oval, but not regularly so, and generally the posterior are relatively narrower than the anterior. In position they agree with the callosities of the domestic horse.

Dimensions of the Limb Callosities of *Equus Prjevalskii*.

No.	Anterior.				Posterior.			
	Length.		Breadth.		Length.		Breadth.	
	mm.	mm.	mm.	mm.	mm.	mm.	mm.	
3,087	...	32	...	20	...	22	...	8
3,088	...	37	...	18	...	26	...	10
3,081	...	38	...	24	...	27	...	8
3,091	...	49	...	16	...	34	...	9
3,090	...	61	...	16	...	34	...	12
3,092	...	50	...	16	...	31	...	10
3,093	...	50	...	13	...	16	...	5
3,071	...	64	...	21	...	38	...	10
3,072	...	23	...	5	...	22	...	10
3,073	...	44	...	14	...	32	...	8
3,074	...	43	...	16	...	38	...	9

THE COAT AND ITS COLOUR.—The hair of the Prjevalsky horse is changed in winter and in summer. The first specimen known to science, captured by Prjevalsky and described by Poliakov, was in its winter coat, and, consequently, it was assumed by Poliakov that the hair of *E. prjevalskii* is long and curly. The winter and summer coats differ from each other, not only in length and texture, but also in colour and markings. The colour of the hair of the winter coat is lighter than that of the summer one. Poliakov correctly described the former as yellowish on the back, lighter over the sides and almost white on the under part of the body. Among the skins at the present time in the Zoological Museum both winter and summer coats are illustrated. Of the two living horses brought to the Imperial stables, one (a mare in her second year) had a winter coat, while the other (a stallion in his third year) had already assumed the summer coat. The difference between the two animals appeared to me to be very

remarkable, and I was inclined, at first, to regard it as an individual peculiarity, but a closer study of the skins of Prjevalsky horses of different ages, and killed at different seasons, showed that the adult animals killed in winter had nevertheless a summer coat. This is illustrated by a ten-year old horse (No. 3,094), killed in January, 1895, during the expedition of Roborovsky and Kozlov. If these data are reliable, it may be assumed that the tendency to change the summer coat for a winter one diminishes with increasing age.

In *E. prjevalskii*, a change of hair probably occurs in the spring, and takes place very slowly, as is the case with some of our domestic horses. This can, naturally, only be proved by the observation of living animals. The summer coat is much shorter than the winter one, and it is smooth and not curly. The hair is about as long as that of the onager and the kiang, which it further resembles in colour. The colour of the back is a light reddish-brown. This shade extends over the sides and gradually merges into the yellowish-white of the under part of the body: so that there is no sharp line of demarcation between the back and the flank, and between the flank and the belly. The head is of the same colour as the back, except that the lips and the end of the muzzle in the region of the nostrils are white. Between the nostrils the white colour changes into grey. The ears are light brown at the base, and dark brown at the tip: while the interior is covered with white hair.

When in its winter coat, the Prjevalsky horse has tufts of hair—which Poliakov termed "whiskers"—on the sides of the head. In the summer coat these can hardly be distinguished: the hair of the cheek being of almost the same length as that on other parts of the body. In summer, however, there are long tufts of hair under the jaw, which present the appearance of an elongated beard. The mane, which begins between the ears and extends to the withers, consists of erect hairs of two colours: dark-brown and light grey; the latter being usually shorter than the former, and gathered into tufts. The hair of the mane is harder than the hair of other parts of the body.

Behind the mane the dorsal stripe extends along the entire back, in the form of a narrow (about 5 mm. broad), reddish-brown (darker than the hair of the back), straight band which, like the dorsal stripe of the onager and the kiang, is continued on to the tail (Fig. 4). The dorsal stripe can be fairly readily distinguished running along the dorsal side of the proximal part of the tail between the light grey erect hair of this region, but it can only be plainly seen in those animals which carry the summer

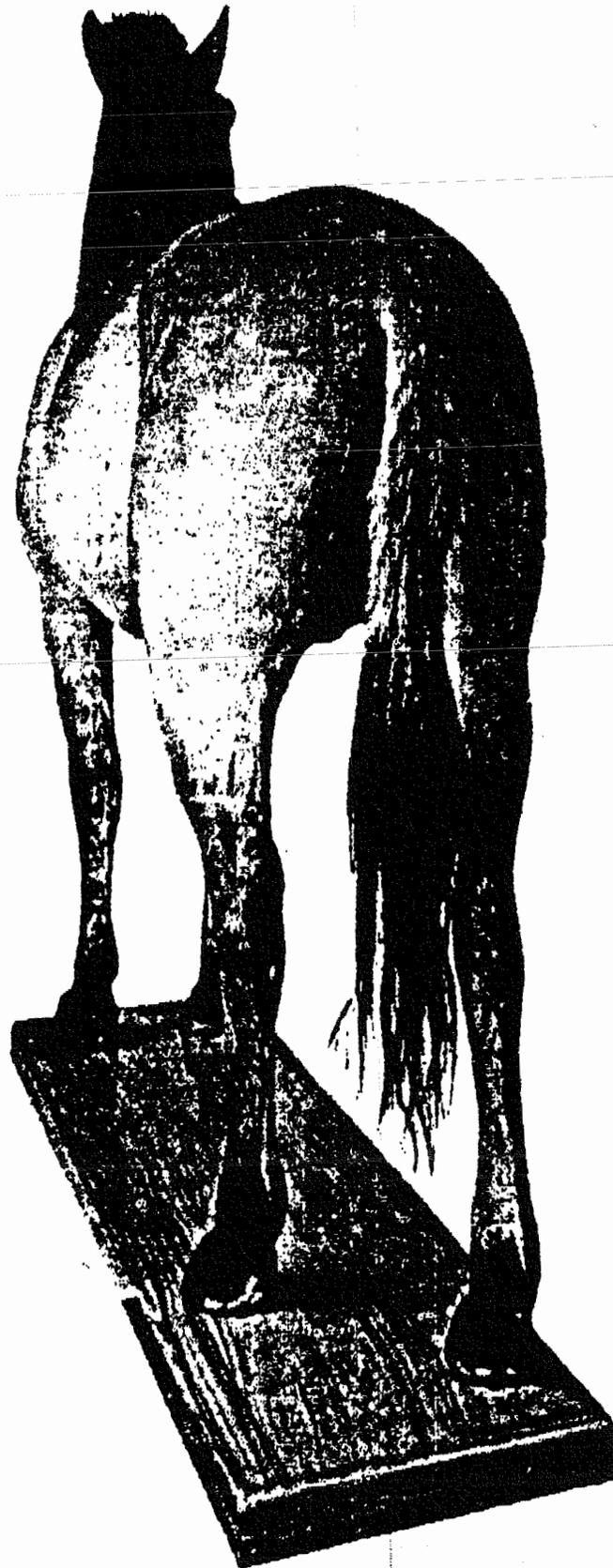


Fig. 4.--*Equus Prjevalskii*. Stuffed specimen.

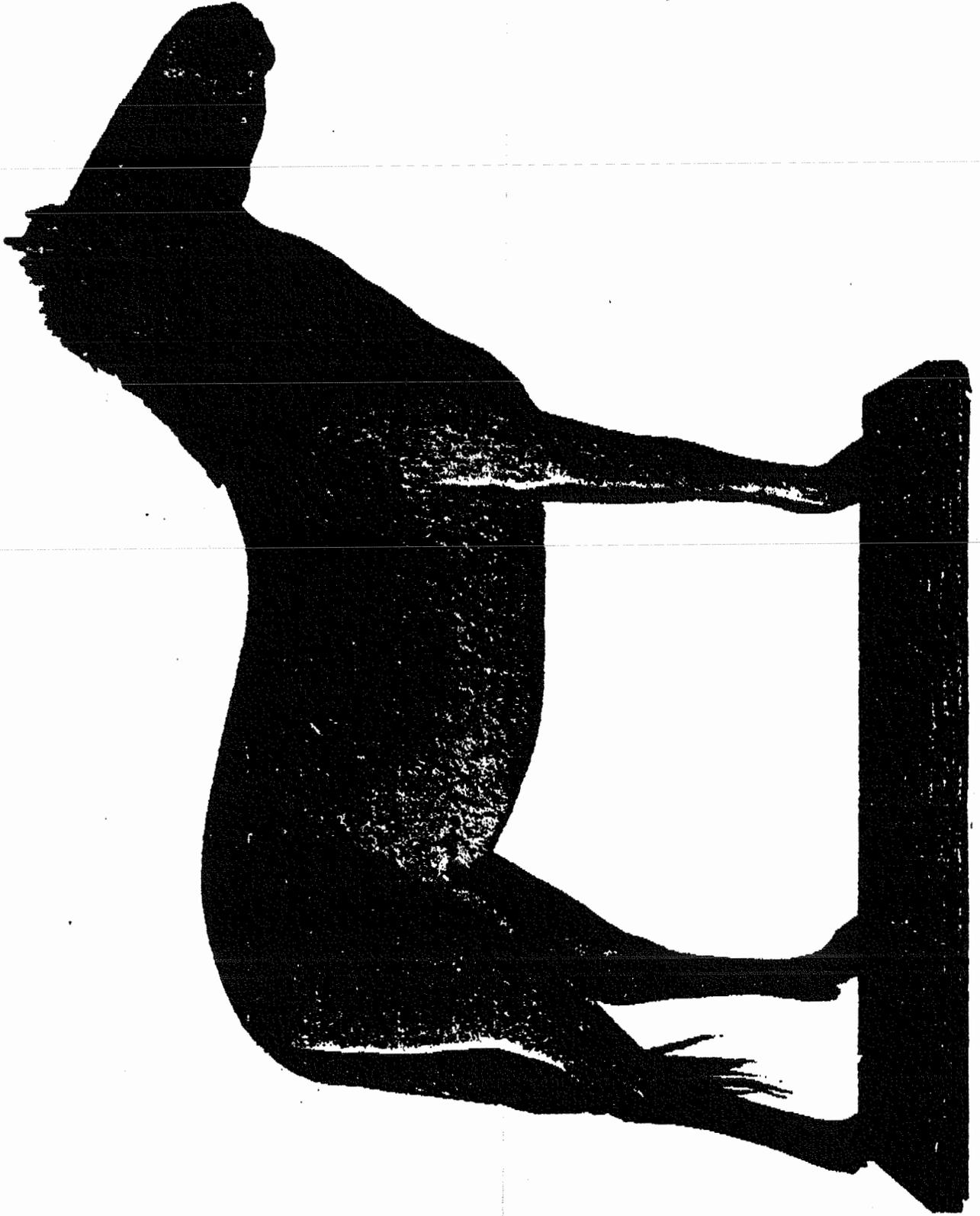


Fig. 5.—*Equus Przewalskii*. Stuffed specimen.

coat. In young animals with a winter coat, it can be distinguished only on the hind quarters close to the root of the tail; on which account it escaped Poliakov's notice. No dorsal stripe is mentioned in those later accounts of *E. prjevalskii*, which were founded upon Poliakov's description. Poliakov, however, saw the trace of the stripe on the tail, and described it correctly. Tichonov,* whose description was based upon an examination of the specimen in the University of Moscow (obtained by the Roborovsky-Kozlov Expedition), and on the specimen in the Zoological Museum of the Academy of Science, was the first to give a full and correct account of the dorsal stripe, because he was dealing with examples with a summer coat. Although attaching great importance to this feature, he held that it played no part in the solution of the question as to whether Prjevalsky's horse is a true wild horse or an animal more closely related to the Asiatic wild ass, since the dorsal stripe is met with in both horses and asses, and may be absent in either. The stripe, though darker than the rest of the coat, has the same reddish-brown tinge.

Another interesting feature in the Prjevalsky horse is the transverse shoulder stripe, which is in exactly the same position as that of the domestic ass and its ancestor, the African wild ass. It is not nearly so well marked as it is in the ass, but nevertheless it can be clearly distinguished in the living specimens at Tsarskoe-Selo. Broader and lighter than in the ass, it is of a brown colour; without sharply defined margins; and much more plainly marked in the summer than in the winter coat; although even in the latter it can be recognised. In the accompanying photograph (Fig. 5) the shoulder stripe appears fainter than it was in the actual specimen. Of the two horses at Tsarskoe-Selo, the stallion has a broad brown stripe with distinct margins; but in the young mare, in which the hair of the body is much darker and, consequently, of a greyish tinge in some regions, the stripe is black in colour, much narrower than in the stallion and more sharply defined.

The legs of *E. prjevalskii* are entirely different in colour from those of the Asiatic ass; inasmuch as, in the latter animal, the lower part of the limbs down to the hoofs is always of a light colour, whereas in the Prjevalsky horse the colour is more or less black, according to the age and individual peculiarities of the animal. In young animals, however, the lower part of the limbs is replaced by grey, and, in very rare instances, by white (as was the case in a new-born foal I saw). In adult animals a black ring extends some 80 mm. ($3\frac{1}{4}$ inches) above the hoof. From this to

* Op. cit.

the fetlock, the outer side of the limb is covered with black hairs ; but, on the inner side, the hair is grey with transverse bands, which are present as far up as the knee. Poliakov, referring to the presence of these transverse stripes, states that they are indistinct. This is so in the specimen which served for his description, since it was in the winter coat. In adult animals with a summer coat, on the other hand, they are generally very pronounced, although they may vary considerably in number and arrangement. In certain horses (for instance, No. 3,071), I have counted as many as five transverse bands ; but in foals, in which the legs are not so intensely coloured, they are occasionally absent. Further, in other animals (No. 3,090, for example), they are light in colour and few in number. Transverse stripes are especially well marked in the specimen (No. 3,074) obtained by the brothers Grun-Grjimalo. They do not constitute complete half-rings, but are in the form of two stripes interrupted on the inner side of the limb.

As far as the fetlock, the lower part of the inside of the limb is of a reddish colour, this gradually merging into the black of the outer side. Above the fetlock the reddish tone is lighter, and, becoming gradually paler, is finally as white as the hair of the belly.

The living specimens at Tsarskoe-Selo and Askaniya Nova show many interesting peculiarities, the recital of which I consider to be here necessary. All the following particulars relating to the Tsarskoe-Selo horses have been obtained by personal observation ; but, as I was not able to see the horses myself, the information regarding the Falz-Fein animals has been supplied by Koshevnikoff, to whom I am greatly indebted.

The three-year-old stallion and the two-year-old mare at Tsarkoe-Selo possessed fairly well-marked differences. The general colour of the mare was greyer than that of the stallion, in which there was a reddish shade. The white patches on the abdomen of the stallion were smaller and fewer in number than in the mare, and confined to the flanks ; while on the mare similar patches were also present on the thighs and shoulders. The colour of the neck was the same in both the stallion and the mare. Pale spots were absent from the neck ; this being a peculiarity which distinguishes *E. prjevalskii* from the Asiatic wild ass, the under part of whose neck is whitish. The "whiskers" could be easily distinguished in the stallion, whose winter coat at the time of examination (October 18th) had begun to grow. On the nose of the mare there was a grey patch, consisting of black and white hairs, not sharply defined but gradually merging into the brown

colour of the forehead. The space between the nostrils was of a red-brown colour. The outside of the nostrils was surrounded with white hairs. The lips of both the stallion and the mare were black.

In the mare the black colour of the legs extended above the fetlocks; but, in the stallion, it did not come so high up as these joints, and was, in general, less dark. The mare had four well-marked black stripes on the legs; but stripes were very poorly developed in the stallion. Owing to the presence of a large quantity of yellow hair, the lower part of the legs of the stallion was mottled in colour; whereas, in the mare, it was of uniform black.

Respecting the Prjevalsky horses belonging to Falz-Fein, I quote the following letter from Koshevnikoff *in extenso*:

"Among the interesting animals which are at Askaniya Nova, there are three Prjevalsky horses, and two supposed crosses between a domestic mare and a Prjevalsky stallion.

"All five animals arrived at the Falz-Fein estate in the spring of 1900. In all, five unweaned foals accompanied by four Kirgibz brood mares were handed over. They were obtained as newly-born animals in 1899, and had apparently wintered in Bisk.

"All the specimens were mares. They grazed in the open, in company with the two supposed cross-bred animals and an onager, under the care of a special herdsman. If these wild horses were driven into an enclosure, they would allow no one to approach nearer than four or five yards without becoming excited."

The following is a description of the individual animals:

"No. 1. The largest and darkest coloured. The stable servants of the place consider it to be cream-coloured. Personally, I would say that it is of a dun or fawn colour; but I must admit that the determination of the colour of the Prjevalsky horse is very difficult on account of its indefiniteness, and owing to the vagueness of the terms employed.

"The different parts of the body are differently coloured. The legs are dark and even black below. Callosities are present on all the legs; the anterior ones being above the joint, and the posterior below the joint. On the fore legs there are two not very well marked stripes.

"The muzzle resembles that of an ordinary horse. There is a dark spot on the forehead. The upper lip is white, and the upper part of the nostril is of a whitish-yellow colour.

"The dorsal stripe is well marked and is broader than in the other animals. The tail has no long hair for a distance of two werschok (about $3\frac{1}{2}$ inches) from the root. The mane is erect,

about $\frac{1}{2}$ arschin (7 inches) high, black down the centre and yellow at the sides. A striping, such as Tichonov described as being present in a skin in the Moscow Zoological Museum, is not apparent.

"No. 2. Lighter in colour than No. 1, and smaller (corresponds in height with No. 3). Dorsal stripe narrower. Legs are the same as those of No. 1, but darker low down. Three stripes on each leg. Traces of a fourth stripe on the right fore limb.

"Muzzle white, and whitish-brown farther back. The nose is less convex than in our skin. The mane is dark fox-red (brownish) in the middle, and lighter at the sides; but the difference in colour is not so well marked as in No. 1. The ears are of a fox-red colour, with black points. The shoulders are light. The lower part of the belly is yellowish. The callosities on the posterior limbs are large, long and placed near the posterior border of the limb.

"No. 3 is the lightest coloured specimen. The dorsal stripe is very narrow. By their colour, the light parts of the body remind one very much of the light parts of the onager. The front of the muzzle is similar in colour to that of the onager. The neck is light brown, and the belly is quite white. The under side of the abdomen, especially close to the legs, is white. The shoulders and buttocks are very light in colour.

"The muzzle is white; the forehead is light brown; and the ears are very light in colour. The nostrils are dark, as in the rest of the animals. The left fore limb has four stripes; two of the other limbs have three stripes; and one has only two stripes. ~~The lower part of the limb is very dark coloured.~~

"Half-bred (?) horses. According to the statements of the inhabitants of the districts from which the wild horses were brought, two ordinary mares were covered by wild stallions in the Steppe, and the supposed half-breds are the product of this union. Their colour is brown with a dark grey tinge. One animal is light coloured; the other is dark. Dorsal stripes are present. The muzzle is white, and, in one of the animals, the region of the nose is pure white. There are no stripes on the legs. The mane long and the forelock short, as if it had been sheared off. No double colouring is seen in the mane. The tail is like that of an ordinary horse."

According to the foregoing description of the external characters of *E. prjevalskii*, Poliakov's diagnostic signs* should be altered as follows: Mane short, no forelock, dorsal stripe and transverse shoulder-stripe present, and the proximal part of the tail bristly.

* Op. cit. p. 2.

**THE PHENOTYPIC APPROACH
IN GENETIC MANAGEMENT OF
PRZEWALSKI'S HORSE**

Frank. P.G. Princée (National Foundation for Research in Zoological Gardens, Amsterdam), Waltraut Zimmerman (Cologne Zoo), Oliver A. Ryder and James M. Dolan (Zoological Society of San Diego)

INTRODUCTION

A basic rule in breeding management of wild animal species under captive or semi-wild conditions is to avoid selective breeding. Managers should not actively induce selection on the captive population. One of the main arguments against selection is that in general humans can not determine which genetic or phenotypic characteristics are of advantage in either captive or wild environment (except for some lethal genes). And even when humans can determine the selective advantage of certain characteristics, these advantages might be restricted to today's environment. Each environment changes in time, seasonally, annually and irregularly. What is of advantage today, might be deleterious tomorrow, and vice versa.

Almost every wild population has animals that carry genes that are of less advantage. These same animals might also carry genes that have high selective advantages. Selection not simply acts on one gene, but on the entire genome (i.e. all the genes). Survival chances of an individual are not only determined by its 'bad' genes but also by its 'good' genes.

Under captive conditions rare alleles (whether 'good' or 'bad') might come to expression due to (1) unnatural selective pressures caused by the captive environment, (2) selection imposed by managers, (3) inbreeding and (4) genetic drift. Furthermore, new combinations of 'wild' genes can be formed. These different conditions might result in a larger variance in phenotypes in captivity than observed in the wild. This is no reason for selection as all these animals represent genes of the wild population.

'DOMESTIC-LOOK' IN PRZEWALSKI'S HORSES

Severe human selection in combination with inbreeding has occurred in the captive population of Przewalski's horses. This certainly will have resulted in 'new' phenotypes, i.e. phenotypes that are not observed in the wild. Inbreeding and human selection may

even have caused the homozygous expression of rare alleles that are usually only seen in domestic horse breeds.

Part of such 'new' phenotypes, on the other hand, may be due to the genetic influence of the Mongolian domestic mare and other founders which were probably not pure bred (e.g. 18 Bijsk 8). The 'domestic' phenotypes are regarded by a number of people as undesired. It is suggested by the EEP Przewalki's horse group, in consultation with the International studbook keeper Jiri Volf, that a mild selection against these characteristics be initiated (the 'phenotypic approach').

This approach contradicts the new views in genetic management of wild species in captivity. The main strategy in what we will call here the 'genetic approach' is to maintain as many of the original wild genes as possible. Selection against certain phenotypic traits which are due to 'domestic genes' might result in the loss of wild genes. This can be regarded as the most important objection against the 'phenotypic approach'.

One could wonder why the 'genetic approach' accepts the presence of 'domestic' genes in the population of a wild species. This seems to be contradictory with respect to the fact that the main goal of this approach is to preserve 'wild' genes. The following arguments can be given:

1. Hybridization between the Przewalski's horses and Mongolian horses resulted in fertile offspring. Thus, we might expect that they did not differ dramatically in genetic constitution i.e. *Equus przewalskii* and *E. caballus* might share a large number of genes.
2. Furthermore, the domestic horse influence in individual Przewalski's horses is small, and one should take into account that a relative small number of genes is involved in phenotypic characters as coat colour, coat patterns and manes.
3. Although, the domestic horse influence is small, a large number of Przewalski's horses carry domestic genes. This means that selection against domestic genes is not feasible. Such a strategy would imply that most of the horses would be excluded from breeding and that the breeding population would be based on 'pure-bred' Przewalski's horses, that belong to highly inbred lines. Furthermore, the few pure-bred horses do not represent all the founders. Thus, selection against domestic genes would also result in the loss of wild genes.
4. Regarding the survival success of feral horses, domestic characters in Przewalski's horses also will probably have no influence on the success of re-introduction. Furthermore, this domestic influence originates from a domestic race that is bred and kept under almost the same environmental conditions as that of Przewalski's horses. And, if domestic horse genes are not favored in reintroduction they will be selected against.

This means that from the population genetics point of view the domestic horse influence can be neglected and the Przewalski population should be managed as wild species.

WHY A PRZEWALSKI'S HORSE SHOULD LOOK LIKE A PRZEWALSKI'S HORSE

The wish to breed horses that resemble the phenotypes of wild Przewalski's horses as have been described in literature is a result of human perception rather than of biological science. But this should not mean that the 'human factor' has to be neglected and 'wild species' management should, in this specific case, prevail in breeding management. Curator, geneticist or zoo-visitor, everyone has a certain perception of what a Przewalski's horse should look like. Images that are imprinted in human brains.

This means that visitors of re-introduction areas, semi-wild reserves and zoological gardens expect to see a horse that resembles their imagination of the last 'wild' horse. Presenting horses that show several domestic external features will disappoint visitors and might encourage several groups in the community (and the common visitor) to doubt the capacities of zoological gardens and conservation groups with respect to the feasibility of education and re-introduction programs. This can seriously hinder modern zoos and conservation groups in performing their activities.

Genetic management that takes into account the 'Przewalski-look' might contradict with new strategies in 'wild species' management, but on the other hand the current population does not consist of 'true' wild individuals as probably not all founders were pure bred and a domestic horse has been bred into the population. A compromise in breeding management where a mild phenotypic selection is carried out without losing wild genes could be tolerated. Regarding the number of animals, it is not a priori impossible to set up such a breeding strategy.

RECOMMENDATIONS

The following guidelines with respect to mild phenotypic selection are recommended:

1. The original descriptions of wild-caught Przewalski's horses (Poljakoff 1881, Salensky 1902) should be used as a basis in phenotypic selection. This, however, does not mean that all Przewalski's horses showing phenotypic traits not seen among the wild-caught specimens should be excluded from breeding. Recombination and inbreeding in the small population may have caused the expression of (rare) wild genes that are not frequently expressed in the wild. These genes belong to gene pool of the wild population and are a part of its adaptive potential, and thus, they should not be completely removed from the captive population. Their frequency, however, may be kept within reasonable limits by (mild) selection.

2. Genetically important horses i.e. horses that carry a large number of unique 'wild' alleles, should never be excluded from breeding by phenotypic selection, not even when they are suspected to be carriers of domestic traits. Reduction of the influence of such traits may be achieved by selection on the offspring of these genetically important animals. Pedigree analysis (gene drop or peeling) can identify those horses that represent uniquely important sources of genetic variation from founder individuals.
3. Given the pattern of inheritance in domestic horses and analysis of the studbook data it is very likely that 'fox' colour in *Equus przewalskii* just as in domestic horses is inherited by a recessive allele on a single locus. This is a testable concept. Fox carriers are and will always be in the population. Whenever possible, the individuals of pairs that produce 'foxes' should be recombined to breed with non-fox carriers.
4. Care should be taken with respect to phenotypic selection against features of which inheritance patterns are unknown. It is recommended that genealogical studies and/or experimental matings are carried out prior to any selection procedure.
5. It is very difficult to draw a line between 'wild' and 'domestic' look. It is recommended that selection should not be carried out against horses that show just single 'domestic' characteristics but preferably against horses that show several domestic characteristics simultaneously e.g. hanging manes and white star and black nose.
6. The 'phenotypic approach' should be regarded as an experiment. This means that monitoring and evaluation are required. Based on such evaluations it should be decided whether to continue with this additional type of genetic management. It is recommended that horses that are excluded from breeding for selective reasons, should remain available until the 'phenotypic approach' is evaluated. Thus, for the time being they should only temporarily be removed from the population.

EPILOGUE

The overall goals of both 'genetic' and 'phenotypic' approaches in management of the Przewalski's horse population are the retention of genetic diversity. The 'phenotypic' approach does not necessarily imply that less genetic diversity will be retained than by a 'genetic' approach. The captive population of Przewalski's horses has (nearly) reached its carrying capacity. This will limit the number of horses that are allowed to breed and the number of offspring that can be produced. This means that one may have to make choices with respect to select animals for breeding. Genetic and phenotypic criteria can be considered in such a selection procedure e.g. in those cases that candidate breeders are genetically equivalent, the horse that is not suspected of carrying a domestic trait may be preferred.

Recommendations on phenotypic selection have to be considered as guidelines rather than rules. In reality the phenotypic approach will be a compromise between practice and guidelines. Furthermore, physical health and fertility of individual horses will also affect both 'genetic' and 'phenotypic' approaches.

Finally, it must be stressed that this paper is intended to be used for discussion rather than it is intended to be the management strategy for Przewalski's horses.

PRZEWALSKI'S HORSE

Equus przewalskii

**GLOBAL CONSERVATION PLAN
DRAFT**

A SPECIAL REPORT TO THE PROFESSION

**POSITIVE HORSE IDENTIFICATION
PART 3: COAT COLOR GENETICS**

Ann Trommershausen-Smith, Ph.D.



EQUINE PRACTICE — IDENTIFICATION

A system of classification of horse coat colors and markings is described and its importance in identifying individual animals is defined. Basic genetic structures are presented. The construction of genetic models is described and genetic terminology is defined. Significant genes in determining coat color are presented and each color gene is described with its relationship to a specific coat color. The genetic formula which results in individual colors is given. Color illustrations of specific coat colors and their genetic delineations are included. A method of assigning coat color by genetic formula is given. Tables present genetic formulas and color definitions and the genetic makeup of specific coat colors in horses.

A SPECIAL REPORT TO THE PROFESSION

Positive Horse Identification Part 3: Coat Color Genetics

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This is the third and final contribution in this series on methods of identification being presented in Equine Practice. The considerations offered here give practitioners considerable help in defining color precisely and presenting suggestions for solving identification problems important to the profession, the horse industry and individual clients.

The Editors

□ A system of classification of horse coat colors and markings is important in any program of identification of horses as individual animals. In order to have accurate and uniform application of the terminology for color classes, the system should stress recognition of basic, definable characteristics and should minimize the importance of subtleties which cannot be clearly defined. A scheme of coat color classification based on recognition of the effects of the alleles of seven genes provides the necessary rigor,

and with training can be uniformly applied by anyone to define most of the common colors encountered in horses.

Basic Genetics

For every living thing millions of instructions called *genes* are used for its growth, appearance and maintenance. It is not possible to see a gene, even with the most sophisticated microscope available. We recognize the presence of genes because of their effects on the organism in ways that we can see or measure.

In order to understand coat color genetics, one must first learn to pick out the conspicuous characteristics effected by each gene. This can be likened to observation and study of a basket of mixed fruit. At first glance we may see a melange of shapes, colors and textures, but with a second glance the trained eye can see the distinctive presence of apples, oranges and bananas. Similarly, the potpourri of horse colors can be focused into a structured subject by attention to the effects of seven different genes.

Every cell contains a duplicated set of genes. Each set is derived from the single sets contributed at conception to a single cell by both the mother and the father. The gene sets in a cell contain similar, but not necessarily identical, information. For ex-

ample, both sets may contain a gene determining hair structure, but one set may contain the instructions for straight hair and the other for curly hair. The alternative forms of each gene are called *alleles*. If both alleles are identical, then the animal is said to be *homozygous* at that gene; if the alleles are dissimilar, then the animal is said to be *heterozygous* at that gene. Information about the homozygosity or heterozygosity for various genes can be inferred from information about parents and/or progeny and can be used for predicting the outcome of matings. For most of the alleles of horse coat colors one cannot tell by looking at an animal whether or not it is homozygous at each coat color gene, so zygosity information will not be critical for purposes of identification. Sometimes, however, information about coat colors of parents may be used as an indication of incorrect parentage or erroneous identification, so some familiarity with genetic relationships may be useful.

Both sets of genes function simultaneously in the cell. Often when the gene pair is heterozygous, one allele may be visibly expressed but the other is not. The expressed allele in a heterozygous pair is known as the *dominant* allele, the unexpressed one as the *recessive* allele. The term dominant is given an allele only to describe its relationship to related alleles, and is not to be taken as an indication of any kind of physical or temperamental strength of the allele or the animal possessing it. Likewise, possession of a recessive allele does not connote weakness.

For simplicity in constructing models, geneticists symbolize genes by letters such as A, B and so on. A dominant allele of a gene can be symbolized by an underlined capital letter, e.g., A, and the recessive by an underlined lower case letter, e.g. a. For each of the seven genes of horse coat color to be considered, only two alternatives will be considered for each.

In any animal expressing the dominant allele of a gene, it cannot be determined by looking at the animal whether the second allele is a dominant or a recessive one. The presence of a recessive allele may be mask-

Continued

ed by a dominant allele, which leads to the expression "hidden recessive". Dominant alleles are never hidden by their related recessive alleles.

Gene W: Inability to Form Pigment in Skin and Hair

This gene and the gene G, to be discussed in the next section, will be presented first because they have alleles whose actions can obscure the actions of the other coat color genes. If either allele W of the W gene or allele G of the G gene is present in the hereditary material of a horse, it is impossible to determine its other coat color genes by superficial examination, so the colors these alleles produce can be simply dealt with at the onset of this discussion.

In the presence of the dominant allele W, a horse from birth will typically lack pigment in skin and hair. The skin is pink, the eyes blue or brown, and the hair white. Such a horse is termed white (Fig. 1A). Sometimes such a horse is called albino.

The W allele is only rarely encountered. All non-white horses are ww.

Gene G: Exclusion of Pigment from Hair

Everyone is familiar with the process of progressive silvering of human hair color in which the hair color of youth, such as blond, brunette or redhead, turns to gray or white with age. Horses show a similar phenomenon of hair silvering with age in a color called gray (Fig. 1B). In horses, gray is controlled by the dominant allele G.

A young horse with a G allele will be born any color but gray and will gradually become white or white with red or black flecks as an aged animal. Earliest indications of change to gray can be seen by careful scrutiny of the head of a young foal, since often the first evidence of the gray hairs will be seen around the eyes (Fig. 1C). In intermediate stages of the graying process, the horse will have a mixture of white and dark hairs, a most confusing stage for trying to identify color.

In contrast to white (W) horses, gray horses

are born pigmented, go through lightening stages, but always contain pigment in skin and eyes at all stages of coloration change.

A gray horse will be either GG or Gg. It is not possible to tell by looking at the horse whether it is homozygous for G. For simplicity in notation, a horse expressing a dominant allele can be symbolized as, for example, G. Use of a single allele designation in this paper for color assignment implies that no information about the second allele of the pair is available. All non-gray horses will be gg. For homozygous recessive colors, both alleles are written in the notation for color assignment, since a horse showing a color or pattern produced by recessives is by definition homozygous for the recessive alleles.

Since gray is produced by a dominant gene, at least one parent of a gray horse must be gray. If a gray horse does not have a gray parent, then it should be seriously considered that the purported parentage is incorrect.

Gene B: Black Hair Pigment

The first step for defining the coat color of a horse which is neither gray nor white is to decide if the animal has any black pigmented hairs. These hairs may be found either in a distinctive pattern on the points (such as legs, mane and tail), or black hair may be the only hair color (with the exception of white markings) over the entire body. If a horse has black hair in either of these patterns, then the animal possesses an allele of the B gene which contains the instructions for placing black pigment in hair. Geneticists symbolize this allele of the B gene B. The alternative allele to B is b. Allele b allows black pigment in the skin but not in the hair. The pigment conditioned by the b allele makes the hair appear red.

If an animal has no black pigmented hair, it has the genetic formula bb. Basically, a bb animal will be some shade of red ranging from liver chestnut to dark chestnut (Fig. 1D) to chestnut (Fig. 1E), or sorrel (Fig. 1F). Manes and tails may be lighter (flaxen), darker (not

black), or the same color as the body. These pigment variations of red cannot yet be explained by simple genetic schemes. Furthermore, the shades of red are not consistently defined by breeds or regions of the country, so usage of specific terms for the shades of red can be confusing. Thus it is strongly urged that this group of colors be lumped under the term red.

Since the red animal is not gray and not white, its genetic formula in terms of the three genes discussed so far is ww, gg, bb. Notice that when two red horses are bred together, (ww, gg, bb x ww, gg, bb), the offspring should also be red (ww, gg, bb). If the offspring has black pigment (B), or is gray (G) or white (W), then the parentage as given is most likely incorrect.

Gene A: Distribution of Black Pigmented Hair

The gene that controls the distribution pattern of black hair is known as A. The allele A in combination with B will confine the black hair to the points to produce a bay (Fig. 1G). Various shades of bay from dark bay or brown through mahogany bay, blood bay to copper bay and light bay exist. The genetics of these variations has not been defined. Any bay horse will include A and B in its genetic formula as well as ww and gg.

The alternative allele a does not restrict the distribution of black hair and thus in the presence of the allele B of the B gene a uniformly black (Fig. 1H) horse is produced. In most breeds of horses, the a allele is rare, so black horses are infrequently seen.

Many black horses will sun-fade, especially around the muzzle and flanks. Such animals may be called brown, but since the term brown can be used for several genetic combinations (various reds, bays and dark bays (Fig. 1I), as well as blacks), usage of the term brown is strongly discouraged. A possible exception might be to allow the usage of the term seal brown for those black animals in which the yellowish areas around the muzzle and flanks are relatively constant throughout all seasons.

Neither A nor a affects either the pigment

or its distribution in red (bb) horses. Thus it is not possible to determine by examination of coat color which alleles of the A gene a red horse has.

Gene C: Pigment Dilution

An allele of the C gene, known as c^{cr}, causes pigment dilution. Fully pigmented horses are CC. Heterozygous horses (Cc^{cr}) have red pigment diluted to yellow but black pigment is not affected. A bay (B, A) becomes a Buckskin (Fig. 2A) by dilution of the red color body to yellow without affecting the black color of the mane and tail. The genetic formula for a buckskin is ww, gg, A, B, Cc^{cr}. A red horse (bb) becomes a palomino (Fig. 2B) by dilution of the red pigment in the body to yellow with mane and tail being further diluted to flaxen. The genetic formula for a palomino is ww, gg, bb, Cc^{cr}. A genetically black horse (B, aa) can carry the dilution allele without expressing it, since Cc^{cr} only affects red pigment.

In homozygous condition, c^{cr}c^{cr} completely dilutes any coat color to a very pale cream with pink skin and blue eyes. Such horses are often called cremello (Fig. 2C), also perlino or albino. Typically, such horses are the product of the mating of two dilute-colored animals such as palominos or buckskins. Cremello may be difficult to distinguish from white unless critical judgments can be made about hair color. The hair of c^{cr}c^{cr} animals will be cream-colored, whereas the hair of W horses will be white. As with W and G horses, for c^{cr}c^{cr} horses it is not possible to determine which alleles of other genes are present.

The c^{cr} allele does not exist in some breeds of horses such as Arabians and Thoroughbreds. In those breeds all animals are CC.

Gene D: Dun Pattern and Pigment Dilution

The D gene determines a second kind of dilution of coat color and its effects can be confused with those of c^{cr}. However, there are several important differences of the effects of D and c^{cr} on color. First, D dilutes

Continued



Fig. 1A — Dominant white (Ww). This horse has been white from birth. Note pink skin, clearly seen around mouth, nostrils, eyes. Eyes are brown in this horse, but may be blue in other cases.



Fig. 1B — Gray (G). This gray Arabian stallion was foaled a non-gray color and turned white with age. In comparison with Ww horse, note black skin around mouth, nostrils and eyes.



Fig. 1C — Gray (G) pony mare with her red tobiano foal turning gray (Gg, bb, TotO). Note rings around eyes of gray hair interspersed with red color. When mature, it will be impossible to ascertain that the foal was red at birth, and the spotting will only be evident as a pink-skinned pattern in the skin.

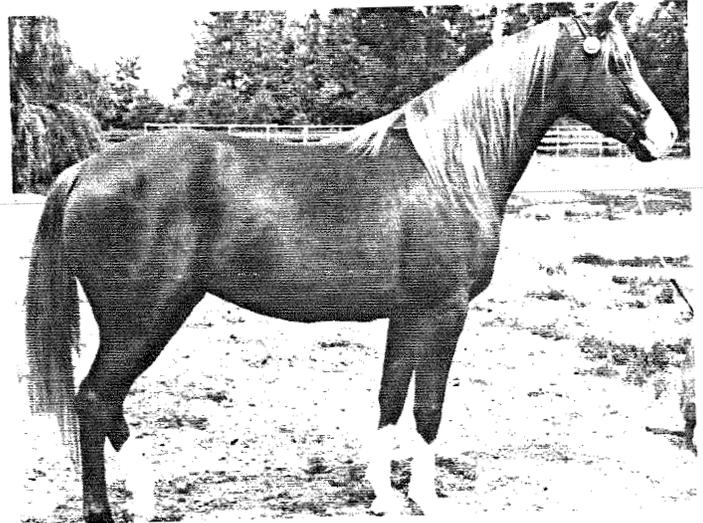
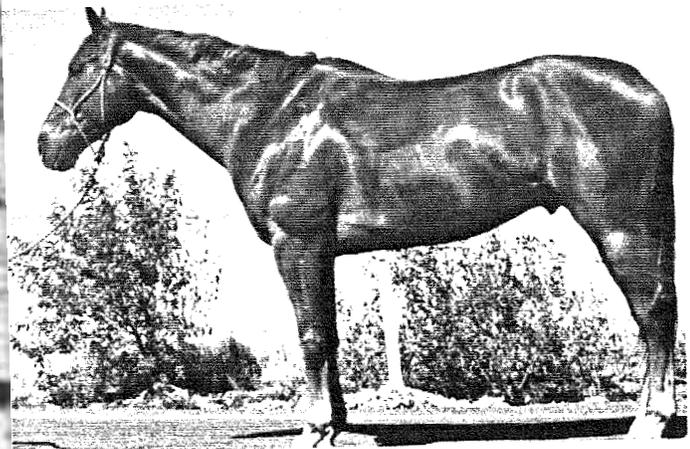


Fig. 1D — Dark chestnut (bb) Arabian mare, Tamasina. For purposes of identification, this color as well as the next two (E, F) are best referred to as red in order to avoid differences in regional and breed specific terminologies for the red series.

Fig. 1E — Chestnut (bb). Thoroughbred gelding, Mr. Maz Jr. For identification this color should be called red.



Fig. 1F — Sorrel (bb). Thoroughbred gelding, Flying Comedian. This horse is registered as a chestnut, but Western regional terminology would describe this light color variant as sorrel. In order to avoid confusion, the use of the term red is preferred.



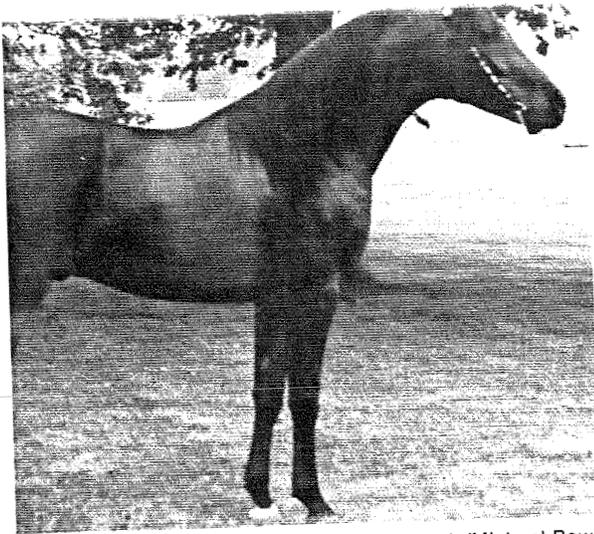


Fig. 1G — Bay (A, Bb). Arabian stallion, Aurtal. (Michael Bowling photograph).

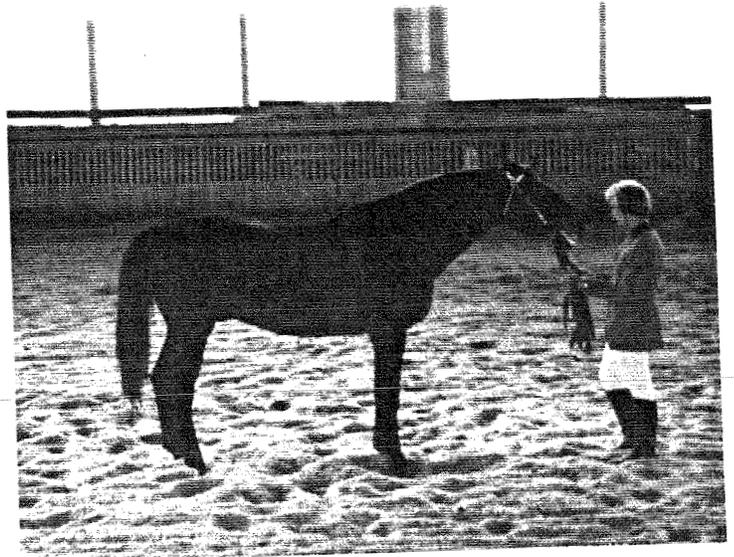


Fig. 1H — Black (aa, B). Trakehner stallion.

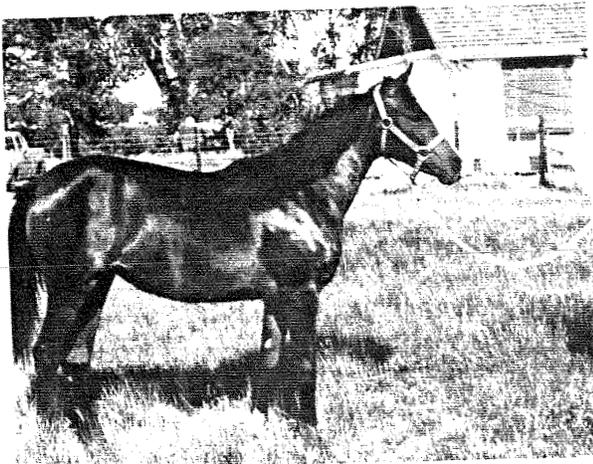


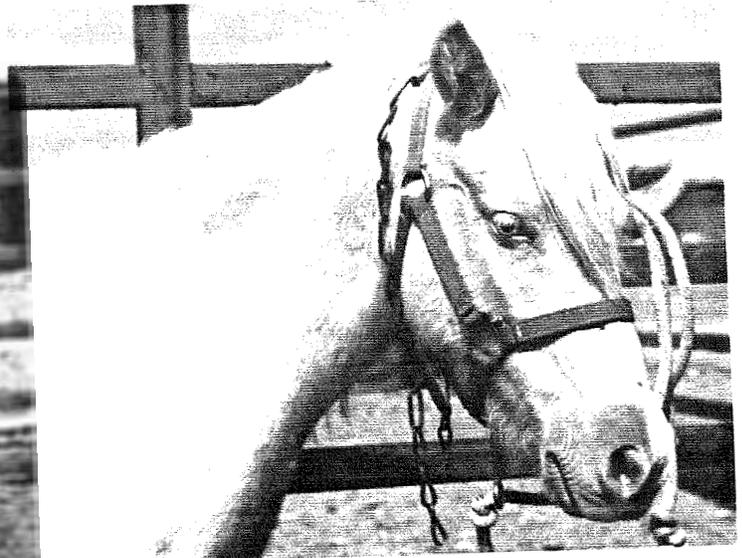
Fig. 1I — Dark bay (A, B). Arabian mare, Narah Bint Nezhah. This color may variously be called dark bay, black bay, mahogany bay or brown. In order to obviate confusion, it is suggested that the basic color be simply described as bay in recognition of the black pigment in an obvious points pattern.



Fig. 2A — Buckskin (A, B, Cc^{cr}) pony mare. Note that this horse is basically a bay, but the areas of red pigment have been diluted to yellow.

Fig. 2B — Palomino (bb, Cc^{cr}) pony mare. The presence of a dilution gene dilutes red pigment to yellow.

Fig. 2C — Cremello (c^{cr}c^{cr}) pony mare. Compare with figures of Ww and G horses. Note the cream-colored hair, pink skin and blue eyes as the group of special characteristics of cremello.



both black and red pigment on the body, but does not dilute either pigment in the points. Red body color is diluted to a pinky-red, yellowish-red or yellow; black body color is diluted to a mouse-gray. Second, in addition to pigment dilution, a predominant characteristic of the allele D is the presence of a particular pattern which includes dark points, dorsal stripe (list), shoulder stripe and leg barring. Third, homozygosity for D does not produce extreme dilution to cream as does c^{cr}.

This pigment dilution pattern is called dun. In an otherwise red horse, the D allele produces a pinkish-red horse with darker red points known as a red dun or claybank dun (ww, gg, bb, CC, D). In an otherwise bay animal, the D allele produces a yellow or yellow-red animal with black points known as a buckskin dun (ww, gg, B, A, CC, D) (Fig. 2D). An otherwise black animal with the D dilution allele is a mouse gray color with black points known as a mouse dun or grulla (ww, B, aa, CC, D).

The effect of D and c^{cr} can be easily confused in A, B horses so care must be taken in identification. It is possible for an animal to have both the c^{cr} and D dilutions, a situation which may be difficult to distinguish except by breeding tests.

D is found only in a few breeds of horses, and probably in the United States would only be seen in stock horse breeds, as well as in some ponies. All Arabians and Thoroughbreds, for example, would be dd.

Gene To: Tobiano Spotting Pattern

Several different white spotting patterns exist in horses, but so far only that of tobiano (Fig. 2E) has been clearly shown to be conditioned by a single gene. Tobiano spotting, symbolized by To, is a variable restricted pattern of white hair with underlying pink skin which can occur with any coat color. The pattern is present at birth and stable throughout life. In general, white extends from the neck crest, withers or top of the croup in an apparent top-to-bottom distribution on the body. The white areas may merge

to form an extensive white pattern of generally smooth outline. The legs are white, but the head is usually dark except for a facial marking pattern.

Other Coat Color Patterns and Markings

In addition to the coat colors and patterns already discussed, the presence of other distinctive features should be noted for any horse being identified, even though their genetics has not been adequately defined. Some distinguishing features to be noted include the following:

- White face and leg markings are commonly found on most horses and should be precisely described.

- One or both blue or partial blue eyes (Fig. 2F) can be found on any color horse, not just whites and cremellos, and should be noted.

- A horse with a mixture of white and dark hairs of any color is known as roan (Fig. 2G). The extent of roaning can vary from a few hairs in the flank to extensive involvement of the body. In the most extensively roaned horses, a typical pattern seen is that in which the body is silver due to a high percentage of white hair, but the legs and head are dark due to the preponderance of non-white hair. Roaning may be present at birth or may not be conspicuous until the first foal coat is shed. Generally, roaning is not a progressive silvering phenomenon as is gray, although often the summer coat may appear lighter than that of winter. Young gray horses can mistakenly be classified as roan, but information about the color of the parents may help clarify the situation, since a gray will have at least one gray parent. A roan may or may not have obviously roaned parents.

- Several variable spotting patterns collectively known as Appaloosa (Fig. 2H) spotting can be found in any coat color. The spotting patterns include leopard, blanket, snowflake and roan. Permanent identification of Appaloosas can be difficult, since the white patterns may not be stable from birth. In

general, besides white spotting, appaloosas can be recognized by striped hooves mottled skin (especially evident around muzzle and eyes) and prominent white sclera.

● A stable pattern of variable white spotting known as overo (Fig. 2I) is characterized by white on the belly or sides of the midsections which appears to extend upward to, but not including, the center line of the back. White may also occur on the side of the neck and flank as separate areas or merged with midsection white. Large white areas characteristically have a jagged outline. At least one, and usually all four legs are colored, but they may have white markings. It is possible for a horse to have both the overo and tobiano spotting patterns (as well as appaloosa) and a precise definition of such a coat color may be difficult.

Assignment of Coat Color by Genetic Formula

In order to define the color of a horse in a systematic way, one must learn to assign genetic symbols to the horse to be identified. With study and practice this becomes easy. Careful application of genetics to coat color definition can gloss over any inconsistencies due to regional or breed definition, age or season.

Defining the coat color of a horse is a stepwise process. The first step is to determine if either G or W is present. If yes, then the animal is gray or white and this is the end of the color identification task.

If the horse is neither gray nor white, then assignment of alleles of the other genes can be made to define the color. First, one must decide if the horse has B or not. If B, then it must be decided whether the horse has A or not. If the animal does not have B, then a decision about A cannot be made. If none of the colors is diluted and if no spotting pattern is present, these decisions about B and A will define the colors bay, black and red.

If dilution of the basic colors to yellow, light red, mouse gray or cream is present, then further definition can be made with addition of the alleles of C and D to the basic

TABLE 1
Genetic Formulas and Color Definitions

Genetic Formula	Color
<u>W</u>	White
<u>G</u>	Gray
<u>B</u> , <u>A</u> , <u>CC</u> , <u>dd</u> , <u>gg</u> , <u>ww</u> , <u>toto</u>	Bay
<u>B</u> , <u>aa</u> , <u>CC</u> , <u>dd</u> , <u>gg</u> , <u>ww</u> , <u>toto</u>	Black
<u>bb</u> , <u>aa</u> , <u>CC</u> , <u>dd</u> , <u>gg</u> , <u>ww</u> , <u>toto</u>	Red
<u>B</u> , <u>A</u> , <u>C</u> <u>c^{cr}</u> , <u>dd</u> , <u>gg</u> , <u>ww</u> , <u>toto</u>	Buckskin
<u>bb</u> , <u>C</u> <u>c^{cr}</u> , <u>dd</u> , <u>gg</u> , <u>ww</u> , <u>toto</u>	Palomino
<u>c^{cr}</u> <u>c^{cr}</u>	Cremello
<u>B</u> , <u>A</u> , <u>CC</u> , <u>D</u> , <u>gg</u> , <u>ww</u> , <u>toto</u>	Buckskin dun
<u>B</u> , <u>aa</u> , <u>CC</u> , <u>D</u> , <u>gg</u> , <u>ww</u> , <u>toto</u>	Mouse dun
<u>bb</u> , <u>CC</u> , <u>D</u> , <u>bb</u> , <u>ww</u> , <u>toto</u>	Red dun
<u>B</u> , <u>A</u> , <u>CC</u> , <u>dd</u> , <u>gg</u> , <u>ww</u> , <u>To</u>	Bay tobiano
<u>bb</u> , <u>CC</u> , <u>D</u> , <u>gg</u> , <u>ww</u> , <u>To</u>	Red dun tobiano

formula containing W, G, B and A. In the absence of white spotting these decisions will define the colors palomino, buckskin, cremello, red dun, buckskin dun and mouse dun.

If a white spotting pattern is present which meets the definition of tobiano, To can be assigned to the genetic formula.

The outcome of decisions about the genes W, G, B, A, C, D and To results in the assignment of alleles for each gene. Each assignment should be carefully reviewed to consider if the chosen alleles are likely to be found in the breed of horse being identified. Some of the genetic formulas and their color definitions which can be assigned by this process are shown in Table 1.

The final step in the coat color identification process is to add any other pertinent markings and patterns to the description such as face and leg markings, roaning, appaloosa and other spotting. Using the genetic system for coat color identification, most of the colors found in horses can be identified. Horses which cannot be defined may rarely be encountered, but a systematic appraisal of the genes likely to be found will provide a better identification than descriptive adjectives lacking a defined basis.

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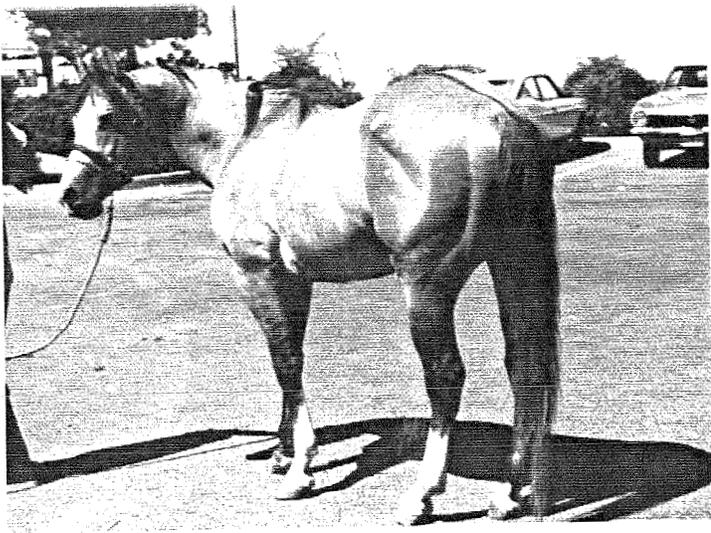


Fig. 2D — Buckskin dun (A, B, D). Compare with buckskin (A, B, Cc^{cr}). Note the dun pattern (dorsal stripe, shoulder patch, leg barring on front legs) associated with the D dilution factor.

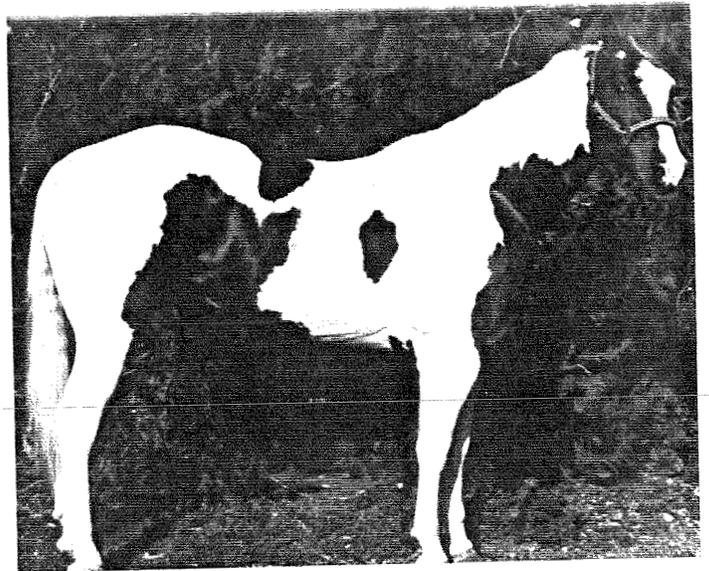


Fig. 2E — Red tobiano (bb, Toto) Paint stallion, Dandy Diamond.

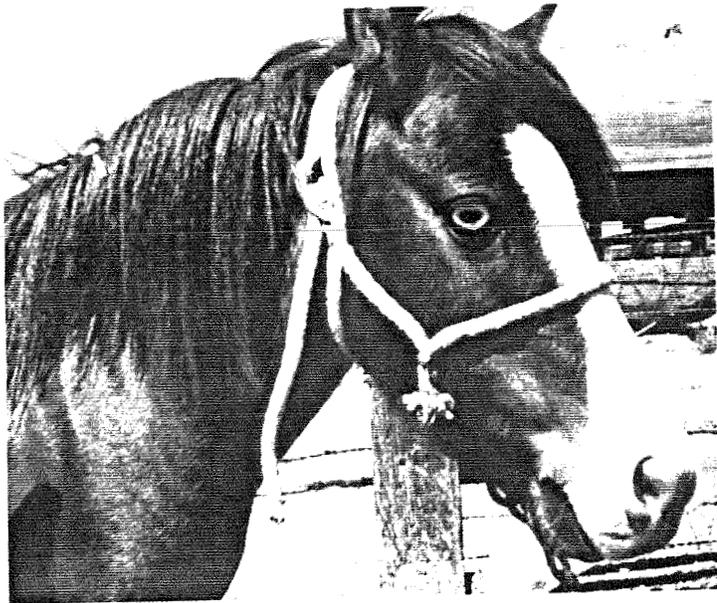


Fig. 2F — Blue eye on a bay pony mare.

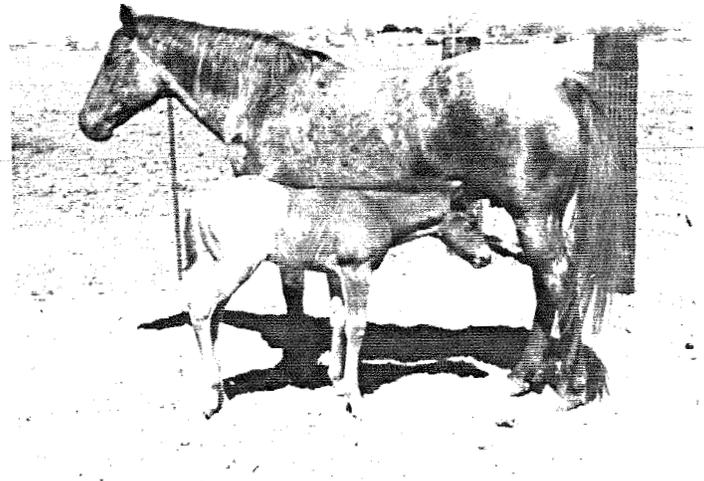


Fig. 2G — Red (bb) roan Quarter horse mare, Miss Bar Depth and her red roan foal, Peppermint Pati Kid.

Fig. 2H — Black (aa, B) appaloosa stallion, Twice as Bright.

Fig. 2I — Bay (A, B) paint overo stallion, Forecast Too.

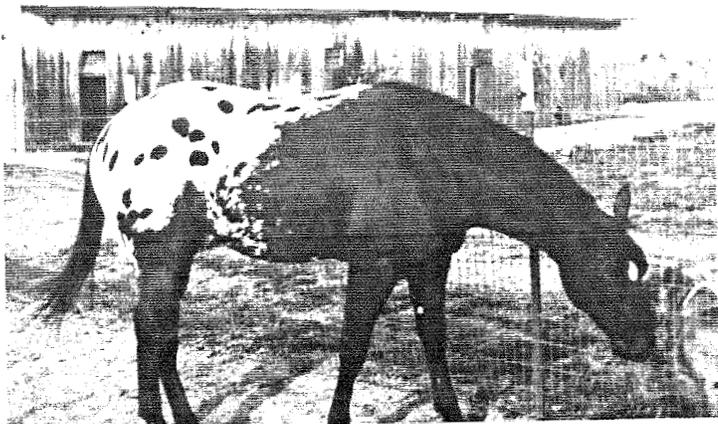


TABLE 2
Alleles and Actions of Horse Coat Color Genes

Gene	Alleles	Observed Effect of Alleles in Homozygous and Heterozygous Condition
W	<u>W</u> <u>w</u>	<u>WW</u> : Lethal <u>Ww</u> : Horse typically lacks pigment in skin, hair and eyes and appears to be white. <u>ww</u> : Horse is fully pigmented.
G	<u>G</u> <u>g</u>	<u>GG</u> or <u>Gg</u> : Horse shows progressive silvering with age to white or flea-bitten, but is born any non-gray color. Pigment is always present in skin and eyes at all stages of silvering. <u>gg</u> : Horse does not show progressive silvering with age.
B	<u>B</u> <u>b</u>	<u>BB</u> or <u>Bb</u> : Horse has ability to form black pigment in skin and hair. Black pigment in hair may be either in a points pattern or distributed overall. <u>bb</u> : Horse has black pigment in skin, but hair pigment appears red.
A	<u>A</u> <u>a</u>	<u>AA</u> or <u>Aa</u> : If horse has black hair (<u>B</u>), then that black hair is in a points pattern. <u>A</u> has no effect on red (<u>bb</u>) pigment. <u>aa</u> : If horse has black hair (<u>B</u>), then that black hair is uniformly distributed over body and points. <u>a</u> has no effect on red (<u>bb</u>) pigment.
C	<u>C</u> <u>c^{cr}</u>	<u>CC</u> : Horse is fully pigmented. <u>C c^{cr}</u> : Red pigment is diluted to yellow; black pigment is unaffected. <u>c^{cr}c^{cr}</u> : Both red and black pigments are diluted to pale cream. Skin and eye color are also diluted.
D	<u>D</u> <u>d</u>	<u>DD</u> or <u>Dd</u> : Horse shows a diluted body color to pinkish-red, yellowish-red, yellow or mouse gray and has dark points including dorsal stripe, shoulder stripe and leg barring. <u>dd</u> : Horse has undiluted coat color.
To	<u>To</u> <u>to</u>	<u>ToTo</u> or <u>Toto</u> : Horse is characterized by white spotting pattern known as tobiano. Legs are usually white. <u>toto</u> : No tobiano pattern present.

Conclusion

With colors from bright to dull and patterns from delicate to gaudy, domestic horses provide a fascinating variety of choices for both aesthetic and scientific appreciation, as well as a task for horse identifiers. An understanding of the effects of each of a series of coat color genes, as well as their combined results, is important for competent identification of horse coat colors. It is not necessary to be an expert at applying rules of genetics so that outcomes of matings can be predicted, but the major distinguishing features of each of the various coat color genes should be clearly understood. Familiarity by horse identifiers with horse coat color genetics should ultimately result in clearly defined and consistent identification of horse coat colors (Table 2). ■

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Fox colour in Przewalskii horses (*Equus przewalskii*)

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 National Foundation for Research in
 Zoological Gardens,
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I. Fox colour in captive-born generations

COLOUR	GENERATION												Total
	0	1	2	3	4	5	6	7	8	9	10	11	
ff	28	34	30	32	19	36	91	195	327	483	317	86	1736
ff?	0	0	0	2	1	0	1	1	8	11	4	3	31
Total	28	34	34	36	20	48	99	208	347	500	325	89	1768

II. Mating combinations that resulted in fox-coloured offspring.

SIRE	DAM										
	0072	0082	0119	0189	0247	0344	0372	0386	0506	0529	0530
0081	0	1	0	0	0	0	0	0	0	0	0
0118	0	0	1	0	0	0	0	0	0	0	0
0120	1	0	0	0	0	0	0	0	0	0	0
0185	0	0	0	0	1	0	0	0	0	0	0
0187	0	0	0	1	0	0	0	0	0	0	0
0281	0	0	0	0	0	0	2	0	0	0	0
0293	0	0	0	0	0	0	0	0	0	2	0
0314	0	0	0	0	0	0	0	1	0	0	0
0466	0	0	0	0	0	0	0	0	0	0	0
0499	0	0	0	0	0	0	0	1	1	0	0
0517	0	0	0	0	0	0	0	0	0	0	1
0519	0	0	0	0	0	0	0	0	0	0	0
0523	0	0	0	0	0	2	0	0	0	0	0
0571	0	0	0	0	0	0	0	0	0	0	0
0584	0	0	0	0	0	0	0	0	0	0	0
0689	0	0	0	0	0	1	0	0	0	0	0
0739	0	0	0	0	0	0	0	0	0	0	0
1153	0	0	0	0	0	0	0	0	0	0	0
Total	1	1	1	1	1	3	2	2	1	2	1

DAM

SIRE	0540	0554	0576	0578	0582	0629	0838	0847	0864	1020	1060
0081	0	0	0	0	0	0	0	0	0	0	0
0118	0	0	0	0	0	0	0	0	0	0	0
0120	0	0	0	0	0	0	0	0	0	0	0
0185	0	0	0	0	0	0	0	0	0	0	0
0187	0	0	0	0	0	0	0	0	0	0	0
0281	0	0	0	0	0	0	0	0	1	0	1
0293	0	0	0	0	0	0	0	0	0	0	0
0314	0	0	0	0	0	0	0	0	0	0	0
0466	0	0	0	0	0	0	0	0	0	1	0
0499	0	0	0	0	0	1	0	0	0	0	0
0517	0	0	0	0	1	0	0	0	0	0	0
0519	2	0	0	0	0	0	0	0	0	0	0
0523	0	0	3	0	0	0	0	0	0	0	0
0571	0	1	0	0	0	0	0	0	0	0	0
0584	0	0	0	1	0	0	0	1	0	0	0
0689	0	0	0	0	0	0	0	0	0	0	0
0739	0	0	0	0	0	0	1	0	0	0	0
1153	0	0	1	0	0	0	0	0	0	0	0
Total	2	1	4	1	1	1	1	1	1	1	1

SIRE	1246	DAM Total
0081	0	1
0118	0	1
0120	0	1
0185	0	1
0187	0	1
0281	1	5
0293	0	2
0314	0	1
0466	0	1
0499	0	3
0517	0	2
0519	0	2
0523	0	5
0571	0	1
0584	0	2
0689	0	1
0739	0	1
1153	0	1
Total	1	32

III. Distribution of fox/non-fox offspring over both sexes in matings that produced fox coloured offspring.

Current selection: (sire="0081") and (dam="0082")

COLOR	SEX		Total
	F	M	
	0	1	1
ff	1	0	1
wf	0	1	1
Total	1	2	3

Current selection: (sire="0118") and (dam="0119")

COLOR	SEX		Total
	F	M	
	1	1	2
ff	0	1	1
wf	0	1	1
Total	1	3	4

Current selection: (sire="0120") and (dam="0072")

COLOR	SEX		Total
	F	M	
ff	1		1
Total	1		1

Current selection: (sire="0185") and (dam="0247")

COLOR	SEX		Total
	F	M	
	2	6	8
ff	0	1	1
Total	2	7	9

Current selection: (sire="0187") and (dam="0189")

COLOR	SEX		Total
	F	M	
	3	2	5
ff	0	1	1
Total	3	3	6

Current selection: (sire="0281") and (dam="0372")

COLOR	SEX		Total
	M		
	1		1
ff	2		2
wf	1		1
Total	4		4

Current selection: (sire="0281") and (dam="0864")

COLOR	SEX		Total
	F	M	
ff	0	1	1
wf;ataxia?	1	0	1
Total	1	1	2

Current selection: (sire="0281") and (dam="1246")

COLOR	SEX		Total
	F	M	
	1	0	1
ff	0	1	1
Total	1	1	2

Current selection: (sire="0293") and (dam="0529")

COLOR	SEX		Total
	F	M	
	3	3	6
ff	1	1	2
Total	4	4	8

Current selection: (sire="0314") and (dam="0386")

COLOR	SEX		Total
	F	M	
	1	0	1
ff	0	1	1
Total	1	1	2

Current selection: (sire="0466") and (dam="1020")

COLOR	SEX		Total
	F	M	
	1	2	3
ff	0	1	1
Total	1	3	4

Current selection: (sire="0499") and (dam="0386")

COLOR	SEX		Total
	F	M	
	6	4	10
ff	1	0	1
Total	7	4	11

Current selection: (sire="0499") and (dam="0506")

COLOR	SEX		Total
	F	M	
	5	5	10
ff	0	1	1
Total	5	6	11

Current selection: (sire="0499") and (dam="0629")

COLOR	SEX		Total
	F	M	
	4	1	5
ff	1	0	1
Total	5	1	6

Current selection: (sire="0517") and (dam="0530")

COLOR	SEX		Total
	F	M	
	5	2	7
ff	0	1	1
wf	1	0	1
Total	6	3	9

Current selection: (sire="0517") and (dam="0582")

COLOR	SEX		Total
	F	M	
	2	5	7
ff	0	1	1
Total	2	6	8

Current selection: (sire="0519") and (dam="0540")

COLOR	SEX		Total
	F	M	
	0	2	2
ff	1	1	2
Total	1	3	4

Current selection: (sire="0523") and (dam="0344")

COLOR	SEX		Total
	F	M	
	2	4	6
ff	1	1	2
Total	3	5	8

Current selection: (sire="0523") and (dam="0576")

COLOR	SEX		Total
	F	M	
	1	3	4
ff	0	3	3
Total	1	6	7

Current selection: (sire="0571") and (dam="0554")

COLOR	SEX		Total
	F	M	
	3		3
ff?	1		1
Total	4		4

Current selection: (sire="0584") and (dam="0578")

COLOR	SEX		Total
	F	M	
ff	2	1	3
	0	1	1
Total	2	2	4

Current selection: (sire="0584") and (dam="0847")

COLOR	SEX		Total
	F	M	
ff	3		3
	1		1
Total	4		4

Current selection: (sire="0689") and (dam="0344")

COLOR	SEX		Total
	M		
ff	1		1
Total	1		1

Current selection: (sire="0739") and (dam="0838")

COLOR	SEX		Total
	F	M	
ff	1	1	2
	1	0	1
Total	2	1	3

Current selection: (sire="1153") and (dam="0576")

COLOR	SEX		Total
	M		
ff	1		1
Total	1		1

V. Expected frequencies of fox-coloured offspring per generation.

Assumption: Fox-colour is single-locus recessive trait that occurred in the wild population of Przewalskii horses (*Equus przewalskii*).

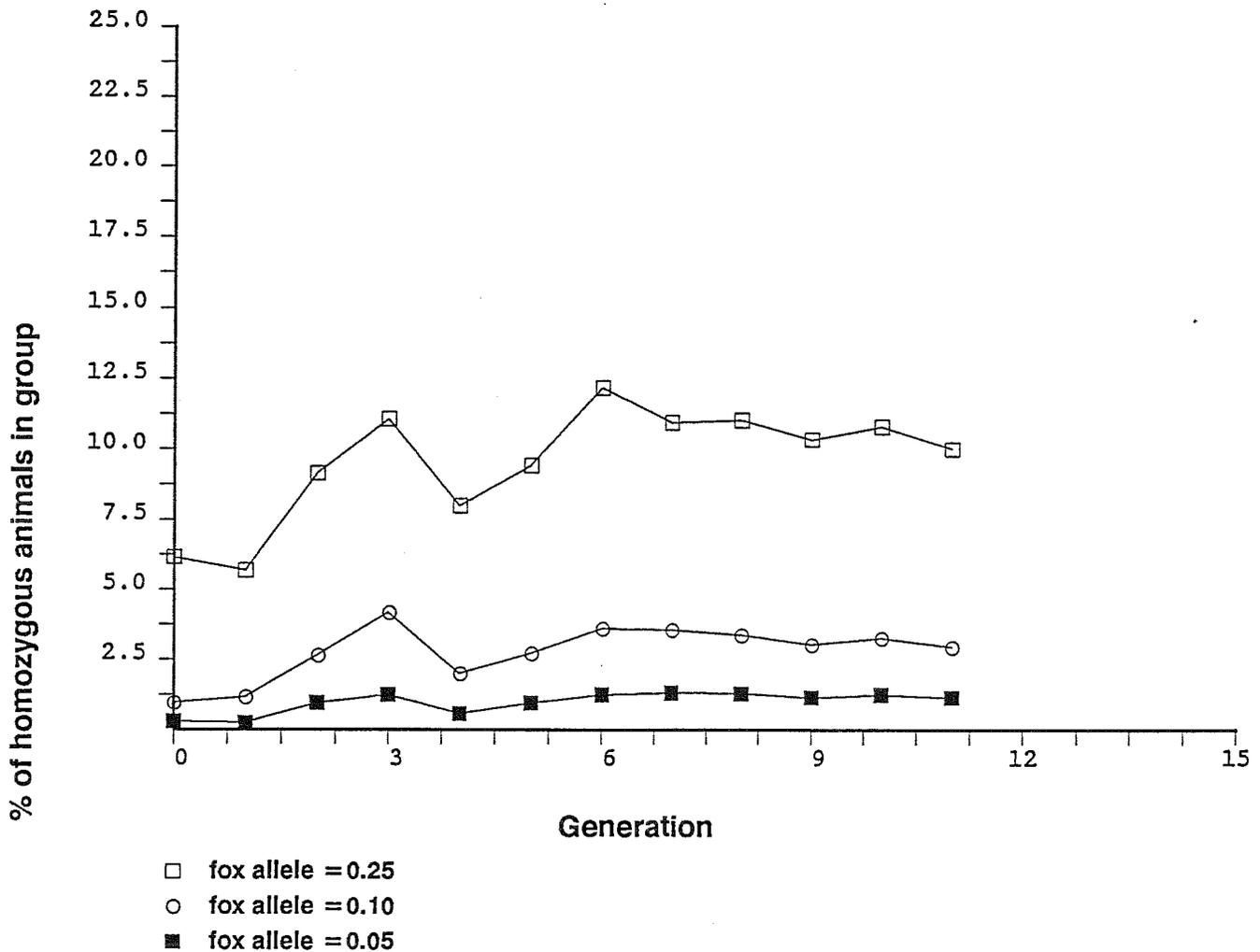
Simulations: GeneFlow simulation program, 250 iterations, one locus, 2 allelic variants: fox and non-fox.

Genotypes of founders assigned according Monte Carlo simulations, based on initial frequencies of the fox-allele of 0.25, 0.10 and 0.05 the in source population, respectively. Genotypes of captive-born are based on Mendelian segregation.

Each iteration the number of animals, homozygous for the fox-allele, in generation groups is determined. Finally the average number of 'fox-coloured' animals per generation group, and the variance over all iterations is calculated.

Percentage of fox coloured animals per generation

different initial frequencies in wild

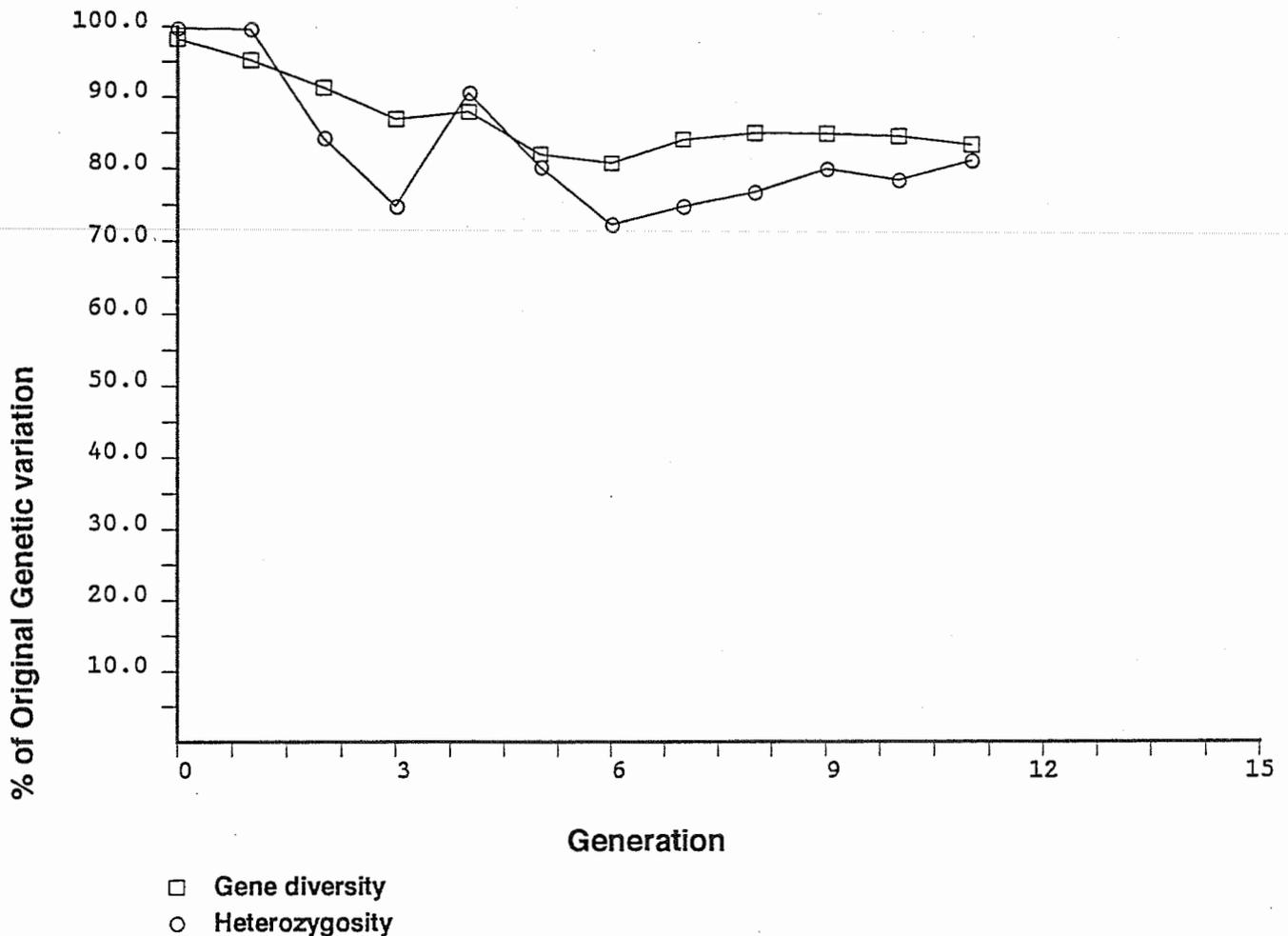


VI. Genetic variation per generation group in the captive population.

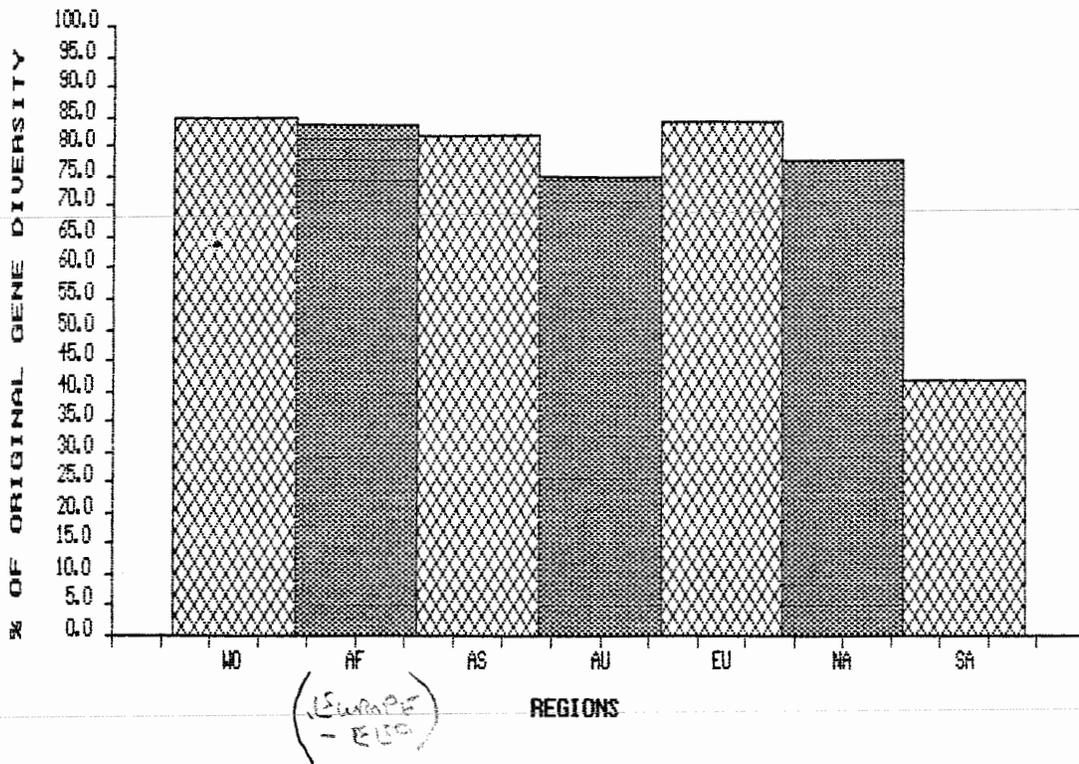
Simulations: GeneFlow simulation program, 50 iterations, 25 loci with each five equally distributed (i.e. in source population) allelic variants. Proportion of heterozygotes (or heterozygosity) and gene diversity are determined each iteration in generation groups and the current (sub-)populations. Finally the averages and variances per group are calculated.

Genetic variation per generation.

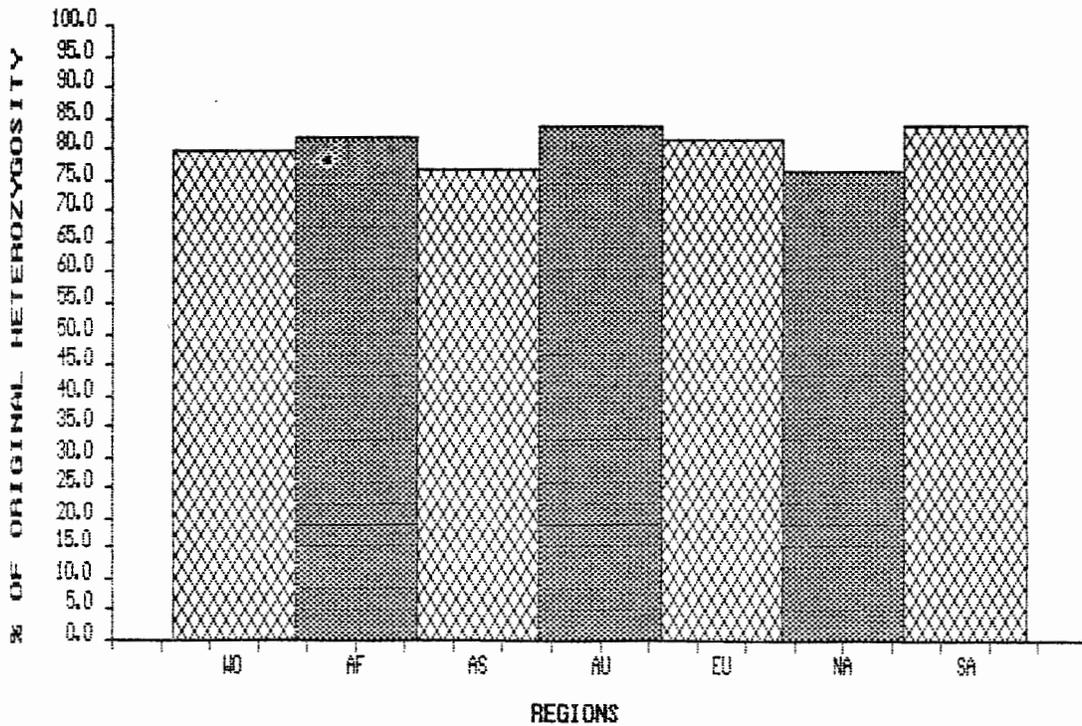
in Przewalskii horses



GENE DIVERSITY IN REGIONAL POPULATIONS OF EQUUS PRZEWAŁSKII



HETEROZYGOSITY IN REGIONAL POPULATIONS OF EQUUS PRZEWAŁSKII



BEMERKUNGEN ZUM ERSCHEINUNGSBILD VON EQUUS PRZEWALSKII, POLJAKOV, 1881
DAS ZUCHTZIEL DES EEP

REMARKS ON THE PHENOTYPE OF EQUUS PRZEWALSKII, POLJAKOV, 1881
THE BREEDING GOAL OF THE EEP

Poljakov, J.S. 1881: in: Ann.nat. Hist., Ser. 5 Vol VIII, p. 23-24

Supposed new Species of Horse from Central Asia

Our specimen of *Equus Przewalskii* is about three years of age; in size it is no bigger than the kulan and djiggetai; its head is nearly of the same length as that of those animals, but lower, and better shaped near the end of the muzzle and nasal bones, with shorter ears than those of the wild ass. Its size is decidedly small in proportion to its head. In shape it takes after the horse; its legs are relatively thick for the size of its body, its hoofs rounder and broader, and its tail better furnished with hair, than in the case of the wild ass. Its colour is dun, with a yellowish tinge on the back, becoming lighter towards the flanks, and almost white under the belly. Its hair is long and wavy, brick-red on the head and nasal bones, of the same colour but longer on the cheeks and about the lower jaw. The extremity of the nose is covered with almost white hairs, a remarkable contrast to the brick-red on the upper part of the head. A short upright (hogged) mane extends from between the ears to the withers, of a dark brown colour, with long yellowish hairs on the margins. It has no stripe of the same colour as the mane along the back, as all Asiatic asses and dun horses have, and a hardly perceptible one along the pelvis. The upper half of the tail is of the same colour as the back; it is longer, thicker at the root, and more bushy than that of any kind of ass; halfway down the tail yellowish hairs are mixed with the brown; and the extremity is dark brown or nearly black. The fore legs are brown near the hoofs and on the knees; and oblique indistinct bars of brown hair extend down the legs. The prevailing colour of the lower parts of the fore legs is brown, a peculiarity never known to occur with wild asses, these having only a narrow barely distinguishable brown margin round the upper rim of the hoof. Dark hairs also occur on the hind legs about the hoofs and much higher.

translated by Mr. E. Delmar Morgan

Mohr, E. 1967: in Equus, 1 (2), p. 350-396. Bemerkungen zum Erscheinungsbild von Equus przewalskii, Poljakov 1881

Remarks on the phenotype of Equus przewalskii, Poljakov 1881

Whether all imported foals were really lacking domestic horse blood is difficult to prove, but hardly taken for granted. Not without good reasons reports haunts people's minds from the beginning up to date that there existed crosses between pure wild bred and domestic mongolian horses in the wild.

At the second Przewalski-Symposium in Berlin-Friedrichsfelde BANNIKOV being consulted answered analogously: ' Especially in the northern habitat of the Przewalski horse crosses with domestic horses took place in the way that wild animals were captured and bred with the domestic ones. As the Characteristics of the wild animals remained well in the offspring it is quite possible, that such hybrids were mixed under the animals that were transported to Europe. The native people exactly knew the value of the wild horses. He (Bannikov) himself had talked with such an old man who thought that not all foals sent away, were pure-bred ones'.

The diversity and variety of the imports give reasons for the suspicion that not all foals were free of domestic horse blood. Therefore the offspring of the imported animals cannot be regarded as totally pure-bred or in every respect as ideal. Against this tell also the photos existing of those animals. On the other hand we cannot defame any breeding line based on these imports.

In Hellabrunn a lot of horses with "Pascha"-blood (Ask A) were born. It seems that the breeder finally became suspicious about this ancestor. From 1955 on, systematically all horses with "Pascha"-blood were sent away (with 1 exception), mostly to America.

Also the rest of the horses sent from Old-Askania Nova to Germany could not convince. Antonius (1928, 1935) declared his stallion Nr. 188 in Schönbrunn not to be free of domestic horse blood and another one he saw in Alfeld (Ruhe) for a hybrid.

The stallion 191 As, who was sent from Askania Nova to Warszawa was too big, had a broad brushy tail, mostly a hanging mane, a very broad shoulder stripe, nearly none meal-nose, well developed muscles, but no preferences.

Up to 1942 there might have been bred good Przewalski horses in Askania Nova. At least for the horses that have been exported to Poland and Germany considerable doubts are legitimate regarding their pure-breed.

The most important characteristics for the judgement of the phenotype are today mane and forelock conditions, the tail with the short hairs in the upper part, colour distribution at belly and nose, dorsal stripe, shoulder stripe and stripes at the legs.

(translated)

The Prjevalsky horse is about the same size as a small domestic horse. The adult stallion stands about 124 cm at the croup; and the length of his trunk is 127 cm. By his general conformation and in the respective proportions of certain parts of the body, he reminds one very much of the wild ass (*E. hemionus* Pall.) and of its variety, the kiang (*E. hemionus* Pall. var. kiang, Moorkroft); but the Prjevalsky horse has a relatively larger head than the wild ass. The proportion of the length of the head to that of the body is as 1:2.21. In the onager the proportion is as 1:2.29; and in the kiang as 1:2.25. As regards the shape of the head, the Prjevalsky horse closely resembles the onager and the kiang: a fact already referred to by Poliakov, who added, however, that the head "is not so high and is more slender at the end of the muzzle and in the region of the bones of the nose." I can confirm the statement that the head of the Prjewalsky horse is very like that of the onager and kiang; but I can obtain no proof that the end of the muzzle and the region of the nasal bones are more slender than in the Asiatic ass. The craniometrical observations which I made revealed no difference.

The colour of the hair of the winter coat is lighter than that of the summer one. Poliakov correctly described the former as yellowish on the back, lighter over the sides and almost white on the under part of the body. The summer coat is much shorter than the winter one, and it is smooth and not curly. The hair is about as long as that of the onager and the kiang, which it further resembles in colour. The colour of the back is a light reddish-brown. This shade extends over the sides and gradually merges into the yellowish-white of the under part of the body; so that there is no sharp line of demarcation between the back and the flank, and between the flank and the belly. The head is of the same colour as the back, except that the lips and the end of the muzzle in the region of the nostrils are white. Between the nostrils the white colour changes into grey. Behind the mane the dorsal stripe extends along the entire back, in the form of a narrow (about 5 mm, broad), reddish-brown (darker than the hair of the back), straight band which, like the dorsal stripe of the onager and the kiang, is continued on to the tail.

Another interesting feature in the Prjevalsky horse is the transverse shoulder stripe, which is in exactly the same position as that of the domestic ass and its ancestor, the African wild ass. It is not nearly so well marked as it is in the ass. The legs of *E. przewalskii* are entirely different in colour from those of the Asiatic ass; inasmuch as, in the latter animal, the lower part of the limbs down to the hoofs is always of a light colour, whereas in the Prjewalski horse the colour is more or less black, according to the age and individual peculiarities of the animal. In adult animals a black ring extends some 80 mm above the hoof. From this to the fetlock, the outer side of the limb is covered with black hairs; but, on the inner side, the hair is grey with transverse bands, which are present as far up as the knee. In a summer coat they are generally very pronounced, although they may vary considerably in number and arrangement. They do not constitute complete half-rings, but are in the form of two stripes interrupted on the inner side of the limb

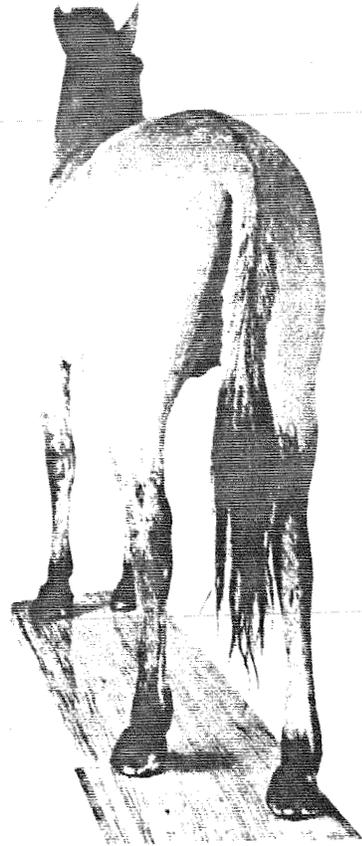
Mohr, E. 1967: in Equus, 1 (2), p. 350-396. Bemerkungen zum Erscheinungsbild von Equus przewalskii, Poljakov 1881

(Remarks on the phenotype of *Equus przewalskii*, Poljakov 1881)

Among all imports of Przewalski foals we found two extreme colour-types; the Englishman calls them "dun" or "bay". Przewalski foals can be as light as sandy-yellow onagers.

Especially in the bay animals characteristics like the "Schwalbenbauch" (swallow-belly) and "Mehlnase" (meal-nose) are conspicuous. Colour paintings in the "Grotto of Lascaux" and others show as well the "Schwalbenbauch" as also the "Mehlnase".

In case the "Mehlnase" is lacking in adult animals, these horses should be suspected not to be free of domestic horse blood. (translated)





Mohr, E. 1967: in Equus, 1 (2), p. 350-396. Bemerkungen zum Erscheinungsbild von Equus przewalskii, Poljakov 1881

(Remarks on the phenotype of Equus przewalskii, Poljakov 1881)

To Askania Nova a very mixed group was imported. The horses that existed there at that time were very non-uniform. Beside few typical animals with all characteristics of the species there were also very dark coloured horses without a meal-nose or only with a slight indication for it.

Disappointing were all the horses that came to Germany or Poland: the outer appearance sheer invites criticism in regard to their pure breed.

In case the meal-nose is lacking in adult animals, these horses should be suspected not to be free of domestic horse blood.

(translated)

The EEP-Commission has decided:

NOT TO BREED WITH STALLIONS, LACKING THE MEAL-NOSE

Picture below: On the left side you see a hybrid between a Tarpan and a Przewalski horse





Mohr, E. 1967: in Equus, 1 (2), p. 350-396. Bemerkungen zum Erscheinungsbild von Equus przewalskii, Poljakov 1881

(Remarks on the phenotype of Equus przewalskii, Poljakov 1881)

Another son of Pascha (187 Ask. A) and the typical female 224 Sidney had a white star, it was 141 Hell. 14 Carlo.

(The other son of Pascha and the female 189 Ask. C Bella was the fox-coloured horse 199 Berlin 3)

By the way, the stallion Nr. 123 who was bred in Washington had a so called "Glasauge" (a lightened iris).

(translated)

Today more and more Przewalski horses are born, who have white markings or lightened iris'.

The EEP-commission decided:

1. Not to breed with horses that have eyes with a lightened iris.
2. Not to breed with stallions that have white stars or other white markings.
3. In the case a foal is born with the above mentioned aberations the parents should no longer breed together but they should be mated to another partner.

Salensky, W. 1907: Prjevalsky's Horse. Hurst and Blacket Ltd.,
London, p. 8-10

The neck is short and broad. It is shorter than the head, to which it bears the proportion of 1:1,12. Measurements show that the proportion of the length of the neck (from the occipital crest to the withers) to its breadth, at the widest part, is as 1:1,06.

The mane, by its length, reminds one of the Asiatic wild ass. As previously stated by Poliakov, it is not very long; begins between the ears, and extends to the withers. Its anterior and posterior portions are short; but about the middle it has a length of from 16 to 20 cm. In his description of a dead Prjevalsky stallion, Grum-Grjimalo states that the mane hangs down on the left side of the neck; but Poliakov describes it as being erect. This apparent contradiction can be explained by the difference in the age of the specimens examined by the two writers. Poliakov's description applies to an animal eighteen months old; whereas Grum-Grjimalo described a ten-year-old stallion. The mane stands erect in all the specimens of different ages in the Zoological Museum; and in no single case does it hang down. In the photograph of an animal described by Grum-Grjimalo - an eighteen months old male - the mane is erect. The forelock of the Prjevalsky horse is about as little developed as it is in the onager and the kiang.

The tail is an extremely interesting feature of the Prjewalsky horse. It is quite peculiar, and resembles neither the tail of the onager nor that of the domestic horse, but is intermediate in form. It differs from that of the onager in that it is not sharply divided into two portions - a proximal part provided with tufts of short hair, and a distal portion covered with long hairs. It differs from the tail of the domestic horse, in that, for a certain distance from the root, its dorsal surface is covered with short hairs. The short stiff hairs on the dorsal aspects of the root are arranged in the form of two converging streaks enclosing a less prominent area, along the center of which is a darker line forming a continuation of the dorsal stripe of the trunk. The hairs of the dorsal surface differ from the long hairs of the tail not only by their coarseness, but also in their colour. In summer they resemble the light-coloured hairs of the edge of the mane.

Horses that are seen on these pictures do neither come up to the species- nor to Salensky's description. On the first table it is clearly shown what Poliakov and Salensky have meant.

As the described erect manes only occur if these hairs are moulted annually (otherwise the mane-hairs grow, become too long and fall aside) it is not a simple characteristic of an outer appearance but also a physiological one that differentiates the wild horse clearly from a domestic one.

The EEP-Commission has decided:

NOT TO BREED WITH HORSES THAT NEVER CHANGE THEIR MANES AND HAVE
THEREFORE A PERMANENT HANGING MANE

THAT STALLIONS WITH TAILS RESEMBLING DOMESTIC HORSES ARE EXCLUDED
FROM BREEDING AS WELL



Mohr, E. 1967: in Equus, 1 (2), p. 394-395. Bemerkungen zum Erscheinungsbild von Equus przewalskii, Poljakov 1881

Remarks on the phenotype of Equus przewalskii, Poljakov 1881

Summary

The facts and considerations I mentionend in this paper have shown that probably not a single Pzrewalski horse living in captivity today can be considered as pure-bred. The same can be said for Przewalski horses who eventually live still in the wilderness. So it makes no sense to give an appreciation of the different lines. Under these circumstances I think that the first 3 points of the resolution of the 2 nd Przewalskhi horse Symposium are totally justified. They say:

1. The Symposium has shown that the phenotype of the Przewalski horse has a high variability, which extent should be studied in the future; this work should be supported.
2. It is too early to determine an obligatory standard, because the breeding base is too small. We should wait until the stock has at least doubled, so that at the next Symposium binding proposals can be made. In the meantime the breeders should work on this problem and keep in contact.
3. Up to this day we should breed with all mares.

25 years have passed and two further international symposia. 1965 there existed 58,75 = 133 Przewalski horses. Today we will have appr. 900, 3 times as much as Dr. E. Mohr has asked for. It is now high time to make our decisions.

PRZEWALSKI HORSES LACKING BLACK PIGMENT AND THEIR PARENTS

Studbook number	Sex	Studbook name	House-name	Date of birth	Date of death	Father	Mother	Last Site
199	M	Berlin 3		17.04.1933	+	187 Askania A Pascha	189 Askania C Bella	1943 Schorfheide
123	M	Wash. 4		27.05.1937	21.01.1957	118 Phil 5	119 Phil. 6	27.05.1937 Washington
74	F	Praha 7	Lucka	01.07.1941	06.09.1964	120 Wash. 1 Horymir	72 Praha 5 Helus	01.07.1941 Praha
184	F	London 8	Ulanova	19.05.1956	21.10.1959	81 Praha 14 Divoch	82 Praha 15 Pusina	19.05.1956 Whipsnade
350	M	London 12	Alpha	24.04.1966	14.10.1982	185 London 9 Tzar	247 Praha 38 Luna	11.07.1968 Colwyn Bay
521	M	Paris 11	Palefroi	16.05.1972	05.06.1987	281 Paris 5 Pacifique	372 Praha 82 Myra	02.07.1973 Thot à Thonac
621	M	Paris 14	Paradis	21.05.1975	15.03.1986	281 Paris 5 Pacifique	372 Praha 82 Myra	28.01.1980 Barcelona
630	M	Howletts 13	Nwr	14.06.1975	17.11.1977	314 Praha 63 Vampir	386 Praha 86 Helga	14.06.1975 Bekesbourne
801	F	Bern 3	Lena	17.03.1977		519 Praha 109 Cyclon	540 Praha 111 Donna	22.10.1981 Habana
884	M	Marwell 44	Bala	30.04.1980		293 Catskill 17 Basil	529 Marwell 6 Lenka	10.03.1981 Tokyo
950	M	Arnhem 10	Djenghis	18.04.1981	28.11.1986	523 Praha 110 Ceylon	576 Arnhem 1 Diane	25.11.1986 TiHo Hannover
955	M	Bern 6	Walo	24.04.1981	14.04.1985	519 Praha 109 Cyclon	540 Praha 111 Donna	25.07.1983 Hohenstadt
1045	M	Marwell 59	Bataar	08.05.1982		293 Catskill 17 Basil	529 Marwell 6 Lenka	17.02.1983 Jersey
1099	M	Howletts 41		17.06.1982	02.07.1987	499 Howletts 2 Ulan	506 Howletts 3 Altai	17.06.1982 Bekesbourne

PRZEWALSKI HORSES LACKING BLACK PIGMENT AND THEIR PARENTS

- 2 -

Studbook number	Sex	Studbook name	House-name	Date of birth	Date of death	Father	Mother	Last Site
1078	M	London 72	Mikhail	14.07.1982	24.07.1986	517 Marwell 3 Haldo	530 London 24 Vashka	21.04.1983 Colwyn Bay
1100	F	Howletts 42		14.07.1982		739 Nürnberg 15 Melchior	838 Howletts 26 Vilan	14.07.1982 Bekesbourne
1183	F	Howletts 49		10.09.1983		499 Howletts 2 Ulan	386 Praha 86 Helga	10.09.1983 Bekesbourne
1191	F	Arnhem 15	Velma	04.02.1984	13.07.1984	523 Praha 110 Ceylon	344 Praha 75 Vela	04.02.1984 Arnhem
1225	M	Arnhem 16	Dimitri	14.05.1984	11.03.1986	523 Praha 110 Ceylon	576 Arnhem 1 Diane	14.05.1984 Arnhem
1230	M	London 79	Brezhnev	16.05.1984	05.07.1985	517 Marwell 3 Haldo	582 London 27 Mirakova	16.05.1984 Whipsnade
1269	F	Howletts 56		11.07.1984		499 Howletts 2 Ulan	629 Howletts 12 Shilka	11.07.1984 Bekesbourne
1299	M	Helsinki 2	Buster	20.12.1984	27.09.1988	584 Marwell 15 Hal	578 Marwell 14 Bella	20.12.1984 Helsinki
1309	M	Arnhem 17	Vasco	28.02.1985	30.09.1985	523 Praha 110 Ceylon	344 Praha 75 Vela	28.02.1985 Arnhem
1330	M	Arnhem 18	Dirk	09.05.1985	11.03.1986	523 Praha 110 Ceylon	576 Arnhem 1 Diane	09.05.1985 Arnhem
1526	M	Paris 31	Octroi	26.03.1986		466 Paris 8 Paturin	1020 Paris 20 Octavie	26.03.1986 Montpellier
1521	M	Paris 27	Palichon	09.04.1986		281 Paris 5 Pacifique	864 Paris 18 Octa	28.09.1986 Pardaillan
1534	F	Helsinki 6	Equus	19.02.1987		584 Marwell 15 Hal	847 London 52 Anulka	19.02.1987 Helsinki
1552	M	Arnhem 21	Vedor	03.05.1987	28.08.1987	689 London 36 Krasnik	344 Praha 75 Vela	03.05.1987 Arnhem

PRZEWALSKI HORSES LACKING BLACK PIGMENT AND THEIR PARENTS

- 3 -

Studbook number	Sex	Studbook name	House-name	Date of birth	Date of death	Father	Mother	Last Site
1576	F	Paris 29	Palote	16.05.1987		281 Paris 5 Pacifique	1060 Paris 21 Pantecote	06.09.1988 Pardailan
	M	Arnhem 24		07.05.1988	09.06.1988	1153 Köln 13 Nathan	576 Arnhem 1 Diane	07.05.1988 Arnhem
	M	Paris 35		13.05.1988	15.09.1988	281 Paris 5 Pacifique	1246 Paris 24 Paciflore	13.05.1988 Paris
	M	Ooij 1	Usch	22.01.1989		1278 Nikolaev 3 Vagur	1314 Lelystadt 2 Nyam	22.01.1989 Lelystadt
	F	Arnhem 26		11.05.1989	24.05.1989	1153 Köln 13 Nathan	576 Arnhem 1 Diane	11.05.1989 Arnhem
	M	Krakow 3	Koral	17.06.1989		1026 Warszawa 17 Step	672 Warszawa 6 Lawenda	17.06.1989 Krakow
	M	Ooij 5	Ocin	1989		1278 Nikolaev 3 Vagur	1462 Norderheide 4 Argun	1989 de Ooij
		Tallinn		1989		636 Askania 25 Graver	953 Tallinn 2 Milly	1989 Tallinn

Further horses lacking black pigment were born in Bekesbourne Lymphe and Askania Nova, still unidentified

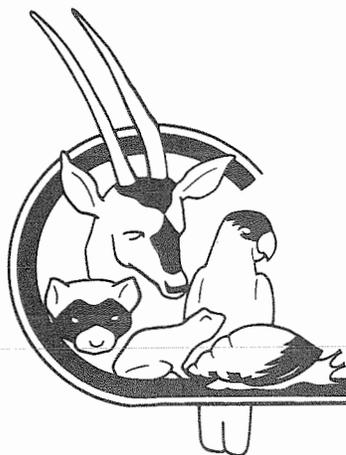
PRZEWALSKI'S HORSE

Equus przewalskii

**GLOBAL CONSERVATION PLAN
D R A F T**

**APPENDIX I:
THE SAN DIEGO DRAFT PLAN TECHNICAL SESSION**

10 February 1990



Captive Breeding Specialist Group

Species Survival Commission
International Union for the Conservation of Nature and Natural Resources

U. S. Seal, CBSG Chairman

October 23, 1989

Dr. Thomas Foose
Conservation Coordinator AAZPA
Minnesota Zoo
12101 Johnny Cake Road
Apple Valley, Minnesota 55124

Dear Dr. Foose,

In preparation for the Fifth International Symposium on the Preservation of the Przewalski's Horse to be held 19-23 May 1990, in Leipzig, German Democratic Republic, the Captive Breeding Specialist Group (CBSG) of SSC/IUCN is organizing a technical working group to produce a detailed genetic and demographic analysis of the studbook population and prepare a report for attendees to the International Symposium. Participants in the technical working group will include experts from the CBSG, the Species Survival Plan in North America, the Europäisches Erhaltungszucht Program, representatives from Great Britain and the Soviet Union, the International Studbookkeeper, and academic scientists. It is intended that the technical working group will both produce a set of recommendations for a Global Management Plan that will preserve the gene pool resources of the captive population and also plan the production of Przewalski's horses with appropriate genetic background for reintroduction programs.

The recommendations will be distributed in advance to those persons planning to attend the Fifth International Symposium in Leipzig and considered at the Leipzig meeting. The zoological institutions that have propagated the species and prevented its total extinction can in

this way take the next step necessary to meet their declared goal of reestablishing the species in nature, simultaneously assuring its long term existence and the preservation of the species gene pool through a managed captive population.

The technical working group will meet December 9-11, 1989 in at the San Diego Zoo, San Diego, California. The meeting will convene at 1 p.m. on Saturday, December 9. Please RSVP to CBSG, and send a copy to Ollie Ryder, San Diego, who will make local arrangements.

CBSG: 612-431-9325 (phone); 612-432-2757 (fax).

Ryder: 619-557-3950 (phone); 619-231-0249 (fax).

I hope that you will be able to attend and contribute to this important meeting that the Zoological Society of San Diego will host.

Sincerely,



U. S. Seal
CBSG Chairman

LIST OF PARTICIPANTS:

Mr. Jonathan BALLOU
 Dr. Bert DE BOER
 Dr. Jim DOLAN
 Dr. Thomas J. FOOSE
 Mr. John KNOWLES
 Dr. Georgina MACE
 Dr. V. N. ORLOV
 Dr. Frank PRINCEE
 Dr. Oliver A. RYDER
 Dr. Ulysses S. SEAL, CBSG
 Dr. Elizabeth THOMPSON
 Dr. Jiri VOLF
 Dr. Waltraut ZIMMERMANN

TECHNICAL WORKING SESSION
San Diego, California
9-11 December, 1989

AGENDA

Saturday, December 9, 1989

- 13:00 Convene
Introductions
Remarks of Chairman, CBSG
Discussion of Agenda
Production of species management masterplans
Regional management plans
 SSP
 EEP
 USSR
Worldwide Population Analyses
 Demography
 Gene extinction
 Other analyses
Coat color variation in Przewalski's horse
Genetics of coat color in domestic horses
- Seal
group
Foose

Ryder
Zimmermann
Orlov

Foose
Thompson
Princeé
Zimmermann
Bowling
- 19:00 Dinner

Sunday, December 10, 1989

- 08:30 pick up from hotel
09:00 re-convene
Selection for phenotypic characters:
 costs and benefits
Genetic goals for world population
Demographic goals for world population
Planning for reintroduction
Interaction of regional management plans
 Coordination function
 Role of Studbook keeper
 Division of responsibility for analyses
Drafting a Global Management Plan Document
- group

19:00 Dinner

Monday, December 11, 1989

- 08:30 pick-up at hotel
09:00 re-convene
Production of Draft Global Management Plan,
 continued
Communicating to all Przewalski's horse owners
 the substance of the Global Management Plan
Additional preparations for Leipzig meeting
- group
- 14:00 adjourn



Captive Breeding Specialist Group

Species Survival Commission
International Union for the Conservation of Nature and Natural Resources

U. S. Seal, CBSG Chairman

MINUTES

PRZEWALSKI'S HORSE GLOBAL MASTERPLAN MEETING

SAN DIEGO ZOO - 9-10 DECEMBER 1989

SATURDAY - 9 DECEMBER

ATTENDANCE: Ulie Seal, Ollie Ryder, Waltraut Zimmermann, V.N. Orlov, Elizabeth Thompson, Ann Bowling, Frank Princee, Nick Reindl, Tom Foose

- RYDER** Introductions. Distributes various handouts; SSP Plans/EEP Plans/Foose-Rockwell Analyses/Zimmermann Compilations and Statements.
- SEAL** States captive program must be to restore species to wild. Need plan when get to Leipzig. A document.
- FOOSE** Presents slide show for overview and orientation of masterplan formulation process. Emphasizes on a holistic strategy that will incorporate captive and wild programs. Ultimate goal of captive propagation should be to support survival of species in natural habitat by reinforcing or restoring populations in the wild. Conservation strategies need to be formulated in terms of viable populations, i.e., consideration of the stochastic problems (environmental, demographic, and genetic) that endanger small populations. Discusses need and benefits of a metapopulation strategy, i.e. interactive management of multiple wild and captive populations. Also advocates a masterplan for the restoration to the wild. Even if reintroductions must be to some extent opportunistic, they should still be evaluated and developed as part of a strategic framework based on principles of population viability and conservation

Minutes

2

biology. Reviews genetic and demographic objectives and management being employed in North American SSP. States need to ultimately decide how regional programs (SSP and EEP) are going to interact to optimize benefits to the species.

RYDER Discusses concordance of databases. FOOSE explains and distributes database used.

SEAL Observes about 500 horses adequate to retain 95% of existing diversity. Are about 900 horses in captivity. So excess of 400 horses to immediately reintroduce. Seal suggests. Seal proposes goal statement: Re-establish Asian wild horse in the wild as a free ranging species with the potential for evolution by adaptation and selection by the year 2000. Also encourages everyone to express views as part of interactive process.

FOOSE Not all 900 in managed program. But at least 500 are.

RYDER Priority has been to insure captive population secure

ZIMMERMANN Do we know how many are healthy?

BOWLING Inquires if 10%/year is healthy increase. Observes other horse populations may increase at up to 20%/year.

PRINCEE What about Baumans semireserves.

SEAL Baumans not part of captive horse community.

RYDER Also observes for formulation of strategy involving wild as well as captive, there are others that need to be involved, e.g. Patrick Duncan, Mark Stanley-Price.

In terms of SSP, refers to Masterplan. Accentuates point that two separate populations in captivity: I.e., with and without domestic mare.

ZIMMERMANN Discusses EEP plan. Husbandry an early problem within EEP. Domestic horse traits and fox color also problems. Many of most valuable stallions infertile. Ataxia problems. Describes selection decisions of EEP. Reports on semireserve opportunity to permit more natural behavior of problem. Goals to minimize inbreeding; by replacing stallions.

RYDER Some questions: In current state of EEP what are goals and objectives and how going to achieve them.

ZIMMERMANN First, to have a healthy population. Secondly to minimize inbreeding. Thirdly to select against aberrant phenotypes, i.e. fox color and where phenotype of domestic mare visible. Selection is various cautious so as not to impair representation of founder lineages. Selection against domestic mare is entirely in terms of phenotypic traits not founder representation of domestic.

RYDER Who decides if phenotype is to be selected against.

FOOSE Are there any cases where an animal is not descended from domestic that has manifested traits that are considered "domestic" and undesirable.

ZIMMERMANN Yes. Also selecting against black nose. Infertile males are pure (non-domestic line) and have high inbreeding coefficients.

THOMPSON How much is known about genetics of these "undesirable" traits?

ZIMMERMANN Don't know. Does describe some of history. Shortest mane is from domestic line.

THOMPSON If going to select, would be useful to know something about the genetics of inheritance of these traits.

SEAL Seems to be a fundamental issue of correlation between phenotype and genotype. Is there a genetic basis for the traits. Also effect on diversity of selecting against phenotype.

SEAL Invites Dr. Orlov to comment on Przewalski's horse programs in the USSR, especially the reintroduction plans.

ORLOV Requests postponement of comments until a little later so he can organize thoughts in English better.

MACE (Via written statement) U.K. committed to maximal preservation of diversity, not disposed toward selection until or unless extreme phenotypic abnormalities appear.

FOOSE Explains set of analyses distributed. Demography: World population increasing at rate of about 10%/year; generation time about 12 years. Genetics: Gene drop analyses indicating founder genomes surviving and target founder values; average relatedness as a measure of genetic importance.

THOMPSON Explains analyses of founder allele survival and genetic importance. Are appreciable non-dom genes in dom-descended horses. Should analyze various groups, e.g. animals approaching demographic senescence, for their genetic importance.

Results summarized in table below (Refer also to attached papers by Thompson).

	Populations			
	World	Non-Dom.	World	N.A. Non-Dom.N.A.
All Alleles	10.48	7.30	9.13	6.64
Non-Domestic Alleles	9.91	7.30	8.67	6.64
Non-Dom. Alleles In Pop. With Dom. Influence	2.61 (i.e., 9.91 - 7.30)		2.04 (i.e., 8.67 - 6.64)	
Origins of These Alleles				
Founders 11 & 12		1.55	1.27	
Other Founders		1.06	0.77	
Non-Dom. Alleles in World Pop. Not in N.A.	1.24 (9.91-8.67)			
Non-Dom. Alleles in Non-Dom. World Pop. Not in Non-Dom. N.A.	0.76 (7.30-6.64)			

FOOSE Presents Lacy's observations that parents always more genetically important than their offspring.

PRINCEE Presents analyses.

ZIMMERMANN Presents slide show of phenotypic variation in horses living and dead.

BOWLING Discusses genetics of coat color in domestic horses. E gene: dominant permits production of black pigment. A gene: dominant causes black to be punctuated (i.e., bay). D gene: Dominant dilutes color (dun). C gene: Dominant dilutes color (palomino); behaves as an incomplete dominant.

Subsequently presents a written statement on coat color in Przewalski's horse:

"The genetic basis of coat color in the Przewalski's horse has never been explicitly demonstrated. We may make working assumptions based on homologies, recognized among other mammals, that color variants in the Przewalski's horse can be explained using loci identified in the closely related domestic horse.

The most commonly encountered color for Przewalski's horse is that of yellowish red body hair with black hair distributed in a points pattern (lower legs, mane, tail) of variable extent, often accompanied by a dark stripe along the dorsal midline, transverse stripe at the withers and bars of striping on the legs at and above the knees and hocks. This color in domestic horses and Przewalski's horse is traditionally called dun. An occasional individual is "fox" colored, lacking black pigment but still retaining the points and striping pattern in red. In domestic horses, this color is known as red dun. Black hair is generally attributed to the presence of eumelanin pigment and red/yellow hair to pheomelanin. Inability to produce eumelanin is attributed to a recessive gene at a locus in the horse now generally referred to as E (extension). Thus the inheritance of the "fox" colored trait in Przewalski's horses would be expected to be inherited as a recessive gene which could be at the E locus.

Other coat color loci recognized in domestic horses such as A, C, D and those of major spotting genes do not appear to vary in Przewalski's horses."

ZMRMN/BOWL Discussion that need to perform breeding experiments (i.e. fox X fox) to elucidate genetics of coat color.

SEAL Not at all obvious why are selecting against fox coat color.

ZIMMERMANN Contends fox color in captivity higher than in wild.

SEAL Inquires what is sample size of wild skins.

Minutes

6

ZIMMERMANN Perhaps 30.

SEAL Sample size not adequate to include trait if frequency low in wild population.

SEAL ET AL. To Thompson, is it possible to calculate cost in terms of other diversity of selecting against fox color trait.

RYDER Is it possible to eliminate gene by selection.

SEAL Is still not clear why select. Is there an end.

RYDER Pros and cons of keeping fox gene:

Pro

Con

Link to other diversity Unattractive

Suggests domestic origin

Increasing in frequency/higher than wild

Associated with bad traits

SEAL Compare inbreeding in fox versus nonfox. Also not convinced frequency of phenotype is increasing.

ZIMMERMANN Have been selecting against fox for 5 years; otherwise would have more.

SEAL Reinforces thought that is important to get horses back into wild in near future to minimize selection voluntary/involuntary.

RYDER Summarizes concerns about retention of diversity but also that phenotype of species is changing under captivity.

SUNDAY - 10 DECEMBER

ATTENDANCE: Ulie Seal, Ollie Ryder, Waltraut Zimmermann, V.N. Orlov, Elizabeth Thompson, Ann Bowling, Frank Princee, Nick Reindl, Tom Foose, Jim Dolan

SEAL Distributes proposed set of goals and objectives for global masterplan.

RYDER Inquires if there are any more general comments that anyone wants to present.

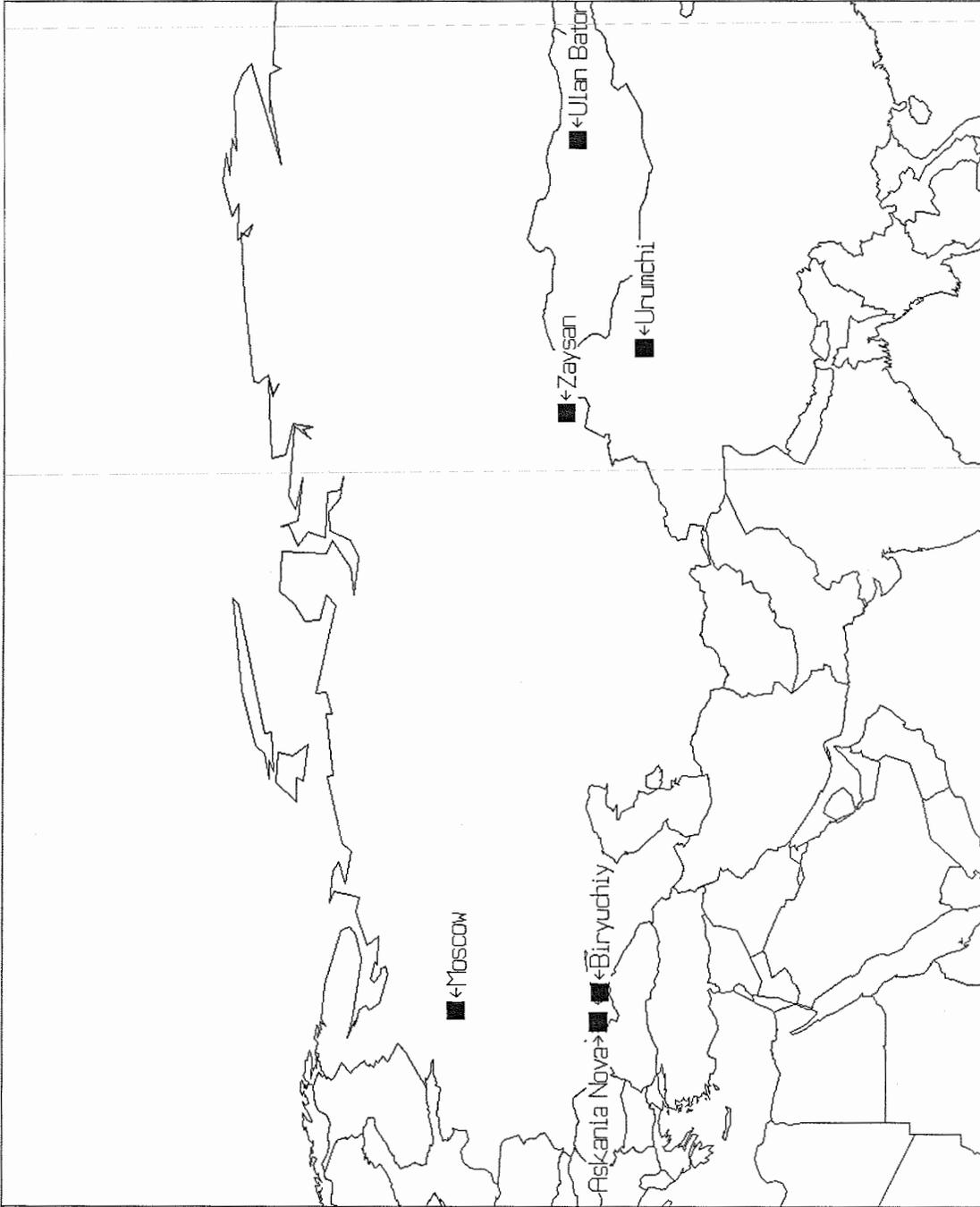
ORLOV Presents statement on USSR plans for reintroduction of Przewalski's horse:

"In recent years the scientists of our Institute and Askania-Nova studied various regions of Mongolia, S.Ukrainian, E.Kazachstan and E.Siberia. Two areas for the future reintroductions were selected: one area in South Ukraine and the other in Mongolia.

In Ukraine, the area is a rather large island in Azov Sea, near the north shore. The name of the island is Birusky (it means the island of old wolf). But there are no wolves now. There are only a few domestic animals on the island, about a dozen cows and a dozen domestic horses. The domestic horses may be removed from the island. Birusky is not real island; it is a spit (a small peninsula) 20 km long and 3-5 km wide. A tall fence isolates the spit from the coast of the mainland. There is a road and horses may be transported to the release site by trucks.

The island is situated not so far from Askania-Nova, about 200 km, and is 1500 km from Moscow. It has a proper geographical location in the steppe zone of S.-E. Europe. It is situated within the boundaries of the historic range of the Tarpan horse. Its vegetation and climate are the same as in Askania-Nova. But average winter air temperature is higher. About 500 hectares are covered by forest and bush. There is some ground water on the island. The total territory of island is more than 10,000 hectares. We believe the ultimate population of Przewalski's horse should be no less than 1000 to 2000 animals.

There are several hundred deer (*Cervus elaphus*) and wild sheep (*Ovis musimon*) in the island. These species were introduced on the island in



the 1930's 30th. The island has had the status of a reserve since that time. As the population of Przewalski's horse increases, the population of deer will have to be reduced. I think, the horses may be introduced in the island next summer.

Besides Birutshy there are two other potential areas for future reintroduction in USSR: one in East Kazakstan near the Lake Zaisan and the other in Dauria steppe in Transbaikalia on the border with Mongolia. Both areas are very good for reintroduction of Przewalski's horse but there are some problems now and we haven't any real projects yet.

In Mongolia, the final choice of the place for reintroduction was made by the agreement with the Mongolian Forest Ministry and USSR Academy of Science in June 1989. The area for the future reintroduction was selected 120 km from Ulan-Bator in the basin of Tola river. The total territory of the reserve is about 20,000 hectares. It is located at an altitude of about 1000-1500 m above sea level. The highest parts are covered with coniferous forest and the rest with steppe. The climate is continental and the winter is very cold. The snow cover is low, from 5 to 15 cm; the annual precipitation is 25 cm on the average. A rather good road connects this area with the city of Ulan-Bator.

We are planning to begin the transportation of the horses from Askania-Nova to Mongolia in 1991. Askania-Nova has already begun the formation of a horse group (about 10 animals) for release into Mongolia."

Also indicates that the steppe is of lower quality than Askania Nova. There are some domestic animals, but only a few horses. A semi-reserve area will be prepared next year for orientation. Release projected for 1991.

RYDER Are there specific plans for number and identity of horses, esp. from Askania Nova, to be reintroduced?

ORLOV About 10 to each site.

RYDER What about horses from zoos?

ORLOV Will use only horses from Askania Nova for Mongolia at first. Subsequently, may be possible to recruit zoo horses for Mongolia if initial releases are successful. Zoo horses could be used for Birutshy.

- PRINCEE** What about preparation of horses, social organization (herd formation versus genetic heritage) etc.
- RYDER** Has already been discussed to some extent by IUCN/FAO/UNEP 1985 Moscow meeting and document. Consensus that acclimatization occur at release site. Considerations important but peripheral to present group and meeting.
-
- SEAL** Inquires if Ryder has information about free-ranging population plans in Australia and Canada.
- RYDER** Yes, MacAlpine in Australia. Independent of small population in Australian zoos.
- In Canada, initial releases (a band) next year on ranch in Alberta prairie. Will be acclimatized and monitored. Are wolves in area. Several ranches interested so large area potentially available. Are 86 and 87 births, currently surplus genetically to SSP population.
-
- SEAL** Will Orlov be at Leipzig
-
- ORLOV** Not certain, possibly.
- SEAL** Should try to obtain written reports from each of the regions developing release programs: USSR/Mongolia, China, Canada, Australia. Ryder will solicit from Calgary, Knowles, AZDANZ, Orlov (will type his report); Maya Boyd, Oswald, and Dolan for China.
- ZIMMERMANN** Expresses concern about Chinese project because of poor quality of the habitat. Oswald, German businessman interested/involved with the Chinese project. Has been trying to recruit horses from European zoos. Will be at Leipzig.
- SEAL** Habitat resembles Red Desert and other viable horse habitat in Western NA.
- ZIMMERMANN** Believes Oswald will solicit horses from Aspinall if EEP and SSP don;t provide them.
- SEAL** Consider Proposed Goals...

MONDAY - 11 DECEMBER

ATTENDANCE: Ulie Seal, Ollie Ryder, Waltraut Zimmermann, V.N. Orlov,
Elizabeth Thompson, Ann Bowling, Frank Princee, Nick Reindl,
Tom Foose, Jim Dolan

SEAL Continues review of goals/objectives/recommendation document. Discussion of distribution (Seal has list agreed to by group). Selection of supporting materials to accompany goals/objectives/recommendation document: selected analyses; Geyer, Thompson, Ryder ZOOBIOLOGY November 1989 paper; list of fox horses, list of SSP and EEP institutions; Orlov documents; blood marker paper;

SEAL Inquires person-by-person if they agree with plan. All state they do as a working document.

RYDER Re-introduces issue of selection and lack of policy on it. Not explicitly or adequately considered in global plan document.

DOLAN Need to define what Przewalski's horse should look like. Is focal issue for management of the Przewalski's horse. Is only taxon where has been introgression of a domestic subspecies.

SEAL Seal attempts to formulate the phenotype problem for further discussion.

RYDER Two kinds of extreme selection have been rejected: random and very narrow type. But between these extremes don't have criteria and don't know what impact of phenotypic selection is on the gene pool.

SEAL Does group agree that any phenotypic selection not compromise the genetic variation of the population? Everyone agrees.

BOWLING What we want is to move toward a fairly uniform phenotype. Aspects of defective conformation are not controversial as breeding criteria; what needs definition is type. Perhaps the old species descriptions may be useful to cite.

RYDER Important if we could agree that selection policy consists of:

- (1) Paramount goal is to preserve founder alleles
- (2) Then stabilizing selection on phenotypic criteria as long as doesn't compromise preservation of all founder alleles.

Think we've agreed that are not going to act in way that causes loss of founder alleles. But still can apply some selection to stabilize phenotype, but need further study to determine limits of selection relative to preservation of genetic variation.

SEAL Requests Ryder, Zimmermann, Princee, Dolan to prepare a document outlining differing views on phenotypic selection and possible conflict with genetic goals. Can be used as a basis then for formulating some recommendations before Leipzig.

Equus przewalskii GLOBAL MANAGEMENT PLAN

TECHNICAL WORKING SESSION

San Diego, California
9-11 December, 1989

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PRZEWALSKI'S HORSE

Equus przewalskii

**GLOBAL CONSERVATION PLAN
D R A F T**

**APPENDIX II:
RELEVANT PAPERS**

10 February 1990

Gene Survival in the Asian Wild Horse (*Equus przewalskii*): I. Dependence of Gene Survival in the Calgary Breeding Group Pedigree

Charles J. Geyer and Elizabeth A. Thompson

Department of Statistics, GN-22, University of Washington, Seattle

The joint probability distribution of the number of distinct (not identical by descent) genes from each founder of the *Equus przewalskii* population that survive in the five horses of the Calgary Zoological Gardens breeding group has been calculated. The dependence structure of this distribution is investigated, and informative marginal distributions are given, among them the distributions of the genetic contributions of each founder to the Calgary horses and the distribution of wild-type genes in these horses. The dependence pattern is found to be complex; there is no substitute for exact calculation of the full joint probability distribution of numbers of surviving genes. Probabilities of gene survival give a more complete summary of the genetic structure of a set of individuals than is provided by more routine measures such as heterozygosity or founder contributions. The feasibility of computing these probabilities for small groups of current individuals descended from few founders via long and complex pedigrees, provides a new approach to assessing such groups, and could be used also in selecting animals to form the founder stock of propagules for future reintroduction programs.

Key words: gene extinction, pedigree analysis, genetic diversity

INTRODUCTION

The Asian wild horse (Mongolian wild horse, Przewalski's horse) *Equus przewalskii* Poliakov 1881 is the only extant species of true horse other than the domestic horse *E. caballus*. There are apparently no longer any Przewalski's horses living outside of captivity. No confirmed sightings of wild Przewalski's horses have occurred in nearly 20 years [Ryder and Wedemeyer, 1982]. There is, however, a captive population now numbering more than 660 individuals. Although large, this population is all descended from just 13 individuals—12 Przewalski's horses and one domestic horse. Of the 12 Przewalski's horse founders, 11 were brought out of the wild in

Received for publication November 13, 1987; accepted June 1, 1988.

Address reprint requests to Charles J. Geyer, Department of Statistics, GN-22, University of Washington, Seattle, WA 98195.

1899–1901 and one in 1948. The domestic horse (denoted DOM) was interbred with one branch of the captive Przewalski's horse population early in the century and unfortunately contributes genes to much of the population. None of the other 12 founders is officially designated in the international studbook [Volf, 1961] as having any domestic horse genes, but an argument based on phenotypic evidence has been advanced [AAZPA, 1987] that one of the founders (studbook number 18) is an F₁-hybrid of a Przewalski's horse and a domestic horse (i.e., half the genes of 18 are domestic horse genes).

The breeding group established by Calgary Zoological Gardens in accordance with the current North American species survival plan (SSP) [AAZPA, 1987] is a prototype for reestablishing a wild population of Przewalski's horses. Five Przewalski's horses, studbook numbers 1085, 1094, 1180, 1260, and 1272, have been placed in a large enclosure where they may freely graze, interact socially, and adapt to the habitat [Ryder, 1988]. For logistic reasons, the five animals chosen for the project were all born in 1982–1984, and three were born in New York and are thus closely related; however, the five Calgary horses do have contributions from all 13 founders. The genetic variability in such a species propagule and the effects of the constricted ancestral genealogy on that variability are of considerable interest.

GENE EXTINCTION IN A KNOWN PEDIGREE

Where a complete population, or species, is descended from just a few founders, the current population must have only a few distinct genes at any autosomal locus. When the genealogy of the population is known, the probability distribution of the number of distinct genes can be calculated. We consider gene extinction relative to the founder pool; founder genes are by definition considered distinct. Of course, these distinct genes may represent the same biochemical allele, and because of unknown previous ancestry of the population founder genes may even be identical by descent, but our interest here is in loss of genes over the known pedigree from the founders to the current animals. In counting the "number of founder genes that survive," we assume that all of these were distinct. A founder gene has "survived" only if a copy of it received by repeated segregations is in some member of the current set of animals under consideration, not just if the same biochemical allele descended from some other founder survives.

Where founders are few and early generations of the pedigree are highly constrained, a particularly interesting aspect of gene extinction (or its converse, survival) is the dependence between survivals of different (sets of) founder genes. If certain genes survive, other homologous genes must have less chance of doing so [Thompson, 1983]. This negative dependence reduces the variance of the number of surviving genes at any autosomal locus, and this in turn increases the precision with which surviving genetic variability in the population can be assessed. Where genetic variability within a particular small group of current individuals is of interest, this dependence can be enhanced. If certain genes are present in the current group, whose genetic variability is constrained by group size or recent common ancestry of the individuals, other founder genes must have a lesser chance of surviving. In this paper we investigate the probabilities of survival of genes of the 13 founders of the Przewalski horse pedigree in the five Przewalski's horses of the Calgary breeding group, with particular reference to patterns of dependence in gene survival. The

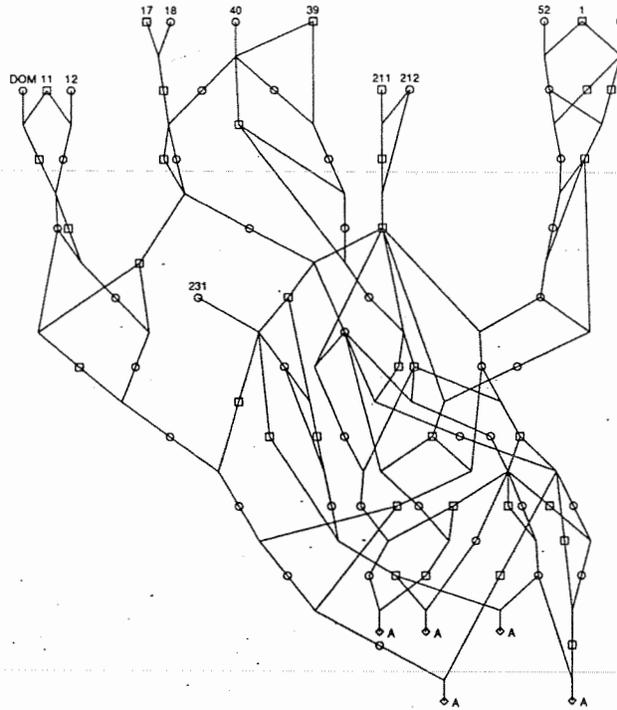


Fig. 1. Pedigree of the Calgary horses. The subpedigree with 17 and 18 deleted was used for peeling. Numbers are studbook numbers of founders. DOM denotes the domestic horse founder. A marks the five Calgary horses.

source of this dependence is thus both the early bottlenecks in the genealogy of the species and also the recent bottleneck involved in selection of the small current group.

The method of peeling [Cannings et al., 1978] permits the computation of probabilities of phenotype combinations on large and complex pedigrees. Thompson et al. [1978] showed how the method can be adapted to obtain exact joint founder gene extinction probabilities.

These algorithms have been refined and implemented in the pedigree analysis software package PEDPACK [Thomas, 1987]. This package is available to researchers from the second author. It requires a Berkeley-like UNIX operating system (with the C shell) and runs now on SUN workstations and on VAXes running Berkeley 4.2 or 4.3 UNIX. Portability to other UNIX environments based on Berkeley UNIX should not be a problem but is not guaranteed. Fairly extensive documentation is available. The package contains programs that calculate likelihoods on complex pedigrees by the peeling algorithm and also programs to draw pedigrees (like Fig. 1).

PEDPACK version 2.2, implemented on a Sun-3/160 workstation with Floating-Point Accelerator, includes a routine *extinction*, whose output is a multidimensional probability distribution of the number of genes (0, 1, or 2) from each founder that survive in a specified current group. Calculation of a gene survival distribution for pedigrees of this size takes about 1 hour of CPU time on this machine, which runs at

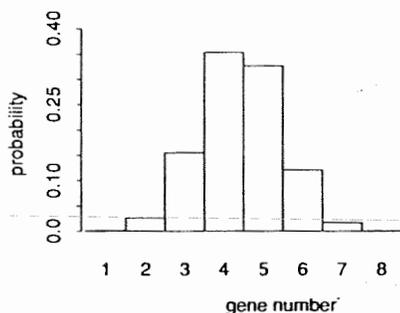


Fig. 2. Distribution of surviving genes. Probabilities that the Calgary horses have a specified number of distinct (not identical by descent) genes.

about 350 KFLOPS (thousand floating-point operations per second) doing double precision arithmetic (which this problem requires). Since the pedigree of the captive Przewalski's horse population is completely known, the probability of gene survival in the Calgary horses can be exactly calculated using this method.

SURVIVAL OF PRZEWALSKI FOUNDER GENES

The captive Przewalski's horses have official names but will be referred to throughout this paper by their studbook numbers [Volf, 1961]. The 12 Przewalski's horses that are the founders of the captive population have studbook numbers 1, 5, 11, 12, 17, 18, 39, 40, 52, 211, 212, and 231. The domestic horse founder is referred to by the notation DOM. Since two of the founders, 17 and 18, had only one mating, to each other, and only one offspring, 113, we can reduce the pedigree by removing 17 and 18 and making 113 a founder. No information about gene survival is lost by this procedure since if one gene from 113 survived it is equally likely to be from 17 or 18, and if two survived they are one from 17 and one from 18. This reduced pedigree has 12 founders (1, 5, 11, 12, 39, 40, 52, 113, 211, 212, 231, and DOM), one of which (DOM) is considered to have all domestic horse genes and one of which (113), if the argument that 18 is a hybrid is accepted, has either no domestic horse genes or one at any autosomal locus with equal probabilities. All of the rest of the founders are considered here to be pure Przewalski's horses. The complete pedigree of the Calgary horses (82 individuals including 17 and 18) is shown as a marriage node plot in Figure 1.

There were in the twelve founders of the population at any autosomal locus at most 24 different alleles, 2 in each founder. Considering these founder genes as distinct, we have calculated the probability distribution of the number of these genes that survive in the Calgary horses. We have also calculated the joint probability distribution of the numbers of genes from each founder that survive in the Calgary horses. Since the number from each founder can take any of three values (0, 1, or 2), this distribution has $3^{12} = 531,441$ terms. This is far too many terms for direct examination to be useful, even if only large terms are examined. It takes the 615 largest terms to make up 90% of the probability, 2,252 terms to make up 99%, and 4,505 terms to make up 99.9%.

The pedigree of the Calgary horses (Fig. 1) shows that the founders naturally divide into six groups, which were very closely inbred in the early generations. These groups are (group 1) horses 1, 5, and 52; (group 2) horses 11, 12, and DOM; (group 3) horses 39 and 40; (group 4) horse 113 (the sole offspring of 17 and 18, a group by itself); (group 5) horses 211 and 212; and (group 6) horse 231 (a group by itself). Groups 3 and 4 (horses 39, 40, and 113) are also moderately highly correlated as are groups 4 and 6 (horses 113 and 231); hence, horses 39, 40, 113, and 231 form a moderately highly correlated supergroup. The major subdivisions of the population descended principally from each of these founder groups are often known by the location of the founders. Horses 211 and 212 were owned by the Duke of Bedford and are referred to as the Woburn horses after Woburn Abbey. They contribute a very large fraction of the genes of the Calgary horses. The entire contribution of these two founders passes through the pseudofounder 182, which is the grandson of 211 and the grandson and son of 212. So the contribution of 212 to any of the Calgary horses is exactly three times the contribution of 211. The horses 1, 5, and 52 were located in what is now the Soviet Union and are the founders of the Old Askania Nova line after the estate of Baron Eduard von Falz-Fein. The mare 231 captured in 1948 was taken to the same location, and she and her descendants are referred to as the New Askania Nova line. The horses 11, 12, and DOM were located in Prague and founded the Old Prague line. The other two groups do not by themselves have names, but animals descended principally from 17, 18, 39, and 40 are referred to as the Munich (U.S.) line. In the sequel, we shall use only studbook numbers; the group names have been given to facilitate comparisons with other papers.

We now consider the probability distributions of numbers of genes surviving in the five Calgary horses that come from specified members or groups of members of the reduced set of founders. The first such distribution is that of the total number of

TABLE 1. Distribution of the number of surviving genes from each founder*

Founder	0	1	2	Mean
1	0.6500	0.3431	0.0069	0.3569
5	0.8191	0.1800	0.0010	0.1819
52	0.8190	0.1809	0.0000	0.1809
11	0.9687	0.0312	0.0000	0.0312
12	0.9844	0.0156	0.0000	0.0156
DOM	0.9844	0.0156	0.0000	0.0156
39	0.4544	0.4960	0.0496	0.5952
40	0.5251	0.4383	0.0366	0.5116
113	0.5862	0.3970	0.0168	0.4306
211	0.6019	0.3981	0.0000	0.3981
212	0.1102	0.7375	0.1523	1.0421
231	0.4102	0.5269	0.0630	0.6528

*Probabilities that the Calgary horses have a specified No. of distinct (not identical by descent) genes from specified founders.

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TABLE 2. Distribution of the number of surviving genes from each founder group*

Founders	0	1	2	3	4	Mean
1, 5, 52	0.3316	0.6170	0.0514	0.0000	0.0000	0.7198
11, 12, DOM	0.9375	0.0625	0.0000	0.0000	0.0000	0.0625
39, 40	0.1614	0.5838	0.2416	0.0131	0.0001	1.1068
113	0.5862	0.3970	0.0168	0.0000	0.0000	0.4306
211, 212	0.0167	0.5264	0.4569	0.0000	0.0000	1.4402
231	0.4102	0.5269	0.0630	0.0000	0.0000	0.6528

*Probabilities that the Calgary horses have a specified No. of distinct (not identical by descent) genes from specified groups of founders.

TABLE 3. Joint and conditional distribution of DOM versus the rest of the founders*

	Joint				Conditional	
	0	1	Marginal		0	1
1	0.0013	0.0001	0.0014	1	0.0013	0.0036
2	0.0261	0.0009	0.0270	2	0.0265	0.0597
3	0.1537	0.0040	0.1577	3	0.1562	0.2564
4	0.3489	0.0062	0.3550	4	0.3544	0.3937
5	0.3194	0.0036	0.3230	5	0.3245	0.2311
6	0.1175	0.0008	0.1183	6	0.1194	0.0515
7	0.0166	0.0001	0.0166	7	0.0168	0.0039
8	0.0008	0.0000	0.0008	8	0.0008	0.0001
Marginal	0.9844	0.0156		Mean	4.4040	3.9597

*Left: Joint probabilities that the Calgary horses have a specified No. of genes from horse DOM (No. at top) and a specified No. of genes from the rest of the founders (No. at left). Marginal distributions of the joint distribution are at right and bottom. Right: Conditional probabilities that Calgary horses have a specified No. of genes from the rest of the founders given that they have zero (left column) or one (right column) gene from DOM.

TABLE 4. Joint and conditional distributions of domestic horse genes and Przewalski's horse genes (assuming that besides DOM the only domestic horse genes in the founders come from one grandparent of 113)*

	Joint					Conditional		
	0	1	2	Marginal		0	1	2
1	0.0013	0.0011	0.0000	0.0024	1	0.0015	0.0090	0.0253
2	0.0251	0.0112	0.0003	0.0366	2	0.0286	0.0935	0.1863
3	0.1434	0.0368	0.0006	0.1809	3	0.1633	0.3067	0.3983
4	0.3157	0.0454	0.0005	0.3617	4	0.3595	0.3783	0.3008
5	0.2795	0.0215	0.0001	0.3011	5	0.3182	0.1791	0.0818
6	0.0992	0.0038	0.0000	0.1030	6	0.1129	0.0315	0.0074
7	0.0135	0.0002	0.0000	0.0137	7	0.0153	0.0019	0.0002
8	0.0006	0.0000	0.0000	0.0006	8	0.0007	0.0000	0.0000
Marginal	0.8783	0.1201	0.0016		Mean	4.3682	3.7274	3.2503

*Left: Joint probabilities that the Calgary horses have a specified No. of domestic horse genes (No. at top) and a specified number of Przewalski's horse genes (No. at left). Marginal distributions of the joint distribution are at right and bottom. Right: Conditional probabilities that Calgary horses have a specified No. of Przewalski's horse genes given that they have zero, one, or two (No. at top) domestic horse genes.

genes surviving from all founders. It is shown as a histogram in Figure 2 (and in numerical form in Table 5, where it is compared with several approximations). More precisely, it is the probability distribution of the number of distinct genes (and recall that distinct means not identical by descent) that exist at a specified autosomal locus in the five Calgary horses. There must of course be at least one and at most ten distinct genes. Since the founders had 24 genes, the probability that k distinct genes have survived is also the probability that $24 - k$ distinct genes have become extinct (are not present in the Calgary horses; they may of course be present in some other Przewalski's horses). There is an average of $4\frac{1}{2}$ (4.4127) distinct genes per locus (averaged over all loci). For comparison, the mean number of distinct genes per locus in all living Przewalski's horses (calculated by the same methods using the entire Przewalski's horse pedigree) is 10.4758. Thus the Calgary horses have 42% of the genes existing in the total population of *E. przewalskii*, over 600 individuals. In the Calgary horses two-thirds of all loci (.678) have four or five distinct genes, and almost all loci (.980) have between three and six distinct genes. At just one locus in 1,000 (.0013) is a single allele fixed (identical by descent from the founders) in all the Calgary horses.

Table 1 shows the marginal distributions of the number of distinct (not identical by descent) genes from each founder that have been passed on to the five Calgary horses. These probabilities are, in a sense, the ancestral contributions to the Calgary horses as a group, rather than the contributions to specific horses. Contributions to specific horses can be calculated without peeling the pedigree [Thompson, 1986], but these contributions do not add up to the contributions to the group because of dependence between the contributions. From Table 1 it is easy to see that most of the genetic contribution to the Calgary horses comes from the founders 1, 39, 40; 113, 211, 212, and 231, each of which contributes at least .36 genes per locus averaged over all loci. Just the horses 212 and 231 together contribute a total of 1.69 distinct genes per locus averaged over all loci to the Calgary horses, which is quite large when compared with the average of 4.41 distinct genes contributed by all founders together. Of the rest of the founders none contributes more than .182 genes per locus. Note that in particular the contribution of the domestic horse DOM is only .0156 genes per locus and that at 98.44% of all loci there are no genes from DOM in any of the Calgary horses.

The next table, Table 2, shows the marginal distributions of the number of distinct (not identical by descent) genes from the six groups of founders that have been passed on to the five Calgary horses. This table shows much the same picture as the preceding one. In particular the three horses 211, 212, and 231 contribute almost one-half of the genes of the Calgary horses, an average of 2.09 genes per locus out of an average of 4.41 genes per locus from all 12 founders combined.

DOMESTIC GENES AND PRZEWALSKI GENES

This section deals with joint (bivariate) probability distributions of the number of genes surviving in the five Calgary horses that are domestic horse genes and the number that are wild-type genes (true Przewalski's horse genes). The two tables in this section give the joint distribution of domestic and wild-type genes given two different assumptions about which founders have some domestic genes. The first assumption is that DOM, the domestic horse founder, is the only founder with any

TABLE 5. Distribution of surviving genes (comparison of truth vs. approximations)*

	Truth	Four groups	Six groups	Twelve groups
0	0.0000	0.0001	0.0002	0.0016
1	0.0013	0.0040	0.0079	0.0191
2	0.0262	0.0433	0.0573	0.0814
3	0.1547	0.1708	0.1781	0.1825
4	0.3529	0.3144	0.2899	0.2513
5	0.3256	0.2926	0.2678	0.2293
6	0.1211	0.1385	0.1443	0.1444
7	0.0174	0.0322	0.0453	0.0643
8	0.0009	0.0038	0.0082	0.0205
9	0.0000	0.0002	0.0009	0.0047
10	0.0000	0.0000	0.0001	0.0008
11	0.0000	0.0000	0.0000	0.0001
Mean	4.4127	4.4127	4.4127	4.4127
s.d.	1.0400	1.1891	1.3112	1.5489

*True distribution of the No. of distinct genes in the Calgary horses (truth) compared with the approximation derived by assuming independence of descent from the four groups 1, 5, 52; 11, 12, DOM; 39, 40, 113, 231; and 211, 212 (4 groups), with the approximation derived by assuming independence of descent from the six groups 1, 5, 52; 11, 12, DOM; 39, 40; 113; 231; and 211, 212 (6 groups), and with the approximation derived by assuming independence of descent from each of the 12 founders (12 groups).

domestic horse genes. The second assumption is that founder 18 is an F_1 -hybrid of a domestic horse and a Przewalski's horse, that DOM is domestic, and that the rest of the founders are pure.

Table 3 gives the joint gene survival distribution of genes from horse DOM versus genes from the rest of the founders (which is the distribution of domestic versus wild-type genes if DOM is assumed to be the only impure founder). This table also shows the relationship between the same random variables (numbers of domestic and wild-type genes) in another way—as conditional distributions of the number of surviving wild-type genes given the number of surviving domestic genes. The columns of the table on the right are just the columns of the table on the left normalized (which makes them these conditional distributions). If these random variables were independent, the columns of the table on the right would be the same, which they are clearly not. At the 98.4% of all loci where there are no genes from DOM in the Calgary horses, there are 4.4 distinct genes on the average from the other founders. At the 1.6% of all loci where there is one gene from DOM in the Calgary horses, there are only 4.0 distinct genes on the average from the other founders.

It is interesting to note that the reduction in the number of wild-type genes for a known increase in domestic genes is not one for one. Knowledge that there is one more domestic gene (i.e., one rather than none) only changes the expected number of wild genes by about a half a gene (from 4.4 to 4.0). This occurs because the expected number of all genes is larger ($5.0 = 4.0 + 1$ rather than 4.4); knowing that more domestic genes have survived gives information that fewer Przewalski genes have survived, but also that more genes have survived in total.

Table 4 gives the joint distribution of domestic genes and wild-type genes in the Calgary horses, assuming that horse 18 is a Przewalski's-domestic hybrid (hence that 113 is one-quarter domestic) and that none of the founders except 113 and DOM have any domestic horse genes. This distribution is calculated as follows. From the 12-dimensional distribution of gene survival from founders calculate the three-dimensional marginal distribution of gene survival for DOM versus 113 versus the rest. Then split this three-dimensional distribution into a four-dimensional distribution—that of genes from DOM, domestic genes from 113, wild genes from 113, and genes from the other 10 founders—as follows. Let $p_0, p_1,$ and $p_2,$ be the two-dimensional probabilities of DOM versus the rest excepting 113 when 0, 1, or 2, respectively, genes of 113 have survived, and let $q_{ij}, i = 0, 1, j = 0, 1, 2$ be the two-dimensional probabilities of DOM versus the rest excepting 113 when i domestic horse genes from 113 and j wild-genes from 113 have survived. Then the transformation

$$\begin{aligned} q_{00} &= p_0, & q_{01} &= \frac{3}{4}p_1, & q_{02} &= \frac{1}{2}p_2, \\ q_{10} &= \frac{1}{4}p_1, & q_{11} &= \frac{1}{2}p_2, & q_{12} &= 0 \end{aligned}$$

defines the four-dimensional distribution. In words, these equations say that if one gene from 113 has survived then it is domestic with probability $\frac{1}{4}$ and wild with probability $\frac{3}{4}$, and if two genes from 113 have survived then they are one domestic gene and one wild gene with probability $\frac{1}{2}$ and two wild genes with probability $\frac{1}{2}$. (Trivially, there cannot be 3 genes, 1 domestic and 2 wild, from 113, and the probability of no genes from 113 surviving is the same whether it is denoted p_0 or q_{00} .) Finally, calculate from this four-dimensional distribution the two-dimensional marginal distribution, one dimension being the two domestic horse variables (from DOM and from 113) and the other dimension being the two Przewalski's horse variables (from 113 and from the rest). This two-dimensional marginal distribution is what is shown in Table 4. Not shown are the means of the marginal distributions in Table 4. The mean number of domestic genes per autosomal locus in the Calgary horses is 0.1233, and the mean number of wild-type genes is 4.2894. For comparison the means of the marginal distributions in Table 3 are 0.0156 for the mean number of domestic genes and 4.3971 for the mean number of wild-type genes.

Notice that here again the reduction in the number of wild-type genes for a known increase in domestic genes is not one for one. As in Table 3, an increase of one in the number of domestic genes produces a decrease in the expected number of wild-type genes of about one-half of a gene. The increase from zero to one domestic genes produces a decrease of $0.7 = 4.4 - 3.7$ wild genes, and the increase from one to two domestic genes produces a decrease of $0.4 = 3.7 - 3.3$ wild genes.

DEPENDENCE IN GENE SURVIVAL

Gene survivals from different founders (or for that matter from homologous genes in one founder) are negatively correlated: a gene descended from one founder is not descended from another. One illustration of this is in the conditional means of Tables 3 and 4. The more domestic genes survive, the less are expected from the Przewalski founders. However, the dependence is not complete; the reduction in expectation is not one for one. One way to look at the lack of independence between the numbers of genes descended from different founders is to examine how much the

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TABLE 6. Gene survival correlations*

5	52	11	12	DOM	39	40	113	211	212	231	
-0.26	-0.26	-0.04	-0.03	-0.03	-0.01	-0.01	-0.02	-0.02	-0.05	-0.02	1
	-0.14	-0.03	-0.02	-0.02	-0.01	-0.01	-0.01	-0.02	-0.03	-0.01	5
		-0.03	-0.02	-0.02	-0.01	-0.01	-0.01	-0.02	-0.03	-0.01	52
			-0.02	-0.02	0.00	0.00	-0.01	-0.01	-0.02	-0.01	11
				-0.02	0.00	0.00	-0.01	-0.01	-0.01	-0.01	12
					0.00	0.00	-0.01	-0.01	-0.01	-0.01	DOM
						-0.33	-0.15	-0.02	-0.04	-0.04	39
							-0.16	-0.02	-0.04	-0.04	40
								-0.02	-0.03	-0.11	113
									-0.44	-0.03	211
										-0.05	212

11, 12, DOM	39, 40	113	211, 212	231	
-0.11	-0.04	-0.04	-0.12	-0.03	1, 5, 52
	-0.01	-0.01	-0.03	-0.02	11, 12, DOM
		-0.26	-0.10	-0.07	39, 40
			-0.05	-0.11	133
				-0.07	211, 212

11, 12, DOM	39, 40, 113, 231	211, 212	
-0.11	-0.07	-0.12	1, 5, 52
	-0.03	-0.03	11, 12, DOM
		-0.15	39, 40, 113, 231

*Top: Correlation coefficients of the No. of genes from specified pairs of founders that survive in the Calgary horses. Middle: Correlation coefficients of the No. of genes from specified groups of founders (6 groups). Bottom: Correlation coefficients of the No. of genes from specified groups of founders (4 groups).

true (12-dimensional) probability distribution of numbers of genes surviving from different founders differs from the closest distribution that has some independence property. This distribution may be taken to be the product of the marginal distributions of the true distribution, a distribution that is of some interest in itself because the marginal distributions can sometimes be calculated when the joint distribution cannot. The true distribution of the total number of surviving founder genes is compared with a series of approximations in Table 5; these assume, successively, independence of all 12 founders, of the six groups, and of the four supergroups formed when founders 113, 231, 39, and 40 are combined into one group. The approximations produce the correct mean (as they must since the mean of a sum is the sum of the means whether or not the variables are correlated), but all three approximate distributions have too much spread. Their standard deviations are 14% (4 groups), 26% (6 groups), and 49% (12 groups, i.e., individual founders) higher than the truth, because negative correlations substantially reduce the variance of the number of surviving genes. Equivalently, one can say that the tails of these approximate distributions are too heavy, and their centers are too light; the truth is $P(4 \text{ or } 5 \text{ genes}) = .678$, whereas the approximations attribute to this event the probabilities $P(4 \text{ or } 5 \text{ genes}) = .607$ (4 groups), $.558$ (6 groups), or $.481$ (12 groups).

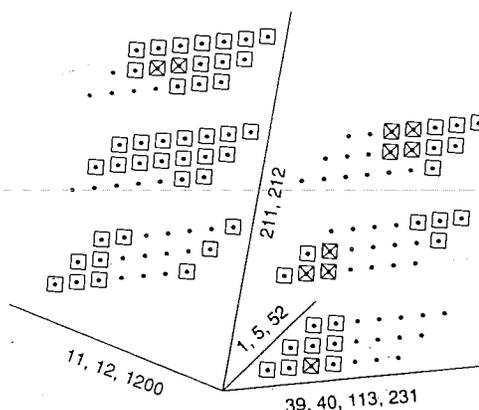


Fig. 3. The event A_3 . Boxes show points of the event A_3 discussed in the text. Crossed boxes show points of A_3 where 80% of the total overestimation occurs. (Note: 1200 is DOM).

We can examine the pattern of correlation in gene survival directly. Table 6 shows the correlation coefficients for numbers of distinct genes surviving from different founders and groups of founders. Note that the only appreciable correlations among founders are those between 1, 5, and 52; between 39, 40, and 113; between 113 and 231; and between 211 and 212. Since the correlation matrix (Table 6) is approximately block diagonal, most of the correlation is within-group correlation, and it seems reasonable to check whether at least the numbers of genes surviving from different groups are almost independent. Table 6 also shows the correlation matrix for the six groups of Table 2. Most of the correlation coefficients are now small, but there are still fairly large correlation coefficients between 113 and the 39–40 group and between 113 and 231. In an attempt to find some groups that are more nearly independent we may continue to collapse several groups into one, starting with the obvious choice, putting 39, 40, 113, and 231 in a single group, reducing the number of groups to four. This is shown also in Table 6. The process of attempting to find groups that are approximately uncorrelated stops here. The three largest correlations, -0.15 between groups 3 and 4, -0.12 between 4 and 1, and -0.11 between 1 and 2, are all about the same size, and collapsing groups to eliminate them would require the collapse of all groups into one group.

We now return to the difference between the true joint distribution and the approximation generated from the 12 independent marginals corresponding to each founder. It is not obvious how best to measure the difference between two distributions. It is not a statistical question, but only of how close an approximation is to the truth, and the answer to this must depend to some degree on the intended use of the approximation. The simplest answer is found by examining the worst case. Suppose that the event A_1 is defined as the union of all simple events for which the independence approximation based on the assumption of independence of gene survival from different founders overestimates the probability. Then the truth is that $P(A_1) = .266$, and the approximation estimates that $P(A_1) = .603$, a very large error indeed, an absolute error of more than one-third, and a relative error of more than 125%. Other events will have smaller absolute errors. Relative errors can be infinite, since there are events of probability zero to which the approximation assigns positive probabilities.

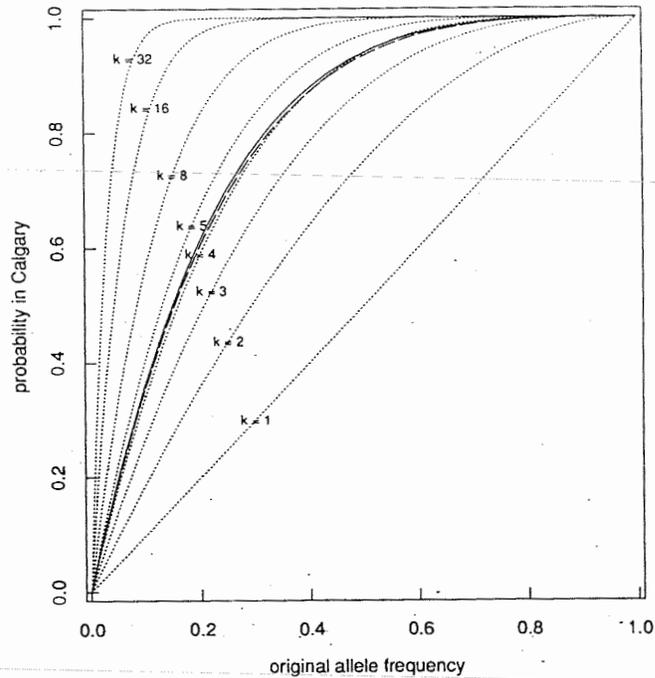


Fig. 4. Probability of allele survival. Horizontal axis, original population frequency p of some allele. Vertical axis, probability $\pi(p)$ of the allele surviving in the Calgary horses. Dotted lines, probability of a gene with population frequency p surviving given that 1, 2, 3, 4, 5, 8, 16, or 32 distinct founder genes survive. Solid line, probability of a gene with population frequency p surviving assuming that DOM is the only source of domestic horse genes (that all of the rest of the founders are pure). Dashed line, probability of a gene with population frequency p surviving assuming that DOM is pure domestic, that 18 is an F_1 -hybrid, and that the rest of the founders are pure).

The true (six-dimensional) probability distribution for numbers of surviving distinct genes from the six groups of founders in the middle panel of Table 6 is somewhat closer to independence. If we look at the event A_2 , defined to be the union of all simple events whose probabilities are overestimated by this independence approximation, then the truth is that $P(A_2) = .322$, and the approximation estimates that $P(A_2) = .473$, an absolute error of .150 and a relative error of 47%. These errors are smaller than before but still large. For the four groups of the bottom panel in Table 6 the worst-case event A_3 has a true probability of $P(A_3) = .247$ and an estimate assuming independence of $P(A_3) = .334$, an absolute error of .088, and a relative error of 35%. The approximation based on an assumption of independence is not so bad as before but is still not very good.

The event A_3 is shown in Figure 3, which shows a four-dimensional plot, the four lines being orthogonal axes, each labeled with one of the four groups of founders under consideration. The point $(0, 0, 0, 0)$ is the point closest to the intersection of the axes, and each step from one dot to the next in the direction of an axis is an increase of one in the number of genes of that group of ancestors that have passed down to the Calgary horses. Although not obvious, the event A_3 is connected. Its

complement is also connected. Most of the probability is on the righthand half of Figure 3. From Table 2 we see that the probability of the event on the righthand side of Figure 3, which is the probability that horses 11, 12, and DOM contribute no genes to the Calgary horses, is 93.75%. Hence the important part of the pattern in Figure 3 is on the righthand side, where the unmarked points form (approximately) a tilted slab. This slab contains all of the points such that the three groups 1, 5, 52; 39, 40, 113, 231; and 211, 212 together contribute a sum of five or six genes to the Calgary horses and most of the points such that they contribute a sum of seven or eight genes. Hence it seems that one deficiency of the approximation is that it fails to yield the correct distribution of the sum of genes contributed by all the founders.

This suggests that it would be interesting to fit a log-linear model to the true distribution that has the correct marginal distributions and the correct distribution for the sum, that is, if P_{ijkl} is the true distribution, then the log-linear model under discussion is the distribution of the form

$$P_{ijkl} = \alpha_i \beta_j \gamma_k \delta_l \epsilon_{i+j+k+l}$$

that has the correct marginal distributions and distribution of the sum. Of course, unlike the assumption of independence of marginals, this is not an approximation that one could actually use, since the distribution of the sum can only be calculated from the true joint distribution. But if the log-linear model fits well it summarizes the deficiency of the approximations obtained on the assumption of independent marginals.

So how well does it fit? The fit is much better than before. For this fit the worst case error occurs for an event A_4 of true probability $P(A_4) = .477$ to which the fit attributes a probability of $P(A_4) = .513$, an absolute error of .036, which is to be compared with the error .088 of the previous fit. This error is less than half as large as before (41%), and this is the first approximation for which the relative error is below 10%. Even this fit leaves a lot of error unexplained. The pattern of residuals for this fit (analogous to Fig. 3 but not shown) shows no obvious regularity. Hence the approximation process must stop here, with the conclusion that dependence is more complex than merely a constraint on total number.

CONCLUSIONS

1. The analysis presented here exemplifies computations that may be of interest for many species isolates, descended from few founders via complex and constrained pedigrees. An analysis of numbers of surviving founder genes provides an additional perspective, which is not encompassed by studies of heterozygosity: inbreeding and kinship within the population [Thompson, 1986].
2. Additionally, the results of this paper can be used to answer questions of the survival of polymorphic variants from the wild population. Supposing that an allele had a population frequency p and that the founder genes are a random sample from the population gene pool, what is the probability that this allele occurs in a current group? Given that there are k distinct founder genes at some locus in the current group, the probability that an allele with population frequency p survives is $1 - (1-p)^k$. The variation of gene survival with original population frequency for various values of k is shown in Figure 4.
3. Of course one usually has no precise knowledge of how many distinct genes survive. So more interesting is the unconditional probability of gene survival

found by summing with respect to the probability distribution P of the number of surviving genes. For the Calgary horses, restricting attention to surviving Przewalski horse (i.e., nondomestic) genes, this is the marginal distribution of wild-type genes shown in Table 3 or Table 4 depending on whether 18 is assumed to be pure or an F_1 -hybrid. The probability $\pi(p)$ that an allele with population frequency p in the original wild population is present in the Calgary horses is

$$\pi(p) = \sum_k (1 - (1-p)^k)P(k).$$

This probability, as a function of p , is also shown in Figure 4. The solid line shows the probability assuming that 18 is pure; the dashed line shows the probability assuming that 18 is an F_1 -hybrid. Note that both of the lines are almost on top of the line ($k = 4$) that assumes that exactly four genes survive. This is not surprising, since the mean number of surviving wild-type genes is 4.3 assuming that 18 is an F_1 -hybrid and 4.4 assuming 18 to be pure. However, the solid and dashed lines are not halfway between the dotted lines for $k = 4$ and $k = 5$, and for large p lie below the line for $k = 4$.

4. Another point to be drawn from Table 3 and Table 4 is that inclusion of 18 as an F_1 -hybrid multiplies the expected number of surviving domestic horse genes (per locus) in the Calgary breeding group by a factor of 8. A similar doubt concerning any founder other than of the group 11, 12, DOM would have as great or greater impact. For these Calgary animals, concerns about the purity of other founders of the *E. przewalskii* pedigree are of far greater significance than the small contribution they have received from the known domestic horse.
5. Another more general conclusion is the importance of analyzing joint probabilities, not just marginal probabilities for each founder alone. The model fitting of the previous section shows that there is no substitute for the exact calculation. One could, of course, use the assumption of independent descent to calculate the mean number of distinct surviving genes. Such a calculation will be exact, as can be seen in Table 5, since the expectation of a sum of random variables is the sum of the expectations whether or not the random variables are independent. However, there is strong dependence in survival of the genes of distinct founders; no marginal probabilities even of groups of founders can provide an adequate approximation to the distribution of the numbers of surviving genes. While part of the dependence pattern can be explained as due to a constraint on the total number of genes that can survive in a small group of current animals, accounting for this factor alone still does not provide adequate approximation.
6. Finally, this report has demonstrated the feasibility of detailed analysis of gene survival in a small group of individuals who are members of a large and complex pedigree. The probability distribution of the number of distinct genes in the population, provided by this analysis, is a direct measure of the genetic diversity of the group, perhaps the best measure that can be computed with available methods. It is possible without peeling to compute the mean contribution of each founder to each individual in a group. But since these contributions are not independent, the mean contribution of each founder to the whole group (what is shown in Table 1) cannot be calculated by summing the contributions to individuals. Moreover, distributions such as the distribution of wild-type genes shown

in Tables 3 and 4, which are of interest, cannot be calculated without peeling. An analysis like this of the genetic diversity of various groups of individuals may be important in providing additional perspectives in selecting individuals to form the founder stock of propagules for future captive breeding or for reintroduction projects.

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Gene Survival in the Asian Wild Horse (*Equus przewalskii*):
II. Gene Survival in the Whole Population, in Subgroups, and
through History.

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Abstract

In populations with a known pedigree exact joint probability distributions of numbers of surviving of genes from each founder can now be calculated for moderately large complex pedigrees (1000-2000 individuals and much inbreeding). The usefulness of such calculations is shown by our analysis of gene survival in the Asian wild horse (*Equus przewalskii*), a species now extinct in the wild with a captive population with 1516 individuals in the known pedigree (twelve generations). We calculate the genetic diversity of subsets of the current population interesting to the North American Species Survival Plan, trace the loss of genetic diversity in this species through its history in captivity, and determine genetically important individuals in the North American population, those with relatively high probabilities of having unique copy genes (genes not found in any other living individual in North America).

Keywords: gene extinction, gene survival, pedigree analysis, genetic diversity, *Equus przewalskii*

1 Introduction

This paper continues the application of new methods of gene survival calculations to the pedigree of the Asian wild horse (Mongolian wild horse, Przewalski's horse) *Equus przewalskii* Poliakov 1881, which we began in the first paper of this series [Geyer and Thompson, 1988]. The main feature of this paper is several improvements in our computer programs that allow us to do calculations on much larger pedigrees than before and consequently apply gene survival calculations to new applications, such as identification of genetically important individuals.

The Przewalski's horse is now almost certainly extinct in the wild [Ryder and Wedemeyer, 1982], but a large captive population exists in zoos and parks throughout the world. The pedigree used for the calculations reported here contained 704 living individuals and 1516 individuals in all. It was current with respect to the North American population as of mid 1987, and perhaps a bit less up to date on the horses in the rest of the world.

This species makes a particularly interesting example for gene survival calculations because the pedigree is large and complex yet originates from only a few founders. This means that gene survival calculations are difficult and also very important.

The whole of the current world population of the Przewalski's horse is descended from just thirteen founders. There are seventy founders recorded in the studbook of the Przewalski's horse [Volf, 1961 et seq.], but only thirteen of these contribute any genes to the current population. Twelve of these founders lived during the first few decades of the century, the last of them dying in 1939. Only one wild horse, a mare,

has been bred into the captive population since then. Although captured as a foal in 1947, she did not have her first offspring that contributes genes to the current captive population until 1960.

Gene survival calculations tell us the probability distribution of the number of surviving genes at a typical (autosomal) locus. By “number of surviving genes” we mean the number of genes in the current population assuming that all of the founder genes were distinct. Of course the founder genes need not have been all different, and could not be all different at a locus where the whole wild population had fewer alleles than the number of founder genes, but any other distribution related to gene survival, for example the probability of survival of a gene with a known frequency in the wild population, can be calculated from the distribution considered here [Geyer and Thompson, 1988]. Throughout this paper when we refer to “distinct” genes we mean genes that are distinct under the assumption that all of the founder genes were different. Another way to say this is that “distinct” genes are genes not identical by descent (through the known pedigree).

The thirteen founders had among them at an arbitrary autosomal locus twenty-six distinct genes. Much of this genetic diversity was lost early in the century and the loss continued until around 1970. Since 1970 the population has been well managed and the loss of genetic diversity has been negligible. Today there are in the whole species an average of 10.476 distinct genes per autosomal locus. In Section 4 we give gene survival calculations for the number of genes surviving in 1930, 1950, 1960, and 1970, which show the course of gene loss in this species.

A peculiarity of the Przewalski's horse pedigree that makes it especially interesting for analysis is that not all of the founders were pure wild-type *E. przewalskii*. Przewalski's horses do interbreed with domestic horses (*E. caballus*) and produce fertile hybrids. One such hybrid was produced at Halle, Germany in 1906. This was 56 (Halle 1) whose dam was a domestic mare, referred to by the abbreviation DOM. [Note here that the horses, DOM excepted, have two or three designations. The first a number, here 56, is the studbook number in the studbook [Volf, 1961 et seq.]. The second is the official name, here Halle 1, formed from the zoo where the animal was born and a sequence number. The third, present only for some animals, is the house name. For example, we will later mention 1124 (Hellabrun 92, Sirtaki) a genetically important horse in the North American population. Sirtaki is his house name.] Of the 1516 horses in the pedigree (including DOM) 978 are DOM and her descendants, all of them through 56.

There were domestic horses in the natural range of *E. przewalskii* in southern Russia, Mongolia, and China throughout historical times. There must have been some interbreeding of *E. przewalskii* and *E. caballus* in the wild, but how much is not known. One of the founders, 18 (Bijsk 8), though officially recorded in the studbook [Volf, 1961 et seq.] as being a Przewalski's horse, is suspected on the basis

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of phenotypic evidence [Dolan, 1982] of having some admixture of domestic horse genes. Although how much, if any, domestic horse ancestry 18 has is unlikely to ever be known for sure, the usual assumption (when 18 is considered impure at all) is that 18 was an F₁-hybrid. Although any of the other founders may also have had some domestic ancestry, there is no particular reason to suspect any one of them, and we give no consideration to the possibility that any of the other founders (besides DOM and 18) were not pure *E. przewalskii*.

Our calculations show that of the 10.476 distinct genes per locus (average) surviving in the current world population, 0.568 come from the domestic mare founder DOM (and hence are for certain not wild-type *E. przewalskii*). Of the remaining 9.908 genes, another 0.270 come from one parent of 18 and hence are also not wild-type if 18 was in fact an F₁-hybrid. This leaves an average of 9.638 wild-type genes per locus.

To provide information for discussions about the management of the North American population of *E. przewalskii* we calculated the the numbers surviving of genes from the various founders that survive in several subsets of the North American population. The breeding program in effect until mid 1988 divided the North American population in to two separate subgroups: those with and those without descent from DOM. In the group with descent from DOM only the mares were bred (to stallions without descent from DOM). The stallions with descent from DOM were never bred. The aim of this policy was to gradually reduce the frequency of domestic genes in the group with descent from DOM without reducing the growth rate of the total population. The effect of this policy, if continued indefinitely, would be to eliminate all DOM genes from the North American population.

As can be seen in the pedigree plot Figure 1 which shows the pre-1970 population, exclusion from the population of genes from DOM necessarily also means exclusion of all genes from the two wild founders 11 and 12 (Bijsk 1 and 2), because all of their descendants are also descended from DOM and vice versa. There are also other genes of wild founders present in North American horses descended from DOM but not in the "pure" horses—those genes that by chance descended to the DOM horses rather than the non-DOM horses. All of these genes were gradually being bred out of the subgroup of the North American horses descended from DOM. There is an average of 8.675 non-DOM genes per autosomal locus in the North American population. In the "pure" (non-DOM) North American population there is an average of 6.639, which is 30 per cent more genes in the total population than in the non-DOM population. Thus the old policy would have eventually resulted in a loss of 2.036 genes per locus. Of these 2.036 genes ~~1.725~~ (62.4 per cent) are genes from 11 and 12 and 0.765 (37.6 per cent) are genes from other founders. The size of this loss was unknown before our calculations were done.

These calculations among other considerations led to a change in policy in 1988

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[Ryder, et al., 1988]. Both mares and stallions with descent from DOM are now bred, although these animals still constitute a special group within the North American species survival plan. Gene flow is one way between the two groups, always from the non-DOM horses to those descended from DOM. Mares with no descent from DOM are never bred to stallions with descent from DOM. This policy still preserves a "pure" group containing no DOM genes and keeps this group growing as fast as possible. The "impure" (DOM-descended) group is, however, managed differently. Within the DOM-descended group the object is no longer to breed out all of the DOM genes eventually making the "impure" group almost the same as the "pure." This group is now being managed to preserve the genetic diversity it contains.

Another example of the value of exact gene extinction calculations is the determination of "genetically important individuals" in the North American population (Section 5). By "genetically important" we mean individuals that are highly likely to have unique copies of founder genes, i.e., genes present in no other individual in the pedigree. Such information is of obvious interest to those planning the breeding of the population. Failure to breed genetically important individuals results in immediate loss of their unique copy genes. Section 5 discusses six horses that are genetically important in the North American population.

Gene survival calculations are, of course, not the only kind of genetic calculations that are used in guiding management decisions for the Przewalski's horse population. Founder contributions are perhaps the most heavily used, because they can be calculated very rapidly with modern recursive methods [Thompson, 1986a] that do not involve either gene drop or peeling. The trouble with founder contributions is that they are in a rough sense the opposite of gene survival. Founder contributions can tell exactly the expected fraction of a specified individual's genes comes from any founder or group of founders. But they cannot shed much light on the contributions of a specific founder to a group in the current population (or the whole population, i.e., gene survival). This is because founder contributions are additive over founders but not over current individuals.

In principle any genetic information, not only founder contributions and gene survival distributions, but also population heterozygosities and allele frequencies can be calculated by simulation methods, so-called "gene dropping." Examples of the gene drop method applied to *E. przewalskii* are calculations of distribution of founder allele frequencies in the 1982 population in a paper by MacCluer et al. [1986] and the calculation of genetically important individuals by Jon Ballou appearing in the 1988 SSP Masterplan [Ryder et al., 1988]. As with all simulation methods, gene drop methods have a "sampling error" that depends on the number of simulations performed. Different runs produce different answers to the same problem. Peeling, when feasible, produces exact answers much faster than gene drop can produce approximations of sufficient accuracy to check peeling.

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A software package PEDPACK [Thomas, 1987, Geyer 1988] to perform these calculations has been implemented. It currently runs on a SUN-3/160 and is available to researchers from the second author. It requires a Berkeley-like UNIX operating system (with the C shell) and runs now on SUN workstations running SUN OS 3.x and on VAXes running Berkeley 4.x UNIX. Some of the calculations also require the S statistical language. Portability to other UNIX environments should not be a problem but is not guaranteed.

2 Gene Survival Methodology

The difficulty of these gene survival calculations has up till now prevented their widespread use. The method of peeling [Cannings et al., 1978, Thompson et al. 1978] which is the heart of the gene survival calculation is of exponential complexity in both time and space. The critical index of the size of a gene survival problem is the size of the maximal cutset encountered in the peeling process. This is at least as large as the number of founders, but can be larger if the pedigree is large and has many loops (different paths of relationship between the same two individuals). For all of the pedigrees involved in the calculations reported here, this maximal cutset size was the number of founders, which was twelve not thirteen as is explained below.

The gene extinction calculation requires memory for at least 3^n double precision floating point numbers where n is the maximal cutset size, which for our problem is over four megabytes of memory, not counting memory for the rest of the program. For pedigrees of this size computing time is not a major problem. Each peeling calculation takes less than an hour of computer time on a SUN-3/160 workstation with Floating-Point Accelerator, which does about one third of a million floating point operations per second.

If we had to do gene extinction calculations using the full pedigree for the Przewalski's horse, the calculations would be impossible. The peeling process would require far too much memory. It is a fortunate fact that there is a procedure, which we call "trimming" the pedigree, that converts the original problem to another problem having the same answer but involving a much smaller pedigree.

The trimming procedure deletes many individuals and matings from the pedigree while preserving some information about the number of removed individuals. It proceeds in five steps.

- Remove from the pedigree all dead individuals that have no living descendants. This obviously has no effect on the gene survival calculations, but in the case of the *E. przewalskii* pedigree takes us from an undoable problem with seventy founders to a reasonable-sized problem (still undoable) with thirteen founders.

- Identify all individuals in the pedigree whose parents are completely descended from living individuals. The term “completely descended” from living individuals means that every gene necessarily comes from some other living individual. Such individuals have no effect on gene survival. Whether they are alive or dead, every gene they have has “survived,” because it is a copy of a gene in some living ancestor. Thus it makes no difference (to gene survival) whether such individuals are alive or dead or whether they are in or out of the pedigree. It is convenient to remove as many as we can and consider all those we cannot remove to be alive. (Some must remain if they are ancestors of other individuals that remain.)
- Remove from the pedigree all matings for which all offspring are alive (or have been marked as “alive” in the preceding step) in the process saving the number of offspring removed for each individual. This does not destroy information about gene survival. If a copy of a specified founder gene has descended to one of the individuals in such a mating, the probability of this copy surviving in one of the trimmed offspring depends only on the number of trimmed offspring. It does not depend on who the other parent of the trimmed offspring is.

This “likelihood factorization” idea has been used before in peeling problems [Thomas, 1986], though usually in problems where the factorization was not exact. Thompson [1986b] used this likelihood factorization method to simplify calculations of gene survival in the Przewalski’s horse on a smaller pedigree (the North American population in about 1975). This calculation, however, did not use a general algorithm for trimming pedigrees; the pedigree was trimmed “by hand” with individuals and matings removed by the programmer, not by the program. The calculations reported here are the first in which this method has been fully exploited in a gene survival calculation, and this is by far the largest pedigree for which an exact gene survival calculation has ever been done.

- Remove as many as possible of the individuals who are no longer (because of removed matings) descended from the founders of the original pedigree, since such individuals make no contribution to gene survival.
- Find individuals having no siblings, having parents who are not related, and having ancestors that have no living descendants except those who are descended from the individual in question. Remove all of the ancestors of such individuals thus making these individuals “pseudofounders.”

In the Przewalski’s horse pedigree the only pseudofounder is 113 (Cincinnati 1). It’s parents, the two founders 17 and 18 (Bijsk 7 and 8) had no other offspring. Eliminating 17 and 18 from the pedigree loses no information. If no genes from

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113 survive then neither do any from 17 and 18. If one gene from 113 survives then it is equally likely to have come from 17 or 18. And if both genes from 113 survive then one is from 17 and one from 18. Thus any question about probabilities of survival of genes from 17 or 18 can be answered from knowledge of the probability of survival of genes from 113.

After all of these steps have been performed a complicated pedigree is usually much smaller. For example, in 1970 there were in the world 174 living Przewalski's horses. Their whole pedigree going back to the twelve founders contained another 49 individuals making 223 in all. This pedigree was already, almost twenty years ago, too complex to peel without trimming (on our computer). Figure 1 shows the result of applying the steps just described to the 1970 pedigree. The trimmed pedigree has just 77 individuals. What is more important, the untrimmed pedigree had 87 matings, and the trimmed pedigree just 27. Both in number of individuals and in number of matings, the trimmed pedigree is only about one third the size of the untrimmed pedigree.

The current (1987) pedigree of 1516 individuals and 513 matings would be completely impossible to peel without trimming. Even the first stage of the trimming procedure would be of little use. Removing all individuals with no living descendants leaves a pedigree with 851 individuals and 395 matings. The likelihood factorization (and the remaining steps of the trimming procedure) get the pedigree down to manageable size: 218 individuals and 76 matings, about one seventh the size of the original pedigree.

Trimmed pedigrees like the one in Figure 1 are interesting not just because they can be used for gene extinction calculations, but also because they show the genetic structure of the population much more clearly than the whole pedigree does, the latter being much too complex to present any clear visual impression. In reading Figure 1 it is important to remember that the living individuals have (by definition) two (not necessarily distinct) surviving genes per locus. Individuals with just one living offspring have one gene surviving in their offspring. Individuals with two living offspring have, on average, one and a half of their two genes surviving in their offspring. Individuals with 3 living offspring have (again, on average) one and three quarters genes surviving, and so forth. An individual like 78 with six living offspring shown in the figure and another 16 not shown has almost all of his genes surviving and so may be thought of as "almost" living (in regard to gene survival). An individual like 143 with just one living offspring (not shown) may be thought of as "half" living. Thus Figure 1 clearly shows the gene flow during the whole early history of the captive Przewalski's horse population.

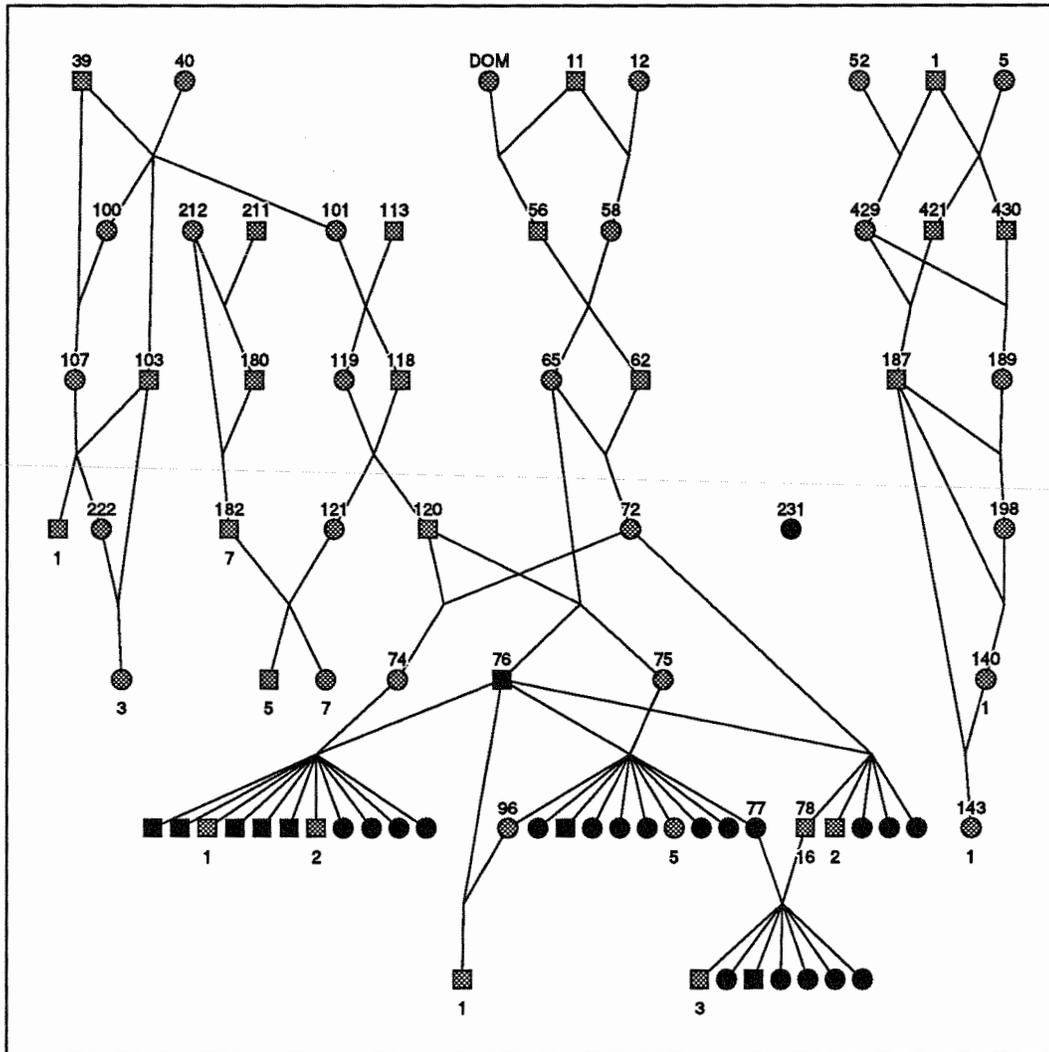


Figure 1: Pedigree of the whole Przewalski's horse population in 1970 after the trimming procedure. Numbers above individuals are their studbook numbers. Numbers below are the number of living offspring an individual had by matings removed from the pedigree by the trimming process. Individuals marked gray were dead in 1970, individuals marked black were alive. The figure is a marriage node plot. Each individual is marked with a large circle (females) or square (males). Each marriage (mating) is marked with a dot. Lines connect each individual to the mating of its parents (going up) and to its own matings (going down).

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Table 1: Distributions of the Number of Surviving Genes in Subpopulations of the Przewalski's Horse Population. Probabilities that a specified subset has a specified number of distinct (not identical by descent) genes at an arbitrary autosomal locus. Subsets: A. The current world population. B. The current North American population (does not include Edmonton). C. All North American females but only males not descended from the domestic horse founder (DOM). D. North American horses not descended from DOM. E. North American males. F. North American males not descended from DOM. G. North American females. H. North American females not descended from DOM. At bottom, mean and standard deviation of the number of distinct genes per locus in each subpopulation.

genes	A	B	C	D	E	F	G	H
3	0.000	0.000	0.000	0.000	0.000	0.001	0.000	0.001
4	0.000	0.000	0.000	0.014	0.000	0.022	0.000	0.018
5	0.000	0.001	0.002	0.116	0.003	0.141	0.002	0.137
6	0.001	0.016	0.020	0.324	0.030	0.343	0.023	0.349
7	0.009	0.083	0.097	0.344	0.125	0.326	0.106	0.330
8	0.052	0.215	0.233	0.164	0.262	0.139	0.244	0.138
9	0.161	0.303	0.305	0.035	0.300	0.026	0.305	0.026
10	0.282	0.242	0.225	0.003	0.194	0.002	0.215	0.002
11	0.281	0.110	0.094	0.000	0.071	0.000	0.085	0.000
12	0.158	0.028	0.022	0.000	0.014	0.000	0.018	0.000
13	0.048	0.004	0.003	0.000	0.001	0.000	0.002	0.000
14	0.007	0.000	0.000	0.000	0.000	0.000	0.000	0.000
mean	10.476	9.129	8.997	6.639	8.769	6.502	8.918	6.514
s.d.	1.309	1.298	1.290	1.058	1.289	1.063	1.285	1.044

3 Gene Survival in Current Population Subsets

This section contains the results of gene survival calculations for the entire current world population of the Przewalski's horse and for a variety of subsets of the North American population that were of interest in discussions of breeding policy in the North American Species Survival Plan. Here and throughout the paper we use "North American population" as a convenient shorthand for the animals in institutions participating in the North American Species Survival Plan, that is, all North American institutions having Przewalski's horses except the zoological park in Edmonton, Alberta.

Table 1 shows the probability distributions of the number of surviving genes (per autosomal locus) in the whole world-wide population of the Przewalski's horse and

Table 2: Mean Number of Surviving Genes from each Founder Group in Subpopulations of the Przewalski's Horse Population. Mean number of genes (both wild type and domestic) per autosomal locus from various founder groups and from all founders that survive in each of the population subsets under consideration. Founder groups: Old Askania Nova (1, 5, 52), Old Prague (11, 12, DOM), Munich-U.S. (39, 40, and 113), Woburn (211, 212), New Askania Nova (231), and all founders together. Subsets: See Table 1.

groups	A	B	C	D	E	F	G	H
1, 5, 52	1.339	1.339	1.339	1.339	1.329	1.329	1.337	1.303
11, 12, DOM	2.121	1.725	1.638	0.000	1.575	0.000	1.638	0.000
39, 40	2.444	1.959	1.948	1.712	1.913	1.686	1.877	1.633
113	1.080	0.974	0.958	0.609	0.925	0.590	0.958	0.609
211, 212	1.741	1.730	1.729	1.729	1.725	1.724	1.724	1.720
231	1.750	1.402	1.385	1.250	1.301	1.174	1.384	1.249
All Founders	10.476	9.129	8.997	6.639	8.769	6.502	8.918	6.514

in specified subsets of the North American population: all combinations of males and females descended and not descended from the domestic mare founder DOM. We give the actual probability distribution rather than the just the mean and standard deviation, which can be quite misleading for a discrete distribution.

From this table we see that the North American population does not yet have all of the genes that are found in the world population. An average of 1.35 genes per locus that are present somewhere in the world population are missing in the North American population. As we shall see from the next two tables, these missing genes are not entirely genes from the domestic mare founder DOM, which have deliberately been bred out of most of the North American population. For non-DOM genes only (Table 3), the North American population is still missing an average of 1.24 genes per locus. This is a bit misleading, since managerial exclusion of genes from DOM necessitates exclusion of genes from 11 and 12 also. If we look only at genes that come from none of the Old Prague founders (11, 12, DOM), the North American population is still missing 0.95 genes per locus that are somewhere in the world population (Table 2). These 0.95 genes, however, need not be in individuals having no descent from DOM. To get a valid comparison it is necessary to calculate the average number of genes per locus in the world population of individuals having no genes from the Old Prague founders (203 individuals in the pedigree we used). This is 7.30 genes per locus, 0.66 genes more than in the North American horses without Old Prague genes. Thus there is still some room for improvement in the genetic diversity of the North American population.

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Table 3: Mean Number of Surviving Wild-type Genes in Subpopulations of the Przewalski's Horse Population. Mean number of wild-type genes per autosomal locus that survive in each of the population subsets under consideration given either of two assumptions about the origin of domestic genes in the population: (1) that the domestic mare founder DOM is the only source of domestic genes and (2) that founder 18 (Bijsk 8) is an F_1 -hybrid. Subsets: See Table 1.

	A	B	C	D	E	F	G	H
DOM only	9.908	8.675	8.568	6.639	8.357	6.502	8.489	6.514
DOM and 18	9.638	8.431	8.329	6.487	8.126	6.355	8.250	6.361
All Genes	10.476	9.129	8.997	6.639	8.769	6.502	8.918	6.514

It is also apparent from Table 1 that the subpopulations D, F, and G, which have no genes from DOM, have fewer surviving genes than the rest, which have some genes from DOM. Again, Table 3 shows that this is the case even if we consider only non-DOM genes. In particular, the North American horses with no descent from DOM have only 6.64 genes per locus (all non-DOM of course), whereas all North American horses have 8.68 non-DOM genes per locus, which is 2.04 more genes per locus than in the horses with no descent from DOM. As mentioned above, part of this difference is unavoidable, since all genes from 11 and 12 are lost when genes from DOM are excluded. Summing a few entries in Table 2 shows that 0.76 of these extra genes are founders other than the Old Prague group, mostly from 39, 40, 113, and 231. Exclusion of genes of DOM from the breeding population results in a large loss of genes, and not just genes from the Old Prague founders. This is the reason for the change of breeding policy mentioned in the introduction.

Figure 2 shows the same phenomenon in graphic form. Shown are the whole world population, the whole North American population, and subsets of the North American population which are all combinations of males, females, or both and inclusion or exclusion of horses descended from DOM. As discussed above, there is a large difference in number of surviving genes between the world population and the North American population. Surprisingly, there is little difference between the whole North American population and any of the subsets that contain any DOM genes at all. The distance separating the five groups in the middle of the figure (the North American groups with any DOM genes), just 0.32 genes per locus, is only about a quarter of the distance between the world population and the North American population, which is 1.23 genes per locus. There is little difference between the number of genes in just the males and the genes in the males and females together. Similarly, the distance separating the three subsets at the bottom of the figure (the North American groups with no DOM

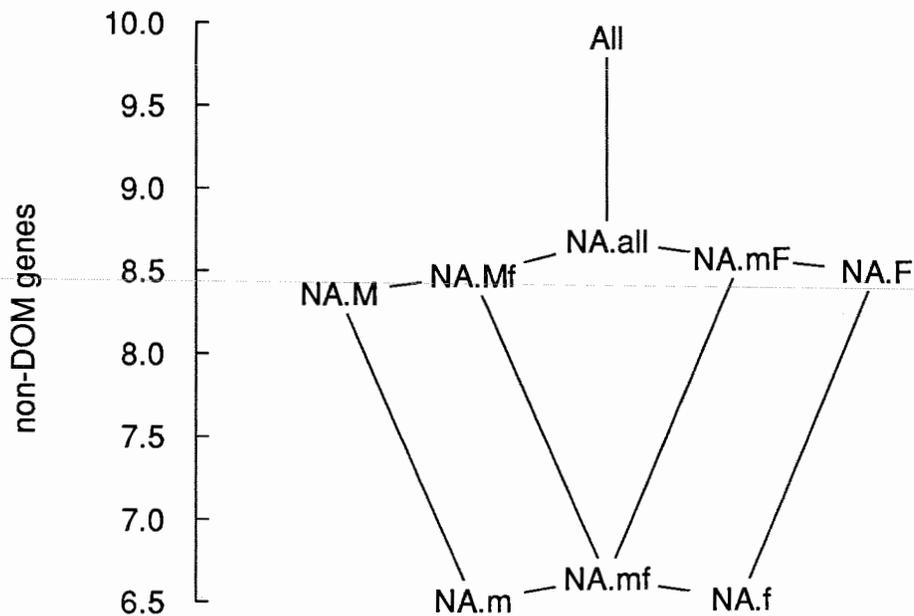


Figure 2: Population Subsets Ordered by Average Number of Non-DOM genes per Locus. Subsets are those tabulated in Table 1 plus one more: (All) The current world population. (NA.all) The current North American population (does not include Edmonton). (NA.Mf) All North American males but only females not descended from the domestic horse founder (DOM). (NA.mF) All North American females but only males not descended from DOM. (NA.mf) North American horses not descended from DOM. (NA.M) North American males. (NA.m) North American males not descended from DOM. (NA.F) North American females. (NA.f) North American females not descended from DOM.

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genes), just 0.14 genes, is much less than the distance separating the middle group from the bottom group, which is 1.72 genes. Any attempt to completely exclude DOM genes even from just part of the population results in the loss of a large number of non-DOM genes.

4 History

The current population of the Przewalski's horse is descended from thirteen founders, twelve Przewalski's horses and one domestic horse and hence there are a maximum of 26 distinct genes (24 wild, 2 domestic) at an autosomal locus. Today the average number of distinct genes at an autosomal locus is 10.476. When were the other genes lost?

Table 4 shows the probability distributions of gene survival at four times in the past (1930, 1950, 1960, and 1970) and at the present. It shows that there was a rapid and steady loss of genes from the beginning of the captive population (about 1900) until 1970 and that the loss since 1970 has been much slower. Note that the coefficient of variation (standard deviation divided by the mean) of the gene survival distribution has steadily increased over time from zero in 1908 when the first of the original founders died. The distribution has gotten (relatively) wider with passing time. The spread increased by 10 per cent between 1970 and today while the mean decreased by only three percent.

Figure 3 shows the mean number of surviving genes per locus from each of six groups of founders. The groups are arranged from bottom to top in order of increasing amounts of gene loss. At the bottom is the number of genes from 231, who died in 1973 so none of her genes were lost before then (and few since). At the top is the Old Askania Nova line from which most of the genes have been lost (1.34 remaining, 4.66 lost out of 6). The other severe loss has been in the line from 17 and 18 in which only 0.61 of the original 4 remain. Of course in this line two genes were lost as soon as 17 and 18 had both died (1935), since they had only one offspring (113 who died in 1943). A similar event occurred in the Woburn line. All of the Woburn genes pass through one individual, 182 (London 6, Neville), who carried on average 1.75 of the original 4 genes of the Woburn founders, 211, 212 (Woburn 6 and 7). Since 182 had 19 offspring almost all of the genes he carried have survived. As shown in Table 2, 1.741 of his 1.75 genes (99.5 per cent) have survived to the present day.

Figure 4 shows the mean number of surviving genes per locus plotted against population size. As long as the world population remained rather small, less than 46 individuals (the peak in 1939 not reached again until 1957), gene loss continued at a rapid rate. Note that the population actually declined throughout the 1940's reaching a low of 27 individuals in 1946 and again in 1950. In early 1963 the population size

Table 4: Distributions of the Number of Genes Surviving in the Przewalski's Horse Population in 1930, 1950, 1960, 1970, and Now. Probabilities that a specified number of distinct (not identical by descent) genes at an arbitrary autosomal locus were present in the population at the date specified. At the bottom are the mean, standard deviation (s.d.), and coefficient of variation (c.v.) for each year

genes	1930	1950	1960	1970	1988
6	0.000	0.000	0.000	0.000	0.001
7	0.000	0.000	0.000	0.002	0.009
8	0.000	0.000	0.001	0.023	0.052
9	0.000	0.000	0.010	0.106	0.161
10	0.000	0.001	0.055	0.252	0.282
11	0.000	0.008	0.167	0.316	0.281
12	0.000	0.049	0.282	0.212	0.158
13	0.000	0.158	0.274	0.075	0.048
14	0.000	0.285	0.154	0.012	0.007
15	0.000	0.290	0.049	0.001	0.000
16	0.000	0.161	0.008	0.000	0.000
17	0.001	0.043	0.001	0.000	0.000
18	0.009	0.004	0.000	0.000	0.000
19	0.066	0.000	0.000	0.000	0.000
20	0.261	0.000	0.000	0.000	0.000
21	0.446	0.000	0.000	0.000	0.000
22	0.217	0.000	0.000	0.000	0.000
mean	20.795	14.473	12.454	10.859	10.476
s.d.	0.888	1.269	1.325	1.241	1.309
c.v.	0.034	0.088	0.106	0.114	0.125

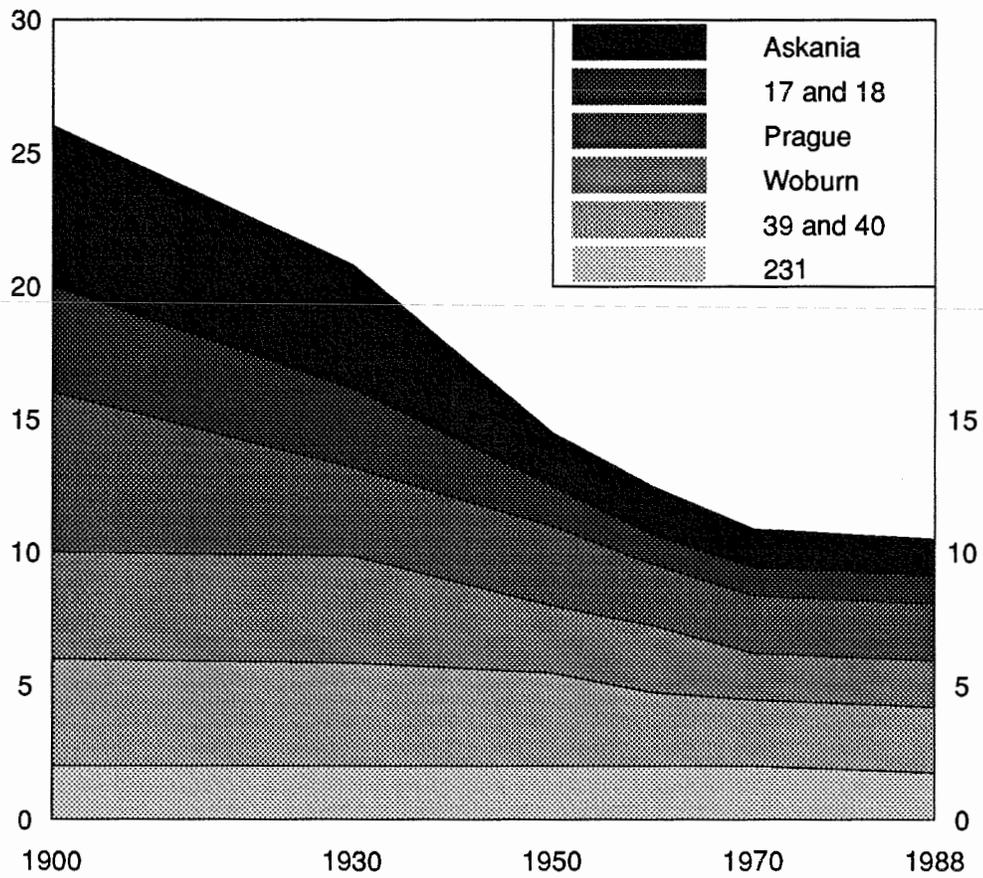


Figure 3: Number of Surviving Genes from Founder Groups through History. The founder groups are Askania (Old Askania Nova line, 1, 5, and 52), 17 and 18, Prague (Old Prague line 11, 12, and DOM), Woburn (Woburn line, 211 and 212), 39 and 40, and 231 (New Askania Nova line).

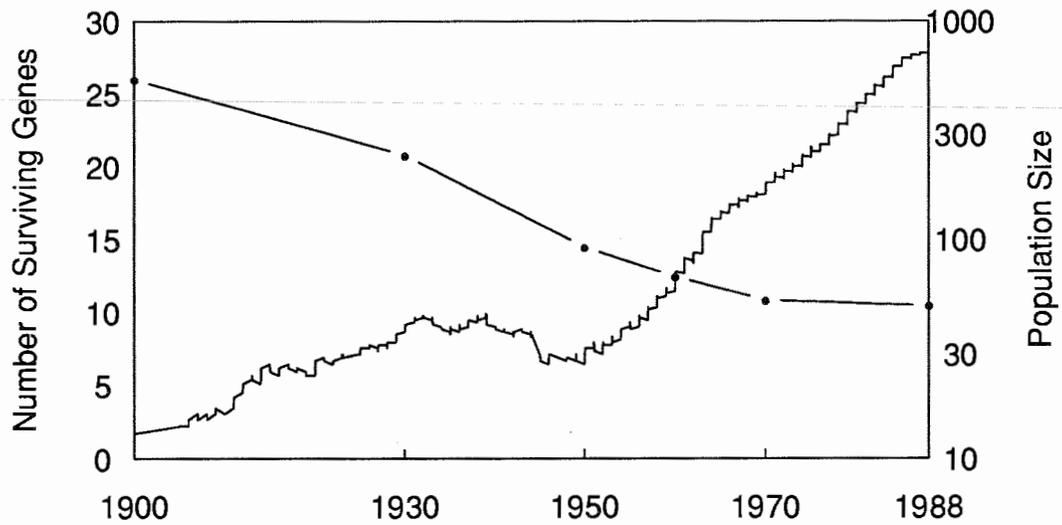


Figure 4: Gene Survival versus Population Size. The declining line is number of surviving genes (axis on left), and the increasing line is population size (axis on right). Note the log scale for population size.

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reached 100 individuals, and since then the population size has doubled about every nine years. At about the same time (1965–70) the rate of gene loss markedly slowed. There has been very little loss since 1970. Note that appreciable gene loss continued for some time after the rapid population increase began. There is a time lag since genes of individuals past reproductive age continue to be lost even if unrestricted population growth preserves most of the genes found in individuals of reproductive age.

Figure 3 makes it clear that almost all of the loss of genetic diversity in the Przewalski's horse occurred over the part of the pedigree shown in Figure 1. On the right side of the figure the Old Askania Nova line descended from the three founders 1, 5, and 52 (Kobdo 1, 5, and C; Vaska I, Staraja, and Staraja II) passes through 5 generations, without any inflow of genes from the rest of the population, down to just two individuals 140 and 143 (Hellabrun 13 and 16, Ella and Selpa) each of which had just one offspring still alive in 1970. It is this severe constriction that caused most of the loss of genes of the Old Askania Nova founders.

From Figure 1 it appears that there were never more than a few of the Old Askania Nova horses, but the figure only shows the horses whose genes are not completely extinct. There were 53 other descendants of the three Old Askania line founders not in the line of descent to the current population (the line through 140). If the three offspring of 140 and 143 were still living, there would only be an average of only 1.550 genes per locus surviving from the Old Askania Nova founders, only 0.211 more than the 1.339 genes per locus that actually survive. On the other hand, if the 53 other descendants were still living, there would be an average of 5.740 genes per locus surviving. Thus the lack of any genetic contribution of the 53 other descendants to the current population resulted in a loss of 4.19 of the 6 genes of the Old Askania Nova founders. Most of these 53 individuals died before 1947, but six died in 1951–55 and one in 1962.

Constrictions similar to the one in the Old Askania Nova line can be seen in the other branches of the pedigree. For each of the other founder subgroups, the Prague line from 11, 12, DOM, the Woburn line from 211 and 212 (Woburn 6 and 7), and the Munich–U. S. line from 39, 40, and 113 (Bijsk A and B and Cincinnati 1), there are no more descendants two or three generations later than there were founders. For two or three generations below the founders the pedigree hardly spreads out at all.

Figures 1 and 3 tell only part of the story of gene loss in this species. There were besides the thirteen founders that have any descendants in the current population 57 other Przewalski's horses captured in the early 1900's that could have added to the genetic diversity of the current population but did not. All of their genes have been lost. Most of these horses, unfortunately, were in private collections and not bred.

Table 5: Genetically Important Horses in the North American Population. Mean number of unique copy genes from specified founder groups and from all founders in the horses 1124 (Hellabrun 92, Sirtaki), 826 (Askania 47, Vata), 831 (Askania 48, Varna), 718 (Marwell 28, Janus), 1166 (Marwell 68, Cleo), and 615 (London 30, Kuporovitch).

	1124	831	826	718	1166	615
1, 5, 52	0.0001	0.0000	0.0000	0.0000	0.0000	0.0000
11, 12, DOM	0.0000	0.0000	0.0000	0.0016	0.0065	0.0190
39, 40	0.0357	0.0011	0.0005	0.0007	0.0030	0.0021
113	0.0000	0.0016	0.0007	0.0011	0.0044	0.0031
211, 212	0.0029	0.0002	0.0001	0.0001	0.0002	0.0000
231	0.0000	0.0226	0.0156	0.0088	0.0352	0.0000
All Founders	0.0387	0.0255	0.0169	0.0123	0.0493	0.0241

5 Genetically Important Individuals

Gene survival calculations can tell us about the genetic importance of individuals or groups of individuals. Suppose that we have specified two population subsets, call them the *reference group* and the *index group*, the latter being a subset of the former. If we calculate the average number of surviving genes (per autosomal locus) in the reference group and in the part of the reference group that excludes the index group, then the difference between these two averages is the average number of genes per locus that are found in the index group but not in any other individuals in the reference group. We call this the number of *unique copy* genes in the index group (relative to the specified reference group).

Table 5 shows the number of unique copy genes for several horses (the ones with the largest number of unique copy genes) in North America relative to the reference group of all North American horses. This is a measure of the genetic importance of these individuals to the North American Species Survival Plan. Some of the “unique copy” genes in these horses do exist in horses living outside of North America, but they are found in no other living North American horses.

From the table it is clear that 1124 (Sirtaki) is important because of the unique copy genes from the Munich line founders 39 and 40 that he carries, that 831, 826, 718, and 1166 (Vata, Varna, Janus, and Cleo) are important because of the unique copy genes of the new Askania Nova founder 231 (Orlitza III) that they carry, and that 615 (Kuporovitch) is important because of the unique copy genes of the Old Prague founders 11 and 12 that he carries (this means, of course that 615 also carries

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genes of the domestic mare founder DOM).

The recognition of the genetic importance of 615 and 718 (first suggested not by our calculations but by simulations by Jon Ballou using the gene dropping method [Ryder, et al., 1988]) coupled with the change in the breeding program allowing stallions with descent from DOM to be bred has already lead to a decision to breed both 615 and 718 again even though both are descendants of the domestic mare founder and thus were not allowed to breed under the policy in force in the last several years. (615 does have two living offspring, both born in 1980, and 718 has two, both born in 1983.)

The four horses (831, 826, 718, and 1166) that are important primarily because of the unique copy genes of 231 they carry are examined in Figures 5 and 6. Just from the numbers in the next-to-last row of Table 5 we see that 1166 is the most important and 718 the least, but why? Figure 5 shows the lines of descent from 231 of all of her North American descendants including these four genetically important horses.

From this pedigree we see that 718 and 1166 are full sibs and so have exactly the same probabilities of having 0, 1, or 2 genes from 231. The sole reason why 1166 is more important than 718 is that she has no offspring yet (she was born in 1983) while 718 has two. The genes that 718 has passed on to his offspring are not unique copy genes. Much the same can be said about 826 and 831. Their relationship to 231 is complicated, but calculations show that their probabilities of having 0, 1, or 2 genes from 231 are quite similar. The main reason why 826 is less important than 831 is that she has more offspring (three for 826 versus two for 831).

This emphasizes the necessity of using the most up-to-date pedigree information available when discussing genetic importance. Every time any individual is born or dies the genetic importance of every individual in the pedigree can change. (One such event has occurred since we did our calculations: 1166 now has one offspring and so is less important than before.)

That genetic importance is not just a matter of how many offspring an individual has, is shown by 718 and 831, which have the same number of offspring, but 831 is two and a half times as important as 718 (0.023 unique copy genes of 231 per locus for 831 versus only 0.009 for 718). This occurs because 826 and 831 are much more closely related to 231 than are 718 and 1166.

A glance at the pedigree shows that these four genetically important individuals are in two closely related pairs, one being 718 and 1166 and the other being 826 and 831. These pairs have kinships relative to 231 of 0.03125 and 0.1680 respectively. (The kinship of two individuals relative to a founder is the probability that a gene drawn at random from each is a copy of a gene in that founder. The sum of the kinships relative to all founders is the kinship.) Although 718 and 1166 are full sibs they are not very closely related relative to 231. Either has exactly the same relative kinship to 826 as they do to each other and almost as large a relative kinship (0.02734)

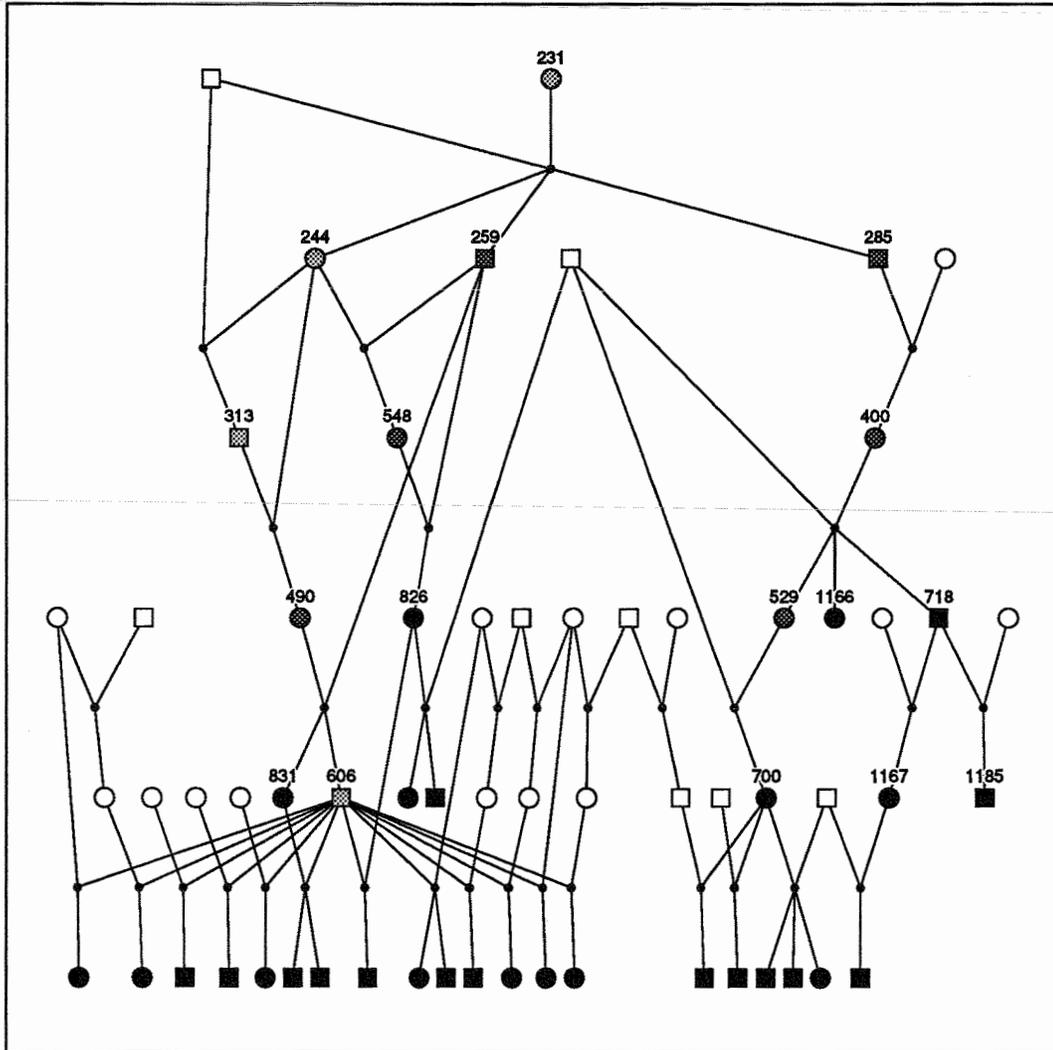


Figure 5: Pedigree of the North American descendants of 231 showing their lines of descent from 231 (Note that descendants of 231 having no descendants in North America are not shown). Numbers above individuals are their studbook numbers. Individuals marked white are not descended from 231. Those marked light gray are dead descendants of 231. Those marked dark gray are living descendants of 231 not resident in North America (259, 490, and 548 are in Askania Nova, 400 and 529 are in Marwell, and 285 is in Munich). Those marked black are living descendants of 231 in North America. The figure is a marriage node plot. Each individual is marked with a large circle (females) or square (males). Each marriage (mating) is marked with a dot. Lines connect each individual to the mating of its parents (going up) and to its own matings (going down).

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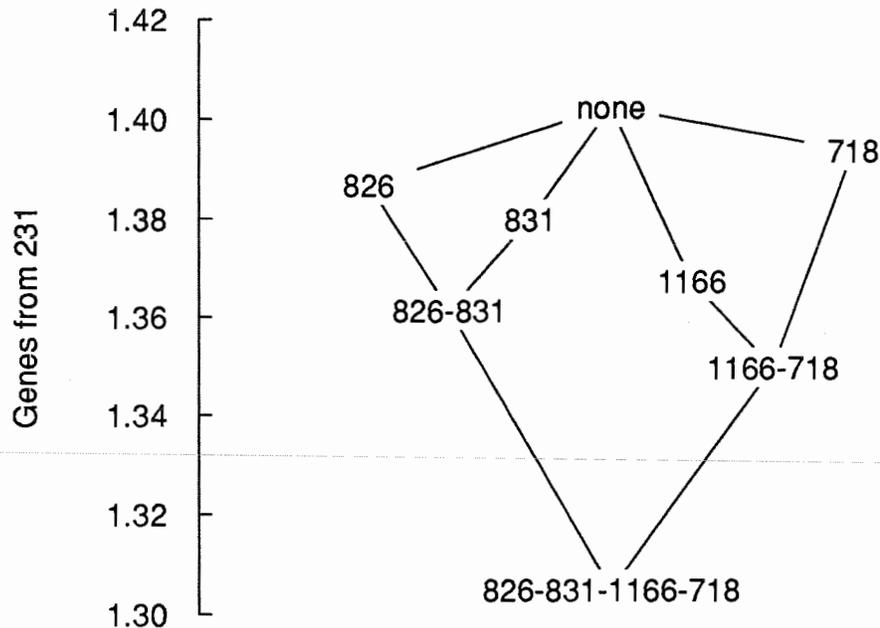


Figure 6: Genetically Important North American Descendants of 231 (Orlitzia III). Plotted are the number of genes of 231 that would remain in the North American population if 826 (Askania 47, Vata), 831 (Askania 48, Varna), 718 (Marwell 28, Janus), or 1166 (Marwell 68, Cleo) were to die without having any more offspring and also the number of genes that would remain if several groups of these were to die. At the top (labeled "none") is the current number of surviving genes of 231 in the North American population.

to 831.

Figure 6 shows the genetic importance of these two pairs, of the four individuals separately, and of the four as a group. Note that in the figure an individual or group is *more* genetically important if it is *lower* down on the figure. This shows that each of the two pairs is important. A large fraction of the unique copy genes in 826 and 831 are not in 718 and 1166 and vice versa. Similarly a large fraction of the unique copy genes in 826 are not in 831 and vice versa. The same cannot be said about 1166 and 718. By herself 1166 is almost as important as together with 718.

6 Conclusion

This paper and its predecessor [Geyer and Thompson, 1988] have demonstrated important applications of gene survival calculations. All are useful tools in the management of a captive population. The genetic diversity of a subset of the current population is an important consideration in deciding whether such a subset is an acceptable breeding group or a suitable group for release into the wild. The time sequence of gene survival in the whole population of *E. przewalskii* as shown in Figures 3 and 4 gives us insight into the management of captive populations that might be a useful example telling us something about managing populations for which genetic information necessary for gene extinction calculations is not available. The calculations of the genetic importance of specific individuals, as discussed in Section 5, has already had an influence on the management of the *E. przewalskii* breeding program, and can be expected to continue to have an important influence. As the individuals mentioned in Section 5 have more offspring and hence become less genetically important, other individuals will become (relatively) more important.

All of these results demonstrate the importance of exact gene survival calculations whenever possible. They contain a very large amount of information about the genetic diversity of a population. Much of what we have discovered about gene survival in the North American population of *E. przewalskii* was not expected before the calculations were done. Only a few of these calculations had even been attempted by other methods, and nothing close to this precision had been obtained previously.

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Blood Markers in Przewalski's Horses

Genetic studies of blood markers in Przewalski's horses

ABSTRACT: Ninety-six Przewalski's horses (*Equus przewalskii*) were blood typed using systems of inherited blood variants known to be highly effective for parentage testing of domestic horses (*E. caballus*). Sixteen red cell antigenic factors detected using sera prepared by alloimmunization of domestic horses were shown to be inherited in six systems (A, C, D, P, Q, and U) and in the same patterns as domestic horses. Family data confirmed autosomal, codominant inheritance at five loci of serum protein variants (Al, Tf, Xk, Pi, and Es) and three loci of red cell proteins (PGM, PHI, and Hb). One serum protein locus (Gc) and two red cell protein loci (PGD and CA) appeared to be monomorphic. Despite the narrow genetic base and high inbreeding coefficients of captive Przewalski's horses, average heterozygosity calculated over 18 loci was estimated to be 0.320 ± 0.05 , which was similar to that found in five breeds of domestic horses.

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PRZEWALSKI'S HORSE (*Equus przewalskii*) is the only living species of wild horse. So-called wild horses found in several regions of the world, such as sparsely populated areas of the western United States, are feral domestic horses (*E. caballus*) and not true wild horses. The two species are visibly distinct and have a difference in chromosomal number² but are quite closely related as shown by studies of cranial and skeletal features¹⁴, chromosomes²², and blood type markers^{7,10,18-20,23,26,30}. The interspecific cross yields fertile offspring²⁷.

Przewalski's horse probably had a range in prehistoric times throughout Europe and into Asia. It is thought to be extinct in the wild and the only remaining examples are about 600 animals in zoo collections (see cover). A studbook maintained by Volf³¹ traces the pedigrees of all animals within about 11 generations to no more than 13 founder animals from Mongolia: 11 animals obtained at the turn of the century, one mare caught in 1947, and a domestic pony mare (*E. caballus*).

Separate breeding lines occur. The Munich line traces its ancestry back to nine of the wild-caught horses. The Prague line includes wild-caught horses, as well as the domestic horse. Munich line breeders have been reluctant to introduce descendants of the domestic mare into their stock and thus separate breeding lines have evolved²¹.

The small number of founders and the iso-

lation of animals in small zoo populations has led to high inbreeding coefficients. In North America the average inbreeding coefficient for the Munich line is 0.273 and for the Prague line, 0.142²¹. Continued inbreeding within small populations is thought to lead to homozygosity and narrow the base of genetic diversity, perhaps rendering the species unable to adapt to environmental changes. The cheetah may become the classic example of such a scenario^{16,17}. Data showing increased juvenile mortality and decreased life-span in Przewalski's horses^{3,4} provide reason for concern for the long-term survival of the remaining zoo populations of this species as well.

Genetic studies of Przewalski's horses may provide important information about breeding management. Knowledge of discrete, assayable genetic variants can be applied to assure accurate animal identification. Genetic variants also can be used to verify parentage, thus ensuring accuracy of the studbook record, the base used to calculate various genetic parameters such as inbreeding coefficients, linkage, drift, and amount of genetic variability in individuals or populations. Analysis of red blood cell surface antigens and electrophoretic/isoelectric focusing studies of blood proteins provide a means to examine genetic variation and to make variability and heterozygosity comparisons with other species. This study presents gene frequency data for 18 loci of Przewalski's horses

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and compares the polymorphisms and average heterozygosity with data similarly obtained for five breeds of domestic horses.

Materials and Methods

Two 10-ml blood samples were submitted from each horse, an ACD anti-coagulant tube to use as a red cell source and a dry tube as a serum source. Blood samples were sent to the laboratory at ambient temperature, then refrigerated until tests were completed. A total of 96 Przewalski's horses was tested (48 females, 48 males), 70 of which were of the Munich line. None of the animals traced to the mare caught in 1947. Thirty-nine horses were tested more than once, some as many as 10 times, affording the opportunity to verify types and extend the markers detected as new techniques and systems were added.

Standard immunological procedures involving hemagglutination and complement mediated hemolysis^{28,29} were used to detect red cell antigens. Reagents were produced by alloimmunization in *E. caballus*, followed by extensive testing and absorption of the immune sera using red cells of domestic horses until each reagent behaved as monospecific. Samples were tested with as many as 40 reagents of different specificities that recognize factors for domestic horses at seven blood group loci. Not all animals were tested for all the factors. The factors summarized in this report are as follows (listed as the system in capital letters, followed by lower case letters for each factor of the system): Aabdefg, Ca, Dabdefghikno, Ka, Pabc, Qa, and Ua. As many as 14 additional reagents were used which have not yet been assigned international nomenclature. Alleles appeared to be similar to those encountered in *E. caballus*; assignment was based on reaction patterns and analysis of family data. Nomenclature used was in accord with that agreed upon for *E. caballus* by the International Society for Animal Blood Group Research (ISABR).

Standard methods of starch^{6,25} and polyacrylamide¹³ gel electrophoresis were used to identify inherited variants at the following loci: albumin (*Al*), transferrin (*Tf*), esterase (*Es*), *Xk*, *Gc*, protease inhibitor (*Pi*), 6-phosphogluconate dehydrogenase (*PGD*), phosphoglucomutase (*PGM*), phosphohexose isomerase (*PHI*), catalase (*Cat*), carbonic anhydrase (*CA*) and acid phosphatase (*AP*). Polyacrylamide gel isoelectric focusing was used for the detection of α -hemoglobin variants (*Hb*)⁸.

When gel variants appeared to be indistinguishable from those of domestic horses, nomenclature used was that agreed upon by ISABR members for *E. caballus*. Variants

designated with square brackets are those for which terminology has not yet been standardized for *E. caballus*. *Tf*-[*E*] is found infrequently in some breeds of domestic horses. Under both starch and polyacrylamide gel conditions, the *Tf*-[*E*] variant migrates just slightly cathodally to *Tf*-*D* and differs from other *Tf* variants in that the two bands characteristic of transferrins are of approximately equal staining intensity, whereas other variants have distinct major and minor bands. This variant corresponds to that called *Tf*-[*E*₂] by others^{10,20}.

Electrophoretically assayed variants that seem to be unique to *E. przewalskii* are identified by braces; e.g., *Tf*-{*D**}; *Tf*-{*I*}; *Es*-{*P*}; *Pi*-{*P*}; *Xk*-{*P*}. *Tf*-{*D**} corresponds to *Tf*-*E*₁ of others^{10,20}. *Tf*-{*I*} may be unique to Przewalski's horses. Under conditions of our gels it seems to correspond in position to an infrequently seen variant of domestic horses designated *Tf*-[*H*₂], but is lighter staining. *Es*-{*P*} is an allele apparently unique to Przewalski's horses, best distinguished with

isoelectric focusing¹¹, but also seen with polyacrylamide electrophoresis. *Pi*-{*P*} is a fast migrating type of protease inhibitor that probably corresponds to *Pi*-*D* in another study²⁰ but was not subdivided under our conditions. The other *Pi* variant observed in these samples is apparently the same as *Pi*-*S*₁ in domestic horses. It has been agreed by ISABR members that the *Pa* locus will now be designated *Xk* and variants will be designated by the *Xk* terminology. *Xk*-*F* and *Xk*-*K* appear to correspond to those variants found in domestic horses; *Xk*-{*P*} under polyacrylamide gel conditions is slightly faster than the slow variant (*Xk*-*S*) seen in domestic horses.

Breed data for domestic horses were taken from Bowling and Clark⁵. For determining gene frequencies of Przewalski's horses, all 96 animals were considered members of one breeding group. Blood group frequencies were calculated as follows: for single factor systems *C*, *P*, *Q*, and *U*, assuming Hardy-Weinberg equilibrium, the frequency of the

Table I. Inheritance of blood factors in Przewalski's horses shown by distribution of phenotypes in offspring from various matings

Mating*	Phenotypes of offspring			
A system (N = 44)	Aa	Aa/Ace	Ace	
Aa × Aa	2	0	0	
× Aa/Ace	14	13	0	
Aa/Ace × Aa/Ace	4	6	3	
× Ace	0	1	1	
C system (N = 45)	Ca		-/-	
Ca × Ca	15		4	
× -/-	18		7	
-/- × -/-	0		1	
D system (N = 44)	Dadn	Dadn/Dcg	Dcg	Dcg/dn
Dadn × Dadn/Dcg	0	2	0	0
× Dadn/Ddn	1	0	0	0
Dadn/dn × Dadn/Dcg	2	6	4	0
× Dcg	0	13	11	0
× Dcg/Ddn	0	1	1	0
Dcg × Dcg	0	0	2	0
× Dcg/Ddn	0	0	0	2
P system (N = 31)		Pac		-/-
Pac × Pac		1		0
× -/-		7		9
-/- × -/-		0		12
Q system (N = 44)		Qa		-/-
Qa × Qa		14		6
× -/-		5		10
-/- × -/-		0		9
U system (N = 44)		Ua		-/-
Ua × Ua		3		1
× -/-		13		11
-/- × -/-		0		16

* N = number of matings for which sire, dam, and offspring were blood typed

null allele was taken as the square-root of the frequency of the null class and the frequency of the named factor was 1 minus the frequency of the null allele; for *A* and *D* by direct counting, assuming no null allele and no ambiguous phenotypes. Allelic frequencies for protein polymorphisms were determined by direct counting from phenotypes, with the addition of family data for *Es* to define animals heterozygous for the null allele. The computer program of Dowling and Moore⁹ was used to calculate Nei's measures of normalized genetic identity (*I*) and standard ge-

netic distance (*D*) between two populations¹⁵. Average heterozygosity also was calculated with this program.

Results and Discussion

Family data showing the inheritance of red cell antigenic markers are shown in Table I. As in domestic horses, factors detected by reagents behaved as autosomal (data not shown) codominants. In the *A* and *D* systems some alleles were determined by a combination of two or three factors (e.g., *Ace*, *Dadn*).

Undetectable alleles acting as recessives to those specificities detected by reagents were present at the *C*, *P*, *Q*, and *U* loci, as in domestic horses. At the *A* locus, both *A^{adf}* and *A^{adg}* were found (as well as *A^{ce}*) but too few families were tested with reagents Ad, Af, and Ag to include in the family data or determine gene frequencies. If reagents had been made using red cells from Przewalski's horses for hetero- or alloimmunization, it is possible that additional variants might have been detected.

Family data for markers detected by electrophoresis and isoelectric focusing are shown in Tables II and III. Markers are inherited as autosomal (data not shown), codominant alleles, as in domestic horses.

Analysis of genetic data for parents and offspring confirmed the studbook record of parentage for all animals in this study. Gene frequency data are given for six loci of red cell antigens in Table IV and for eight other loci of polymorphisms in Table V. Loci that were monomorphic are not included in the tables, but variants found and numbers tested are as follows: *Ka⁻* (92); *PGD^F* (76); *Gc^F* (60); *CA^I* (28).

Many alleles of Przewalski's horse appeared to be shared with *E. caballus*, and the most common variants at each locus were often the most common found in domestic horses as well (e.g., *Aa*, *Ca*, *Xk-K*, *PGD-F*, *PHI-I*, and *Gc-F*). An exception was the higher frequency in Przewalski's horses of

Table II. Inheritance of electrophoretically detected serum protein variants in Przewalski's horses shown by distribution of phenotypes in offspring from various matings

Mating†	Phenotypes of offspring									
Albumin (Al) (N = 44)	A		AB		B					
AB × B	0		4		5					
B × B	0		0		35					
Transferrin (Tf) (N = 45)	{D*}	[E]	F ₂	{D*}[E]	{D*}F ₂	[E]F ₂	{D*I}	[E]{I}	F ₂ {I}	
[E] × [E]F ₂	0	1	0	0	0	0	0	0	0	0
F ₂ × [E]F ₂	0	0	1	0	0	2	0	0	0	0
× F ₂	0	0	2	0	0	0	0	0	0	0
{D*}[E] × {D*}F ₂	0	0	0	1	0	1	0	0	0	0
× {D*I}	0	0	0	0	0	0	0	1	0	0
× [E]{I}	0	1	0	1	0	0	1	1	0	0
{D*}F ₂ × [E]F ₂	0	0	0	1	3	3	0	0	0	0
× {D*I}	0	0	0	0	1	0	0	0	0	0
× [E]{I}	0	0	0	1	0	1	0	0	0	0
× F ₂ {I}	0	0	2	0	1	0	0	0	0	0
[E]F ₂ × [E]F ₂	0	1	1	0	0	1	0	0	0	0
× F ₂ {I}	0	0	5	0	0	7	0	0	2	0
{D*I} × {D*I}	0	0	0	0	0	0	1	0	0	0
[E]{I} × [E]{I}	0	1	0	0	0	0	0	0	0	0
Xk (N = 42)	FK	F{P}		K	K{P}		{P}			
F × K	2	0		0	0		0			
FK × F{P}	4	0		0	1		0			
× K	9	0		9	0		0			
× K{P}	1	1		0	1		0			
K × K	0	0		12	0		0			
× K{P}	0	0		1	1		0			
Esterase (Es) (N = 41)	{P}	I	H	I{P}	H{P}	HI				
{P} × {P}	1	0	0	0	0	0				
× I{P}	1	0	0	1	0	0				
× HI	0	0	0	1	0	0				
× I	0	0	0	2	0	0				
I{P} × I{P}	4	0	0	4	0	0				
× H{P}	0	0	0	1	0	0				
× {P}**	5	0	0	1	0	0				
× HI	0	1	0	0	0	0				
× I**	9**	0	0	10	0	0				
**May have Es-O										
Protease inhibitor (Pi) (N = 41)	{P}	{P}S		S						
{P} × {P}	21	0		0						
× {P}S	10	4		0						
× S	0	1		0						
{P}S × {P}S	2	1		1						
× S	0	0		1						

† N = number of matings for which sire, dam, and offspring have been blood typed. Square brackets [] are used to designate variants found in both *E. przewalskii* and *E. caballus* for which a standard nomenclature has not been determined. Braces { } are used to designate variants apparently unique to *E. przewalskii*.

Table III. Inheritance of electrophoretically detected variants of red cell proteins in Przewalski's horses shown by distribution of phenotypes in offspring from various matings

Mating	Phenotypes of offspring		
Phosphoglucosyltransferase (PGM) (N = 17)	F	FS	S
F × F	1	0	0
× FS	6	4	0
FS × FS	1	3	2
Phosphohexose isomerase (PHI) (N = 13)	I	IS	S
I × I	2	0	0
× IS	4	1	0
× S	0	1	0
IS × IS	1	3	1
α-Hemoglobin (Hb) (N = 18)	I	I/II	II
I × I/II	2	2	0
× II	0	5	0
I/II × I/II	0	1	0
× II	0	1	6
II × II	0	0	1

PGM-F compared to *PGM-S*. Four loci (*Tf*, *Xk*, *Es*, and *Pi*) had alleles apparently unique to Przewalski's horses.

We are not aware of published gene frequencies for red cell antigens of Przewalski's horses, but the specificities are similar to those reported previously. Factor *Qa* has not been previously reported for European zoo animals^{7,18,26}. In our study *Qa* was found only in Munich line animals. Other apparent exceptions seen in red cell antigen data comparisons, particularly in the *A* and *D* systems,

Table IV. Gene frequencies for red cell antigens of Przewalski's horses

Locus	N*	Allele	Freq
<i>A</i>	91	<i>a</i>	0.63
		<i>ce</i>	0.37
<i>C</i> [†]	89	<i>a</i>	0.46
<i>D</i>	92	<i>cg</i>	0.72
		<i>adn</i>	0.25
		<i>dn</i>	0.03
<i>P</i> [†]	90	<i>a</i>	0.24
<i>Q</i> [†]	90	<i>a</i>	0.18
<i>U</i> [†]	90	<i>a</i>	0.18

* *N* = number of horses tested for the specificities
[†] The frequency of the alternative allele (a "negative allele" for which no antiserum is reactive) at these loci is 1 minus the value given here

Table V. Gene frequencies for blood protein polymorphisms in Przewalski's horses

Locus	N*	Marker	Gene freq
<i>Al</i>	96	<i>A</i>	0.09
		<i>B</i>	0.91
<i>Tf</i>	96	{ <i>D</i> *}	0.20
		[<i>E</i>]	0.40
		<i>F</i> ₂	0.30
		{ <i>I</i> }	0.10
<i>Xk</i>	96	<i>F</i>	0.24
		<i>K</i>	0.69
		{ <i>P</i> }	0.07
<i>Es</i>	95	<i>H</i>	0.05
		<i>I</i>	0.29
		{ <i>P</i> }	0.59
<i>Pi</i>	68	<i>O</i>	0.07
		{ <i>P</i> }	0.82
<i>PGM</i>	46	<i>S</i>	0.18
		<i>F</i>	0.77
<i>PHI</i>	36	<i>S</i>	0.23
		<i>I</i>	0.77
<i>Hb</i>	45	<i>S</i>	0.23
		<i>BI</i>	0.46
		<i>BII</i>	0.54

* *N* = number of horses tested. Square brackets [] indicate variants found in both *E. caballus* and *E. przewalskii* for which an internationally uniform nomenclature has not been established. Braces { } indicate variants apparently unique to *E. przewalskii*

can be explained as being due to a more extensive battery of reagents in the present report.

Polymorphisms of serum and red cell proteins are similar to those published previously for Przewalski's horses with a few exceptions that are mostly due to nomenclature differences. We were unable to confirm previous reports of polymorphism for *CA*¹⁰ or *AP*⁷, but have tested relatively few samples for these loci.

We noted polymorphism for *Cat* (*Cat-M* = 21 animals; *Cat-F* = 7 animals), but by Hardy-Weinberg testing this distribution of phenotypes and lack of *Cat-S* types does not fit the domestic horse model in which the *M* phenotype is the heterozygote for *F* and *S* alleles. The population data suggest that the *Cat-M* type of Przewalski's horses be interpreted as homozygous for a slow allele, and the *F* type as heterozygous for a slow and a fast allele. In this model, the homozygous

fast type has not yet been seen by us. Thus, one or both *Cat* alleles of *E. przewalskii* may be different from those of *E. caballus*. We did not include the *Cat* locus in the comparisons of Table VII.

Family data and gene frequencies for four serum (plasma) protein loci were reported by Putt and Whitehouse²⁰ using 130 animals, which was largely a non-overlapping set of individuals with ours. Their technique of isoelectric focusing for diagnosis of *Tf*, *Pr* (*Pi*), *Pa* (*Xk*) and *Es* allowed the discrimination of more variants at *Pi* and *Tf* than reported in this study. In their population, *Tf*-{*I*} and *Tf*-{*D**} were in higher frequency than in ours. In our population, the fastest migrating *Xk* variant (*Xk-F*) was at a higher frequency than the slow one (*Xk-P*), but in their study the frequencies were in a reverse relationship. Whether the same variants were being detected by the two techniques remains to be determined.

Table VI. Number of blood type variants per locus with a gene frequency equal to or greater than 0.001 in *E. przewalskii* and five breeds of *E. caballus*

Locus	Breeds of <i>E. caballus</i> *					<i>E. przewalskii</i> PZ
	TB	AR	ST	MH	QH	
RBC antigenic alleles (33) [†]						
<i>A</i>	5	5	6	8	6	2
<i>C</i>	2	2	2	2	2	2
<i>D</i>	8	8	11	11	12	3
<i>K</i>	2	2	2	2	2	1
<i>P</i>	3	3	3	3	3	2
<i>Q</i>	2	2	2	2	2	2
<i>U</i>	2	2	2	2	2	2
RBC total:	24	24	28	30	29	14
Serum proteins (37)						
<i>Al</i>	2	2	3	3	2	2
<i>Tf</i>	6	5	7	9	10	4
<i>Es</i>	3	4	5	7	7	4
<i>Xk</i>	2	2	3	3	3	3
<i>Pi</i>	8	9	8	8	8	2
<i>Gc</i>	2	2	2	2	2	1
Protein total:	23	24	28	32	32	16
RBC proteins (15)						
<i>PGD</i>	2	3	2	2	3	1
<i>PGM</i>	2	2	2	2	2	2
<i>PHI</i>	1	2	2	3	3	2
<i>CA</i>	2	2	3	2	3	1
<i>Hb</i>	2	2	3	2	3	2
RBC protein total:	9	11	12	11	14	8
Combined RBC & protein total (85)						
	56	59	68	73	75	38

* Breeds are: TB = Thoroughbred, AR = Arabian, ST = Standardbred, MH = Morgan horse, QH = Quarter horse

[†] Numbers in parentheses are total numbers of variants detectable in *E. caballus* with the methods applied

With the exception of *Pi*, the gene frequency data show the loci to be in Hardy-Weinberg equilibrium, despite small population size, inbreeding, and the presence of breeding line traditions that have maintained the Munich line separate. For *Pi* the data showed an excess of *Pi-S* homozygotes and a deficiency for *Pi-FS* ($\chi^2 = 12.46$; $P < 0.01$). It is possible that this effect was due to breeding line differences, although both variants exist in both lines. The *Pi-FS* type might occasionally have been scored in error as *Pi-F*, but since most animals were typed several times, and types carefully rechecked if they did not agree with the previous record, this explanation is not compelling. Perhaps application of the isoelectric focusing technique²⁰, which discriminated five *Pi* alleles for Przewalski's horses, might resolve the apparent conflict.

The number of variants detectable at each locus in Przewalski's horses is compared with the number of variants detectable in five breeds of domestic horses (Thoroughbred, Arabian, Standardbred, Morgan horse and Quarter horse) in Table VI. These breeds can be classified as "riding type," not draft horses or ponies. Thoroughbreds and Standardbreds are primarily bred as sport horses (racing); the others are primarily bred for show ring competition and pleasure riding. Fewer alleles were recognized in the Przewalski's horse samples than those of the domestic horses, noticeably for the *A*, *D*, *Tf*, and *Pi* loci for which 10 or more alleles each have been described in domestic horses.

Measures of normalized genetic identity (*I*) and standard genetic distance (*D*) between two populations¹⁵ for five breeds of domestic horses and Przewalski's horse were

calculated over 18 loci: *A*, *C*, *D*, *K*, *P*, *Q*, *U*, *Al*, *Tf*, *Xk*, *Es*, *Pi*, *Gc*, *PGD*, *PHI*, *PGM*, *CA*, and *Hb*. Average heterozygosity (J_x) for each breed also was calculated. The results are shown in the matrix of Table VII.

The distance measurements showed the domestic horses clustered rather closely at a value of about 0.9 or greater; the relationship of Przewalski's horse to any of the domestic breeds was about 0.7 or slightly greater. These values might be interpreted to indicate evolutionary divergence at the level of subspecies rather than full species¹, which is consistent with other measures of divergence (e.g., skeletal, chromosomal, reproductive performance of hybrids).

Average heterozygosity for Przewalski's horses calculated over 18 loci was estimated to be 0.320 ± 0.050 . This number was slightly higher than that of Thoroughbreds and lower than that of Arabians, Standardbreds, Morgan horses, and Quarter horses, but taking standard error into consideration, the differences were not significant. In light of the narrow genetic base and high inbreeding coefficients of captive Przewalski's horses, this high level of heterozygosity was unexpected. It might be argued that the heterozygosity is an artifact of combining the horses into a single population, ignoring breeding lines. However, with the exception of one locus, the sample tested was determined to be in Hardy-Weinberg equilibrium, so this explanation is not persuasive. The heterozygosity might be due to contamination of the stock with domestic horses. The restricted range of variants found in Przewalski's horses, compared with domestic horses, suggests that the extent of contamination is minimal and not

likely to be more widespread than the one known cross. One is led to speculate what relationship the Przewalski's horse data may have to the recent report¹² of a great excess of genetic variation in 10 inbred strains of mice compared to expectation.

ADDENDUM: In the course of testing more animals, a third *Pi* marker has been found that may explain the deviation from Hardy-Weinberg equilibrium observed with the previous data. In addition, animals descending from the 1947 wild-caught mare have now been typed and found to possess markers *Tf-D*, *Tf-F₃* and *CA-F* as well as markers found in the Prague and Munich lines.

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Table VII. Normalized genetic identity, *I*, standard genetic distance, *D*, and average heterozygosity, J_x^* , for *E. przewalskii* and five breeds of *E. caballus* at 18 loci[†]

	Breeds of <i>E. caballus</i>					<i>E. przewalskii</i>
	TB	AR	ST	MH	QH	PZ
TB	0.313	0.096	0.110	0.081	0.084	0.367
AR	± 0.062	± 0.051	± 0.041	± 0.038	± 0.053	± 0.132
ST	0.909	0.330	0.075	0.054	0.020	0.269
MH		± 0.059	± 0.027	± 0.030	± 0.011	± 0.098
QH	0.896	0.928	0.397	0.021	0.068	0.295
PZ			± 0.052	± 0.011	± 0.032	± 0.108
	0.922	0.947	0.980	0.369	0.054	0.262
				± 0.059	± 0.036	± 0.103
	0.919	0.980	0.934	0.948	0.377	0.246
					± 0.060	± 0.094
	0.693	0.764	0.744	0.770	0.782	0.320
						± 0.050

* Nei's *I* (genetic identity) is below the diagonal. *D* (genetic distance) is above the diagonal. J_x (average heterozygosity) is on the diagonal. Standard error values are given for *D* and J_x .

† Loci and frequency values used for domestic horses were from Bowling and Clark⁵ and for Przewalski's horses from Tables IV and V.

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PRZEWALSKI'S HORSE

Equus przewalskii

**GLOBAL CONSERVATION PLAN
D R A F T**

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10 February 1990

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Recommended breeder code for individual identification of Przewalski-Horses. The code is to use together with the breeder number, e.g.

DE 8 is: 1495 M Denver 8 Gino.

Adelaide	AD	Gdansk-Oliva	GO	München	H
Alma-Ata	AA	Genk	GE	Münster	MU
Anvers	AN	Gramat	GR	Neumünster	NM
Arnhem	AR	Habana	HB	Neuwied	NW
Askania Nova	A	Halle	HA	New York	YO
Barcelona	BA	Helsinki	HL	Nieborow	NB
Bekesbourne- Lympe	HO	Herberstein	HR	Nikolaev	NI
Berlin-Ost	BT	Hilvarenbeek	HI	Norderheide	NO
Berlin-West	BZ	Jersey	JE	Nürnberg	NU
Bern	BE	Karaganda	KA	Oberwil	OB
Bernburg	BG	Karl-Marx-Stadt	KM	de Ooij	OJ
Braniewo	BO	Karlsruhe	KR	Paignton	PG
Bratislava	BR	Keokuk	KE	Paris	PA
Brownsville	BV	Kiev	KV	Peking	PE
Budapest	BU	Kingussie	KI	Pforzheim	PF
Calgary	CG	Kisinev	KS	Poznan	PO
Canyon	CC	Köln	KO	Praha	P
Cardigan	CN	Krakow	KW	Riga	RI
Catskill	CA	Kurgan	KN	Roma-Bordi	RB
Cavriglia	CV	Langenberg	LG	Rostock	RK
Cevennes	CS	Leipzig	LE	Rostov	RO
Chester	CH	Lelystadt	LL	Rotterdam	BP
Chiba	CB	Leningrad	LN	Sababurg	SA
Chicago-Bell- Ranch	CR	Lodz	LZ	Salzburg	SG
Colombo	CO	London	LO	San Diego	SD
Colwyn Bay	CL	Los Angeles	LA	Schwerin	SN
Denver	DE	Lymington	LY	Seul	SE
Dubbo	DU	Marwell	MA	Springe	SP
Duisburg	DG	Memphis	ME	Stuttgart	ST
Edmonton	ED	Midway Manor	MM	Taipei	TI
Front Royal	WN	Minnesota	LK	Tallinn	TA
Frösön	FR	Montpellier	PA	Taskent	TS
		Moskva	MO	Termez	TE

Thot à Thonac	TT
Tokyo	TK
Topeka	TO
Toronto	TR
Urumchi	UR
Weilburg	WB
Whipsnade	LO
Wien	WI
Woburn	WO

About freeze branding

Material: types and numbers of the breeder code (aluminium-blocks, 3x1/2cm)
liquid nitrogen
bowl of styropor (which doesn't conduct heat)
gloves

1. Shave the site of the freeze brand. If the brand should be hidden, it can be placed at the inner side of the thigh, so that it is only readable, if the horse moves its tail.
2. Clean the place with warm water, which contains some rinsing agent, to remove the fat of the skin.
3. Fill the liquid nitrogen into the styropor-bowl and wait until it doesn't bubble any longer
4. Dip in the types and numbers and wait until these are cold enough (N₂ doesn't bubble any longer).
5. Press the types firmly at the shaved and cleaned site: for 1 minute
6. The freeze brand isn't visible until 3 - 4 weeks, when the reactions of the skin are finished. Because of the long winter coat, the brand is mostly not readable during winter.

PRZEWALSKI'S HORSE

Equus przewalskii

**GLOBAL CONSERVATION PLAN
D R A F T**

**APPENDIX IV
REINTRODUCTION CRITERIA**

10 February 1990

The Przewalski horse

and restoration
to its natural habitat
in Mongolia

FAO²³
ANIMAL
PRODUCTION
AND HEALTH
PAPER

61

FAO/UNEP Expert Consultation
held in Moscow, USSR
29-31 May 1985



FOOD
AND
AGRICULTURE
ORGANIZATION
OF THE
UNITED NATIONS
Rome, 1986

CRITERIA FOR SELECTION OF INDIVIDUAL ANIMALS

- I. GENETIC CRITERIA
 1. Studbook registered.
 2. Genetic contribution from all founders should be represented by individuals designated for breeding propagules. This includes genetic contributions from the domestic mare with 6% Domestic Mare Average in the propagule and no individual 15% Domestic Mare. Ages not specified. Average founder contribution should be represented within the female cohort.
 3. Unique individual (in sense of pedigree) should not be designated and thus protect the captive population.
 4. Measure of sanguinity (default to F or the coefficient of inbreeding). Average F of potential offspring in propagules should be 0.3 or 0.25.

- II. HEALTH CONTROL CRITERIA
 1. Top constitution and condition, excellent health status, normal behaviour, correct hoofs, descent of testes.
 2. Vaccinations:
 - a. Virus abortion (Herpes)
 - b. Tetanus
 - c. Rabies
 - d. Horse influenza
 - e. Additional vaccinations according to the local infection situation of domestic horses in Mongolia (*Rickettsia*, *Malleomyces mallei*, and other).
 - f. Additional vaccinations against local infections in the country donating the horses.
 3. Parasites control:
 - a. Roundworms: *Parascaris equorum* e.a. (Mebendazol 10 mg/kg, 7 consecutive days or 500 ppm M. 14 days or Fenbendazol 5 mg/kg 7 days.

Deworming of the animals every 2 months 6 times before the transport, even with negative faeces control test.

- b. Tapeworm, Gastrophilus, (fluke?), and other local parasites (ticks): Treatment only if animals are infested according to the treatment schedule recommended for domestic horses.

Clear up Trypanosoma situation in Mongolia.

- c. Ectoparasites: Mallophagae, ticks, lice, etc.: Animals must be free of ectoparasites during 6 months before transport. Animals from a breeding centre and possibly infected with scabies are generally excluded from a restoration programme.

4. Medical requirements:

Additional to the necessary veterinarian equipment:

- a. Large animal Immobilon
- b. Revivon (3x more than L.A. Immobilon)
- c. Hyaluronidase
- d. Ivermectin
- e. Mebendazol/Fenbedazol
- f. Injectable selenium
- g. Oral vitamin/mineral mixture containing selenium

5. Technical requirements:

- a. Freeze branding tools
- b. Blow pipe and Airinject system (70 metre range). Do not use in any case hot gas systems. Recommend: Telinject System.

CRITERIA FOR SELECTION OF WILD AND SEMI-WILD RESERVES

- I. WILD RESERVES (FINAL RELEASE SITE) (These are taken from the paper of Miller which is included with the collection of papers.)
 1. Historic occurrence - has the Przewalski horse been found here in the past?
 2. Land status - who controls use of the land?
 3. Topography - is the topography suitable for the horse?
 4. Cover - what is the vegetative cover?
 5. Range condition - what is the condition and trend for the forage plants?
 6. Presence of domestic animals - what domestic animals are present and are they competitors or carrying diseases to which the horse is vulnerable. Are domestic and feral horses present and in what numbers and distribution?
 7. Presence of wildlife - what wildlife species are present and are they competitors or disease sources? Are wolves or other predators of horses present?
 8. Human disturbance - what level of human use does the area receive? Are the horses likely to be subject to poaching?
 9. Available water - what quantity and quality of water is available on a year-round basis and at how many sites?
 10. Dispersion and size of the habitat area - what is the size of the available area? How are the resources such as food, cover, and water dispersed and distributed? How much of the area will be unavailable due to topography or seasonal changes?
 11. Potential for expansion - is there a potential to expand the area if the population does well?
 12. Fencing - are there potential problems with existing or planned fences? Will it be possible or necessary to fence the reserve area? What will be the cost?

13. Seasonal habitat - are the seasonal needs of the animal such as wind cover, forage, water, and foaling areas available?

II. SEMI-WILD RESERVE (INTERMEDIATE ADAPTATION SITE)

1. An area of not less than 5000 hectares providing all year round ranging requirements for a group of horses including forage and water. It should provide territory necessary for formation of natural social grouping - harems or bands - which will allow the horses to acquire and demonstrate the normal behavioural patterns of wild horses. If necessary for the survival of the horses in the judgment of the management specialists, additional feeding may be provided.
2. Dry steppe climate which is close to the environmental conditions (or biotope) of the release site in Mongolia.
3. Competent research, breeding, zootechnical, veterinary, and administrative services.
4. Can support several harems or bands which reproduce on a natural selection basis.

**CRITERIA FOR NUMBERS OF PRZEWALSKI HORSES FOR A
REINTRODUCTION PROGRAMME**

1. Should be at least 2 populations initially.

2. Founders for each population:

There should be 20-30 individuals because of harem structure. It is suggested that they be: 15-20 females and 10-15 males over a 1 to 3 age span if yearlings are chosen. The composition will differ for the construction of a band from older animals and would include a stallion and up to 10 mares.

3. Carrying capacity (=Ultimate size for each population)

Suggest: 200 to 1000.

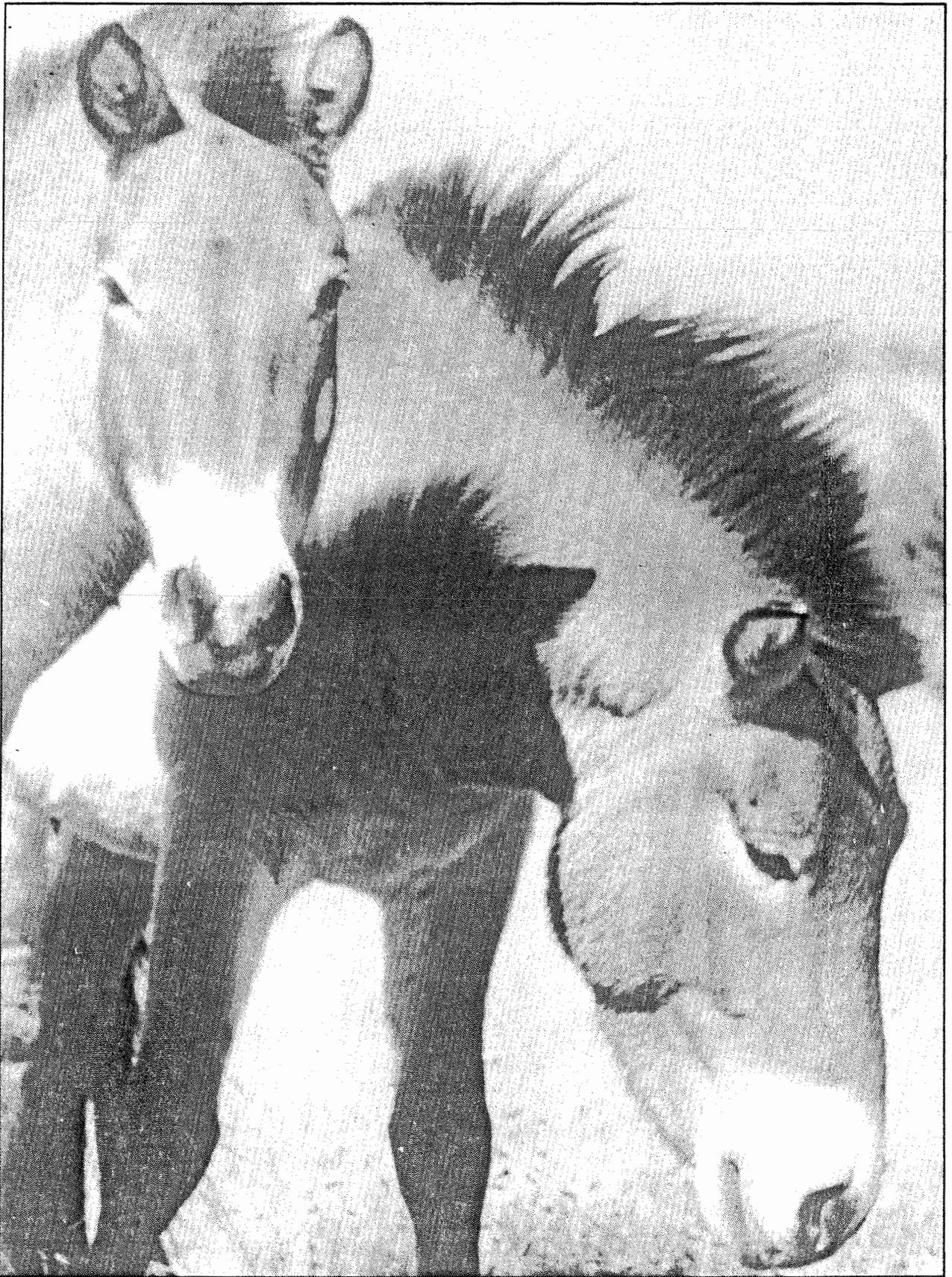
PRZEWALSKI'S HORSE

Equus przewalskii

**GLOBAL CONSERVATION PLAN
D R A F T**

ATTACHMENT I

10 February 1990



Asian Wild Horse Species Survival Plan
Masterplan 1989

Asian Wild Horse Species Survival Plan

**Masterplan
1989**

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Acknowledgements

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A particular debt is owed to Charles J. Geyer of the Department of Statistics, University of Washington, for his calculation of gene survival in population subsets.

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Introduction

Following the meeting of the Asian Wild Horse SSP propagation group in Portland in 1987, a working group was identified to consider the demographic status and the results of gene extinction studies of the SSP sub-populations and produce a draft masterplan for the management of the SSP population. On 1.I.88, the Przewalski's horse census for the SSP population stood at 55.85. The working group met in San Diego March 7-8, 1988, and produced an outline of this draft masterplan for consideration of the Asian Wild Horse SSP Propagation group. In formulating the recommendations for the future management presented here in draft form, consideration was given to the unique aspects of this species in captivity, including the presence of genes from domestic horses in the population and the recent availability of new methodologies for analysis of gene extinction in complex pedigrees.

Genetic Analyses

Pedigrees have been constructed based on the original studbook (Mohr, 1961) and subsequent work of studbook keeper Dr. Jiri Volf at the Prague Zoo (Volf, 1961 *et seq.*). Przewalski's horses have been bred in captivity for twelve generations. Although there were 70 potential founders only thirteen animals left descendants that contribute to the pedigrees of the living animals. As *Equus przewalskiis* thought to be extinct in the wild (Sokolov and Orlov, 1985; Ryder, 1988), there seems to be no possibility to incorporate new founders.

The pedigree of Przewalski's horses in captivity reveals a number of complex features, including bottlenecks, a founder of alleged hybrid ancestry, genetic contributions of a Mongolian domestic mare (in approximately two thirds of living horses worldwide), and a new founder entering the pedigree 54 years after the initiation of captive breeding (Ryder and Wedemeyer, 1982; Dolan, 1982; Volf, 1959 *et seq.*; MacClure, et al., 1986; Geyer and Thompson, 1988). These complexities have resulted in several suggestions for managing the captive population (Heck, 1980; Ryder and Wedemeyer, 1982; Bouman, 1980), but the genetic sequelae of these various plans has been difficult to assess due to the pedigree complexities.

Founder contribution has been calculated by the traditional methods based on data included in the 1987 studbook reflecting the status of the captive population on 1.I.1987 (Figure 1).

Target Founder contributions, calculated to reflect the adjustments necessary when considering that founder genes have already been lost due to bottleneck effects was calculated by the formula:

$$TFC_x = \frac{S_x}{\sum_{i=1}^{13} S_i} \quad (1)$$

TFC_x — Target Founder Contribution of Founder x
 S_x — proportion of Founder x's genome surviving to SSP population

Table 1 presents the founder contributions for the SSP populations and the target founder contributions, which is affected by the proportion of the genome surviving, (determined in this instance from gene drop simulations). These values are depicted graphically in Figure 1. The identification of genetically important animals (individuals possessing unique genes from under represented founders) can be made based on differing computational approaches to the determination of gene extinction probabilities (Geyer et al., 1989). Table 2 contains a listing of individuals that contain founder genes especially useful for achieving the target founder contribution goals. Individuals listed in Table 2 may be useful for either the sub-population possessing genes from #11, #12, and the Mongolian domestic mare, the sub-population lacking genes from

#11, #12, and the Mongolian domestic mare, or both sub-populations. Individuals with founder coefficients greater than the overall sub-population's target founder contribution would, by the production of offspring tend to move the sub-population founder contributions toward the target founder contribution. The distribution of founder coefficients within the SSP population is depicted in Figure 2.

The distribution of genes not identical by descent has been calculated for the entire studbook population and a variety of populations subsets according to the peeling procedure of Cannings and Thompson (1982) which allows the determination of probabilities that 0, 1, or 2 genes not identical by descent from each founder have been transmitted to any individual or set of individuals within the pedigree. These data are presented in Table 3.

Both the gene drop and peeling approaches for examination of gene extinction within pedigree address an issue that founder effect calculations alone cannot, viz., the likelihood that an individual possesses a distinct gene descended from one founder may diminish (or increase) the likelihood of that individual possessing a distinct gene from another founder.

The contributions of some of the founders are inextricably linked. This correlation can be observed qualitatively by an examination of the pedigree. Quantitative estimates of founder contribution concordance can be displayed by the construction of a matrix depicting the numbers of animals with contributions from pairs of founders, and the proportions those animals represent of all living individuals that include contributions from each of the pair of founders (Table 4). This same phenomenon is also apparent in the results of pedigree peeling (Table 5).

A matrix of the coefficients of inbreeding of potential offspring produced as a result of matings between living males and females within the SSP population were calculated (Appendix 1). A matrix of inbreeding coefficients for all possible matings within the world population has also been produced (Canyon Colorado Equid Sanctuary, 1987) but is not reproduced here.

Demographic Analyses

The age structure by sex was determined for the world population (Table 6 and Figure 3), for the SSP population (Table 7 and Figure 4), for the subset of the SSP population possessing genetic contributions from the Mongolian domestic mare as depicted in the International Studbook (Table 8 and Figure 5), and for the SSP population lacking genetic contributions from the Mongolian domestic mare as depicted in the International Studbook (Table 9 and Figure 6).

Age specific survivorships and fertilities were determined for the world Przewalski's horses (Table 10 and Figure 7), for the SSP population (Table 11 and Figure 8), for the subset of the SSP population possessing genetic contributions from the Mongolian domestic mare as depicted in the International Studbook (Table 12 and Figure 9), and for the SSP population lacking genetic contributions from the Mongolian domestic mare as depicted in the International Studbook (Table 12 and Figure 10).

In order to meet demographic and genetic objectives for the SSP, the number of individuals to be managed as a population with a stable age distribution must be defined. This number, referred to as the carrying capacity, is larger than the minimum estimate for a viable population but has an upper limit that incorporates consideration of the facilities and resources available for all taxa in zoological parks. The establishment of the number of individuals for the population at carrying capacity requires delineation of the objectives for genetic management of the population.

Objectives and Their Derivation

Genetic Objectives

Identification of Sub-Populations for Management

The SSP populations of *Equus przewalskii* currently contains two sub-populations that differ in their genetic contributions from founder individuals, their apparent growth rates (Tables 3, 8, 9), and the proportion of their residual genetic variation derived from the Mongolian domestic horse. The extent to which the two sub-groups differ in the number of surviving genes from wild type Przewalski's horse founders (Geyer and Thompson, 1988; Geyer et al., 1989) is presented in Table 10. Although the two population sub-groups identified in the current management plan contain 97.7% (8.997 genes) of the total number of surviving genes in the current SSP population (9.219 genes), the selection against the Mongolian domestic mare results in the selection against wild type genes carried by founders #11 and #12 and would, over time, reduce the number of surviving genes in the SSP population. There are additional unique founder genes surviving in the entire International Studbook pedigree that are not present in the North American SSP population subset. These include genes derived from #11, #12 and the Mongolian domestic mare, but also include genes from other founders (Table 5b). Currently incorporating a mean of 9.129 surviving genes, the North American population (excluding Edmonton) includes 87.1% of the surviving genes from the thirteen founders (Table 3). The proportion of wild type *E. przewalskii* genes surviving worldwide represented within the North American population is 87.5% (Table 5b).

A management plan that strives to preserve the maximum number of genes from the founders in a single population requires introduction of genes from the Mongolian domestic mare into horses whose ancestral contributions lack genetic input from the Mongolian domestic mare. There is reluctance to adopt such an approach, particularly from breeders whose collections consist of Przewalski's horses that lack genetic input from the Mongolian domestic mare as depicted in the International Studbook. The largest single collectively managed population of Przewalski's horses lacking genetic contribution from the Mongolian domestic mare as depicted in the International Studbook resides within North America and is part of the Asian Wild Horse SSP.

However, if two population sub-groups are maintained and separately managed from retention of different combinations of founder genes (e.g., with and without #11, #12 and Mongolian domestic mare), a larger number of genes surviving from the founders could be managed while preserving future options involving the introduction of the genes from the Mongolian domestic mare into the populations lacking genes from the Mongolian domestic mare. Gene flow from the population lacking #11, #12, and the Mongolian domestic mare to the population with genetic contributions from #11, #12 and the Mongolian domestic mare could occur through horses of either sex for the purposes of increasing the number of genes surviving from founders under represented in the subpopulation. Gene flow of wild type founder genes into the SSP sub-population lacking

genetic input from the Mongolian domestic mare may be accomplished by the transfer of selected individuals from outside North America who lack genetic input from #11, #12 and the domestic Mongolian mare.

This later strategy emerged as the consensus plan because it meets the objectives of managing for the survival of the largest possible number of genes possible while still preserving a sub-group of Przewalski's horses lacking genetic contribution from the Mongolian domestic mare as depicted in the International Studbook and thereby preserving options for future management.

The revised management plan now stipulates that stallions as well as mares possessing genetic contributions from #11, #12 and the Mongolian domestic mare be utilized for breeding as is reflected in the breeding recommendations for each institution (see Appendix 1). This reflects a change from earlier strategies.

Managing Genetic Diversity

In the process of producing this masterplan the working group established average heterozygosity as the currency of genetic variability. In addition, the numbers of unique genes from founder individuals (genes not identical by descent) was also utilized as an appropriate measure of surviving genetic variation in the entire captive population and its sub populations.

Temporal Goals for Retention of Genetic Diversity

The Asian wild horse SSP will attempt to preserve 90% of current average heterozygosity for a period of 200 years.

Carrying Capacities

By comparison to extensive work performed by other SSPs, the size of the genetically effective population necessary for achieving the stated genetic objectives of retention of 90% of residual heterozygosity over 200 years is:

$$N_e = \frac{1}{(1 - e^{-(\ln \Delta H/T)})} \quad (2)$$

The census population sizes necessary for retention of average heterozygosity as a function of three different ratios of effective to census population size (N_e/N) have been calculated according to formula (2) and are presented in Table 11. A generation time of 14 years, resulting in a total of 14 generations of management were used in the calculations for estimation of census population size necessary for meeting genetic goals for a population at carrying capacity.

Consideration of these results led to the following consensus suggestions for the carrying capacity of the two sub populations. For the sub-population lacking genetic input from the Mongolian domestic mare, a carrying capacity of 222 animals will meet the above stated goals for the retention of average heterozygosity. For the population with genetic representation from the Mongolian domestic mare and including the wild type genes of founders #11 and #12, a carrying capacity of 111 will be established. The smaller carrying capacity of the sub population with genes from #11, #12 and the Mongolian domestic mare was judged appropriate because: 1) a carrying capacity for the total North American Asian wild horse SSP population of 333 animals represents a realistic goal (Table 13), 2) other regional programs are managing the genetic contributions of #11, #12 and the Mongolian domestic mare in larger populations, i.e., the EEP, 3) the genetic contributions of #11, #12 and the Mongolian domestic mare are at little risk of extinction in the world population (MacClure et al., 1986; Geyer et al., 1989) and 4) gene flow from the sub-population lacking Mongolian domestic mare genes is planned.

Demographic Objectives

Both sub-populations are currently below the designated carrying capacity. The sub-population lacking genes from #11, #12 and the Mongolian domestic mare is currently at an approximate size of 108 animals (49% of carrying capacity). The sub-population possessing genetic contributions from #11, #12 and the Mongolian domestic mare is currently at approximately 48 animals (43% of carrying capacity). Thus, both populations need to continue to grow.

Rates of population growth could be at the rates achieved by the current SSP population since 1975 (Tables 7, 8 and 9). Female demographic parameters are judged to be less artificial than those for males and were chosen for consideration in the population projections. During the period of population expansion a generation time of 10 years has been used for the demographic calculations necessary to manage the population growth to the designated carrying capacities for individuals descended from over represented founders, under represented founders, and for individuals whose founder contributions are at parity. While recognizing that some error is potentially introduced through this method, the working group felt that 1) it was appropriate to distinguish the generation time of the population in its growth phase from the generation time when the population was at carrying capacity and 2) there was concern that a generation time of 14 years, as was recommended for the population at carrying capacity, would not allow for population growth of 10% per year for the total SSP population (16%/year for the sub-population possessing genetic contributions from #11, #12 and the Mongolian domestic mare and 7%/year for the sub-population lacking genetic contributions from #11, #12 and the Mongolian domestic mare).

The number of female offspring required on the average from each individual over its lifetime to sustain the observed rates of population growth are the R_0 's (2.933 for the sub-population possessing genetic contributions from #11, #12 and the Mongolian domestic mare, 2.01 for the sub-population lacking genetic contributions from #11, #12 and the

Mongolian domestic mare and 2.44 for the total SSP population). If we assume or adopt an average growth rate of 10%/year and a generation time of 10 years, the R_0 prescribed would be 2.6, i.e., this value is the number of female offspring required to sustain this rate of population growth. Double this number, i.e., 5 offspring, would represent the total number of offspring that would be required.

However, this required number of offspring really refers to the number of progeny that will themselves survive to reproduce. To determine the number of individuals that must be born in order to produce an average of 5 offspring that survive to themselves reproduce, the survivorship for the total SSP population to age 10 (the generation time chosen for this phase of the population growth curve), $L_x = 0.689$, was divided into 5 (desired offspring). Thus 7.26 ($5 \div 0.689$) represents the total number of offspring that must be born to each animal to insure that 5 will, on the average, survive to reproduce.

Since it was also decided to adopt a 1:2 male:female sex ratio (that is, each reproductive male produces, on average, twice the number of offspring an average reproductive female produces) the best sex distribution of the offspring would be 2/5. This is the average to be sought after and represents the number of offspring indicated in Table 12 for females approximately at parity for their founder contributions.

In order to meet genetic goals, females descended from under-represented founders should on average produce more surviving offspring while females descended from over-represented founder should on average produce fewer surviving offspring. Nonetheless, the average number of offspring surviving to reproduce from all reproductive females should be 2 males and 5 females. These values are presented in Table 12.

Current census populations and estimated carrying capacities for SSP participant institutions are presented in Table 13.

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- Table 13. Current census populations and estimated carrying capacities for SSP participant institutions.

FOUNDER	TARGET FOUNDER CONTRIBUTION		CURRENT FOUNDER CONTRIBUTION	
	SSP NON-DOMESTIC (1)	WORLD (2)	ALL SSP	SSP NON-DOMESTIC
231	0.187	0.168	0.039	0.050
212	0.185	0.120	0.336	0.370
39	0.139	0.126	0.119	0.128
40	0.118	0.107	0.101	0.107
1	0.097	0.060	0.081	0.078
211	0.075	0.048	0.112	0.123
5	0.055	0.032	0.040	0.039
52	0.051	0.031	0.040	0.037
17	0.047	0.052	0.037	0.032
18	0.046	0.052	0.037	0.032
11	*****	0.095	0.029	----
DOM	*****	0.055	0.015	----
12	*****	0.055	0.015	----

Table 1. Target founder contributions for North American populations.
N equals 51. *Note 1:* Based on gene drop of 5000. *Note 2:* Based on Thompson's Gene Extinction Techniques.

Studbook	Founder	Prop. Sim. Sole Rep.
1124	39	0.02900
831	231	0.02400
1124	40	0.01600
826	231	0.01200
718	231	0.01200
268	1	0.01200
615	11	0.00900
868	231	0.00800
830	12	0.00600
615	DOM	0.00600
505	40	0.00600
505	39	0.00600
268	5	0.00600
868	12	0.00500
830	DOM	0.00500
701	39	0.00500
268	52	0.00400
868	17	0.00300
1124	212	0.00300
830	11	0.00300
718	DOM	0.00300
718	40	0.00300
701	40	0.00300
667	12	0.00300
667	DOM	0.00300
615	12	0.00300
942	39	0.00200
942	212	0.00200
868	40	0.00200
700	231	0.00200
667	11	0.00200
667	18	0.00200
615	40	0.00200
505	212	0.00200

Table 2. Genetically important animals. Proportion of 1000 simulations in which each individual was the only representative of the founder shown.

genes	A	B	C	D	E	F	G	H
3	0.000	0.000	0.000	0.000	0.000	0.001	0.000	0.001
4	0.000	0.000	0.000	0.014	0.000	0.022	0.000	0.018
5	0.000	0.001	0.002	0.116	0.003	0.141	0.002	0.137
6	0.001	0.016	0.020	0.324	0.030	0.343	0.023	0.349
7	0.009	0.083	0.097	0.344	0.125	0.326	0.106	0.330
8	0.052	0.215	0.233	0.164	0.262	0.139	0.244	0.138
9	0.161	0.303	0.305	0.035	0.300	0.026	0.305	0.026
10	0.282	0.242	0.225	0.003	0.194	0.002	0.215	0.002
11	0.281	0.110	0.094	0.000	0.071	0.000	0.085	0.000
12	0.158	0.028	0.022	0.000	0.014	0.000	0.018	0.000
13	0.048	0.004	0.003	0.000	0.001	0.000	0.002	0.000
14	0.007	0.000	0.000	0.000	0.000	0.000	0.000	0.000
mean	10.476	9.129	8.997	6.639	8.769	6.502	8.918	6.514
s.d.	1.309	1.298	1.290	1.058	1.289	1.063	1.285	1.044

Table 3. Distributions of the Number of Surviving Genes in Subpopulations of the Przewalski's Horse Population. Probabilities that a specified subset has a specified number of distinct (not identical by descent) genes at an arbitrary autosomal locus. Subsets: A. The current world population. B. The current North American population (does not include Edmonton). C. All North American females but only males not descended from the domestic horse founder (DOM). D. North American horses not descended from DOM. E. North American males. F. North American males not descended from DOM. G. North American females. H. North American females not descended from DOM. At bottom, mean and standard deviation of the number of distinct genes per locus in each subpopulation.

FOUNDER B														
FND A	212	39	211	40	1	231	52	5	18	17	11	DOM	12	
212	141.0 **1**	139.0 0.986	141.0 **1**	139.0 0.986	126.0 0.894	29.0 0.206	126.0 0.894	126.0 0.894	138.0 0.979	138.0 0.979	38.0 0.270	38.0 0.270	38.0 0.270	
39	139.0 0.993	140.0 **1**	139.0 0.993	140.0 **1**	124.0 0.886	29.0 0.207	124.0 0.886	124.0 0.886	139.0 0.993	139.0 0.993	39.0 0.279	39.0 0.279	39.0 0.279	
211	141.0 **1**	139.0 0.986	141.0 **1**	139.0 0.986	126.0 0.894	29.0 0.206	126.0 0.894	126.0 0.894	138.0 0.979	138.0 0.979	38.0 0.270	38.0 0.270	38.0 0.270	
40	139.0 0.993	140.0 **1**	139.0 0.993	140.0 **1**	124.0 0.886	29.0 0.207	124.0 0.886	124.0 0.886	139.0 0.993	139.0 0.993	39.0 0.279	39.0 0.279	39.0 0.279	
1	126.0 **1**	124.0 0.984	126.0 **1**	124.0 0.984	126.0 **1**	21.0 0.167	126.0 **1**	126.0 **1**	123.0 0.976	123.0 0.976	34.0 0.270	34.0 0.270	34.0 0.270	
231	29.0 **1**	29.0 **1**	29.0 **1**	29.0 **1**	21.0 0.724	29.0 **1**	21.0 0.724	21.0 0.724	29.0 **1**	29.0 **1**	12.0 0.414	12.0 0.414	12.0 0.414	
52	126.0 **1**	124.0 0.984	126.0 **1**	124.0 0.984	126.0 **1**	21.0 0.167	126.0 **1**	126.0 **1**	123.0 0.976	123.0 0.976	34.0 0.270	34.0 0.270	34.0 0.270	
5	126.0 **1**	124.0 0.984	126.0 **1**	124.0 0.984	126.0 **1**	21.0 0.167	126.0 **1**	126.0 **1**	123.0 0.976	123.0 0.976	34.0 0.270	34.0 0.270	34.0 0.270	
18	138.0 0.993	139.0 **1**	138.0 0.993	139.0 **1**	123.0 0.885	29.0 0.209	123.0 0.885	123.0 0.885	139.0 **1**	139.0 **1**	39.0 0.281	39.0 0.281	39.0 0.281	
17	138.0 0.993	139.0 **1**	138.0 0.993	139.0 **1**	123.0 0.885	29.0 0.209	123.0 0.885	123.0 0.885	139.0 **1**	139.0 **1**	39.0 0.281	39.0 0.281	39.0 0.281	
11	38.0 0.974	39.0 **1**	38.0 0.974	39.0 **1**	34.0 0.872	12.0 0.308	34.0 0.872	34.0 0.872	39.0 **1**	39.0 **1**	39.0 **1**	39.0 **1**	39.0 **1**	
DOM	38.0 0.974	39.0 **1**	38.0 0.974	39.0 **1**	34.0 0.872	12.0 0.308	34.0 0.872	34.0 0.872	39.0 **1**	39.0 **1**	39.0 **1**	39.0 **1**	39.0 **1**	
12	38.0 0.974	39.0 **1**	38.0 0.974	39.0 **1**	34.0 0.872	12.0 0.308	34.0 0.872	34.0 0.872	39.0 **1**	39.0 **1**	39.0 **1**	39.0 **1**	39.0 **1**	

Linked : 212, 211 231 Independent
 : 39, 40
 : 1, 5, 52
 : 17, 18
 : DOM, 11, 12

Table 4. Summary of Individual Concordance. Example: Contribution from Founders 40 and 212 were present together in 139 animals. This is 98.6% of the animals with any contribution from 40 and 99.3% of the animals with any contribution from 212.

GROUPS	A	B	C	D	E	F	G	H
1, 5, 52	1.339	1.339	1.339	1.339	1.329	1.329	1.337	1.303
11, 12, DOM	2.121	1.725	1.638	0	1.575	0	1.638	0
39, 40	2.444	1.959	1.948	1.712	1.913	1.686	1.877	1.633
113	1.08	0.974	0.958	0.609	0.025	0.59	0.958	0.609
211, 212	1.741	1.73	1.729	1.729	1.725	1.724	1.724	1.72
231	1.75	1.402	1.385	1.25	1.301	1.174	1.384	1.249
All Founders	10.476	9.129	8.997	6.639	8.768	6.502	8.918	6.514

Table 5. Mean number of surviving genes from each founder group in subpopulations of the Przewalski's Horse population. Mean number of genes (both wild type and domestic) per autosomal locus from various founder groups and from all founders that survive in each of the population subsets under consideration (see Table 3). Founder groups: Old Askania Nova (1, 5, 52), Old Prague (11, 12, DOM), Munich-U.S. (39, 40 and 113), Woburn (211, 212), New Askania Nova (231), and all founders together. Subsets: See Table 3.

Age Class	Females			Males		
	Px	Lx	Mx	Px	Lx	Mx
0	0.843	1.000	0.000	0.785	1.000	0.000
1	0.963	0.843	0.000	0.925	0.785	0.000
2	0.968	0.812	0.054	0.051	0.726	0.052
3	0.974	0.786	0.119	0.961	0.691	0.122
4	0.978	0.765	0.162	0.963	0.664	0.194
5	0.981	0.749	0.187	0.963	0.639	0.245
6	0.982	0.734	0.206	0.962	0.615	0.283
7	0.982	0.720	0.215	0.970	0.592	0.344
8	0.982	0.707	0.224	0.985	0.574	0.412
9	0.983	0.695	0.237	0.987	0.565	0.433
10	0.984	0.683	0.244	0.972	0.558	0.412
11	0.985	0.672	0.245	0.956	0.542	0.378
12	0.983	0.662	0.245	0.954	0.518	0.356
13	0.979	0.651	0.236	0.962	0.494	0.367
14	0.976	0.637	0.217	0.960	0.476	0.402
15	0.975	0.622	0.207	0.947	0.456	0.426
16	0.964	0.606	0.207	0.947	0.432	0.430
17	0.943	0.584	0.207	0.959	0.409	0.440
18	0.932	0.655	0.199	0.963	0.393	0.464
19	0.932	0.514	0.181	0.956	0.378	0.483
20	0.930	0.479	0.170	0.947	0.361	0.487
21	0.925	0.445	0.146	0.958	0.342	0.453
22	0.922	0.411	0.117	0.986	0.238	0.385
23	0.905	0.379	0.057	0.963	0.323	0.296
24	0.872	0.343	0.000	0.888	0.311	0.177
25	0.865	0.299	0.000	0.851	0.277	0.078
26	0.884	0.259	0.000	0.888	0.235	0.022
27	0.921	0.229	0.000	0.500	0.209	0.000
28	0.974	0.211	0.000	1.000	0.105	0.000
29	1.000	0.205	0.000	1.000	0.105	0.000
30	1.000	0.205	0.000	0.960	0.105	2.700
31	1.000	0.205	0.000	1.000	1.000	0.000
32	0.750	0.205	0.000	1.000	1.000	0.000
33	0.250	0.154	0.000	0.750	1.000	0.000
34	0.000	0.038	0.000	0.250	0.075	0.000
35	0.000	0.000	0.000	0.000	0.019	0.000
r	=	0.0825		r	=	0.0987
		0.0920				0.1200
λ	=	1.086		λ	=	1.104
		1.096				1.127
R ₀	=	2.564		R ₀	=	4.021
G	=	11.414		G	=	14.102
		9.084				9.521

Table 6. Age-specific survivorships and fertilities for the world population of Przewalski's horses. Data calculated for animals alive on 1.I.1975 and those born since.

FEMALES				MALES			
Age Class	Px	Lx	Mx	Age Class	Px	Lx	Mx
0	0.838	1.000	0.000	0	0.828	1.000	0.000
1	0.966	0.838	0.000	1	0.987	0.828	0.000
2	0.977	0.810	0.051	2	0.986	0.817	0.045
3	0.984	0.790	0.110	3	0.982	0.805	0.124
4	0.985	0.777	0.156	4	0.978	0.790	0.174
5	0.982	0.766	0.182	5	0.977	0.773	0.183
6	0.981	0.752	0.212	6	0.977	0.755	0.213
7	0.980	0.737	0.249	7	0.983	0.738	0.291
8	0.978	0.722	0.265	8	0.994	0.725	0.360
9	0.976	0.706	0.262	9	1.000	0.721	0.376
10	0.974	0.689	0.247	10	0.991	0.721	0.329
11	0.969	0.671	0.220	11	0.971	0.714	0.240
12	0.963	0.650	0.197	12	0.959	0.693	0.250
13	0.971	0.627	0.190	13	0.952	0.665	0.260
14	0.990	0.608	0.190	14	0.941	0.632	0.270
15	1.000	0.602	0.190	15	0.935	0.595	0.297
16	0.938	0.602	0.185	16	0.931	0.556	0.343
17	1.000	0.565	0.176	17	0.916	0.518	0.324
18	1.000	0.565	0.142	18	0.897	0.474	0.330
19	0.818	0.565	0.150	19	0.889	0.425	0.340
20	1.000	0.462	0.130	20	0.917	0.378	0.356
21	1.000	0.462	0.120	21	0.972	0.347	0.458
22	1.000	0.462	0.100	22	1.000	0.337	0.502
23	1.000	0.462	0.070	23	1.000	0.337	0.468
24	0.857	0.462	0.000	24	1.000	0.337	0.450
25	1.000	0.396	0.000	25	1.000	0.337	0.350
26	1.000	0.396	0.000	26	1.000	0.337	0.000
27	1.000	0.396	0.000	27	1.000	0.337	0.000
28	1.000	0.396	0.000	28	1.000	0.337	0.000
29	1.000	0.396	0.000	29	1.000	0.337	0.000
30	1.000	0.396	0.000	30	0.970	0.337	0.000
31	1.000	0.396	0.000	31	1.000	0.327	0.000
32	0.750	0.396	0.000	32	0.750	0.327	0.000
33	0.250	0.297	0.000	33	0.250	0.245	0.000
34	0.000	0.074	0.000	34	0.000	0.061	0.000
35	0.000	0.000	0.000	35	0.000	0.000	0.000
r	=	0.0807		r	=	0.1011	
		0.0900				0.1210	
λ	=	1.084		λ	=	1.106	
		1.094				1.129	
R ₀	=	2.440		R ₀	=	3.907	
G	=	11.053		G	=	13.481	
		8.835				9.317	

Table 7. Survivorships and fertilities by sex for Przewalski's horses for the SSP population. Data calculated for animals alive on 1.I.1975 and those born since.

Age Class	FEMALES			MALES		
	Px	Lx	Mx	Px	Lx	Mx
0	0.878	1.000	0.000	0.836	1.000	0.000
1	0.940	0.878	0.000	1.000	0.836	0.000
2	0.985	0.825	0.118	1.000	0.836	0.000
3	1.000	0.813	0.168	1.000	0.836	0.400
4	1.000	0.813	0.189	1.000	0.836	0.750
5	1.000	0.813	0.260	1.000	0.836	0.750
6	1.000	0.813	0.418	1.000	0.836	0.750
7	1.000	0.813	0.558	1.000	0.836	0.750
8	1.000	0.813	0.600	1.000	0.836	0.750
9	1.000	0.813	0.575	1.000	0.836	2.400
10	1.000	0.813	0.600	1.000	0.836	0.500
11	1.000	0.813	0.125	1.000	0.836	0.125
12	1.000	0.813	0.000	1.000	0.836	0.000
13	1.000	0.813	0.000	1.000	0.836	0.000
14	1.000	0.813	0.000	1.000	0.836	0.000
15	1.000	0.813	0.000	1.000	0.836	0.000
16	1.000	0.813	0.000	1.000	0.836	0.000
17	1.000	0.813	0.000	1.000	0.836	0.000
18	1.000	0.813	0.000	1.000	0.836	0.000
19	0.750	0.813	0.000	0.750	0.836	0.000
20	0.250	0.609	0.000	0.250	0.627	0.000
21	0.000	0.152	0.000	0.000	0.157	0.000
22	0.000	0.000	0.000	0.000	0.000	0.000
23	0.000	0.000	0.000	0.000	0.000	0.000
24	0.000	0.000	0.000	0.000	0.000	0.000
25	0.000	0.000	0.000	0.000	0.000	0.000
26	0.000	0.000	0.000	0.000	0.000	0.000
27	0.000	0.000	0.000	0.000	0.000	0.000
28	0.000	0.000	0.000	0.000	0.000	0.000
29	0.000	0.000	0.000	0.000	0.000	0.000
30	0.000	0.000	0.000	0.000	0.000	0.000
31	0.000	0.000	0.000	0.000	0.000	0.000
32	0.000	0.000	0.000	0.000	0.000	0.000
33	0.000	0.000	0.000	0.000	0.000	0.000
34	0.000	0.000	0.000	0.000	0.000	0.000
35	0.000	0.000	0.000	0.000	0.000	0.000
r	=	0.1463 0.1550		r	=	0.2487 0.2740
λ	=	1.158 1.168		λ	=	1.282 1.315
R ₀	=	2.933		R ₀	=	5.998
G	=	7.356 6.498		G	=	7.202 5.867

Table 8. Survivorships and fertilities by sex for Przewalski's horses for the subset of the SSP population possessing genetic contributions from the Mongolian domestic mare as depicted in the International Studbook. Data calculated for animals alive on 1.I.1975 and those born since.

Age Class	FEMALES			MALES		
	Px	Lx	Mx	Px	Lx	Mx
0	0.827	1.000	0.000	0.826	1.000	0.000
1	0.954	0.827	0.000	0.985	0.826	0.000
2	0.978	0.789	0.034	0.984	0.814	0.038
3	0.984	0.772	0.096	0.979	0.800	0.103
4	0.983	0.759	0.148	0.975	0.784	0.150
5	0.980	0.746	0.170	0.974	0.764	0.165
6	0.979	0.731	0.187	0.974	0.744	0.200
7	0.978	0.716	0.206	0.981	0.725	0.261
8	0.976	0.700	0.215	0.994	0.711	0.400
9	0.973	0.682	0.216	1.000	0.706	0.375
10	0.970	0.664	0.216	0.991	0.706	0.350
11	0.966	0.644	0.210	0.970	0.700	0.198
12	0.962	0.622	0.194	0.958	0.679	0.150
13	0.971	0.598	0.181	0.951	0.650	0.143
14	0.990	0.581	0.177	0.940	0.618	0.154
15	1.000	0.575	0.177	0.935	0.581	0.159
16	1.000	0.575	0.176	0.931	0.543	0.164
17	1.000	0.575	0.173	0.916	0.506	0.173
18	1.000	0.575	0.142	0.897	0.463	0.178
19	0.800	0.575	0.083	0.889	0.415	0.216
20	1.000	0.460	0.075	0.917	0.369	0.334
21	1.000	0.460	0.050	0.972	0.339	0.459
22	1.000	0.460	0.025	1.000	0.329	0.503
23	1.000	0.460	0.010	1.000	0.329	0.469
24	0.860	0.460	0.000	1.000	0.329	0.309
25	1.000	0.396	0.000	1.000	0.329	0.092
26	1.000	0.396	0.000	1.000	0.329	0.000
27	1.000	0.396	0.000	1.000	0.329	0.000
28	1.000	0.396	0.000	1.000	0.329	0.000
29	1.000	0.396	0.000	1.000	0.329	0.000
30	1.000	0.396	0.000	0.970	0.329	0.000
31	1.000	0.396	0.000	1.000	0.319	0.000
32	0.750	0.396	0.000	0.750	0.319	0.000
33	0.250	0.297	0.000	0.250	0.239	0.000
34	0.000	0.074	0.000	0.000	0.060	0.000
35	0.000	0.000	0.000	0.000	0.000	0.000

r	=	0.0657	r	=	0.0870
		0.0710			0.1020
λ	=	1.068	λ	=	1.091
		1.074			1.107
R ₀	=	2.013	R ₀	=	3.044
G	=	10.644	G	=	12.803
		9.083			9.282

Table 9. Survivorships and fertilities by sex for Przewalski's horses for the subset of the SSP population lacking genetic contributions from the Mongolian domestic mare as depicted in the International Studbook. Data calculated for animals alive on 1.I.1975 and those born since.

	A	B	C	D	E	F	G	H
DOM only	9.908	8.675	8.568	6.639	8.357	6.502	8.489	6.514
DOM and 18	9.638	8.431	8.329	6.487	8.126	6.355	8.250	6.361
All Genes	10.476	9.129	8.997	6.639	8.769	6.502	8.918	6.514

Table 10. Mean number of surviving wild-type genes in subpopulations of Przewalski's horses. Mean number of wild-type genes per autosomal locus that survive in each of the population subsets (see Table 3) in consideration of two scenarios concerning the origin of domestic genes in the population: (1) The domestic Mongolian mare is the only source of domestic genes or (2) in addition to the Mongolian domestic mare, #18 Bijsk 8 (the Cincinnati mare) is an F_1 hybrid.

H	Ne	MVP if $N_e/N =$		
		.3	.5	.7
.95	137	456	273	195
.90	67	222	133	95
.85	43	144	87	62
.80	32	105	63	45
.75	25	82	49	35

Table 11. Minimum population sizes required for retention of average heterozygosity as a function of three N_e/N ratios.

MALES: PER INDIVIDUAL/LIFETIME			FEMALES: PER INDIVIDUAL PER		
Under represented	Parity	Over represented	Under represented	Parity	Over represented
4 / 12	4 / 10	4 / 8	2 / 6	2 / 5	2 / 4

Table 12. Number of offspring desired for Przewalski's horses from individuals possessing contributions from under-represented founders, over-represented founders, and founders whose contributions are at designated levels. (Key: # males / # females)

INSTITUTION	- 11, 12, DOM CC = 222 Cur. Pot.	+ 11, 12, DOM CC = 100 Cur. Pot.	Physical Capacity
Catskill	3 / 11		3 / 12
Chicago	1 / 0		?
Denver	4 / 3		3 / 4
Front Royal	2 / 0	2 / 9	8 / 18
Memphis	1 / 4		2 / 5
Minnesota	4 / 0	9 / 12	4 / 6
New York	5 / 12		5 / 12
San Diego Zoo	1 / 4		1 / 4
San Diego Wild An. Pk.	17 / 14		7 / 20
Topeka	6 / 6	0 / 1	4 / 8
Gruenerwald	2 / 1		?
Calgary	1 / 3	2 / 1	3 / 6
Bell Ranch		4 / 0	4 / 0
Woodland Park			?
Toronto	1 / 0	1 / 4	2 / 5
White Oak			?
Tampa			?
Winnipeg			?
Miami			?

Table 13. Current census populations and estimated carrying capacities for SSP participant institutions.

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- Figure 2. Distribution of founder coefficients in Przewalski's horses.
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- Figure 10. a) Age-specific survivorships for Przewalski's horse of each sex, b) female fertilities and c) male fertilities for the subset of the SSP population possessing genetic contribution from the Mongolian domestic mare as depicted in the International Studbook.

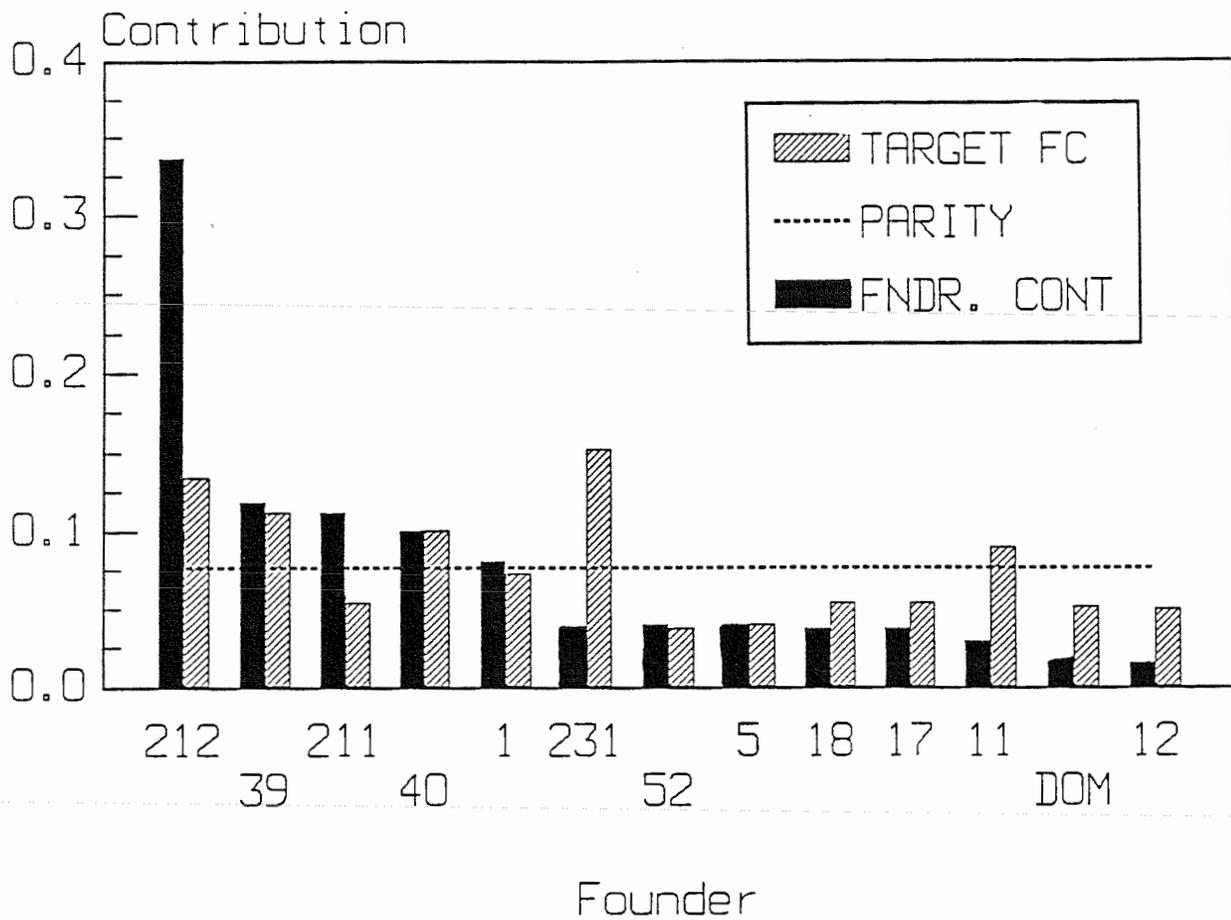


Figure 1. Founder contribution, proportion of founder's contribution surviving to SSP population and target founder contributions for Przewalski's horses.

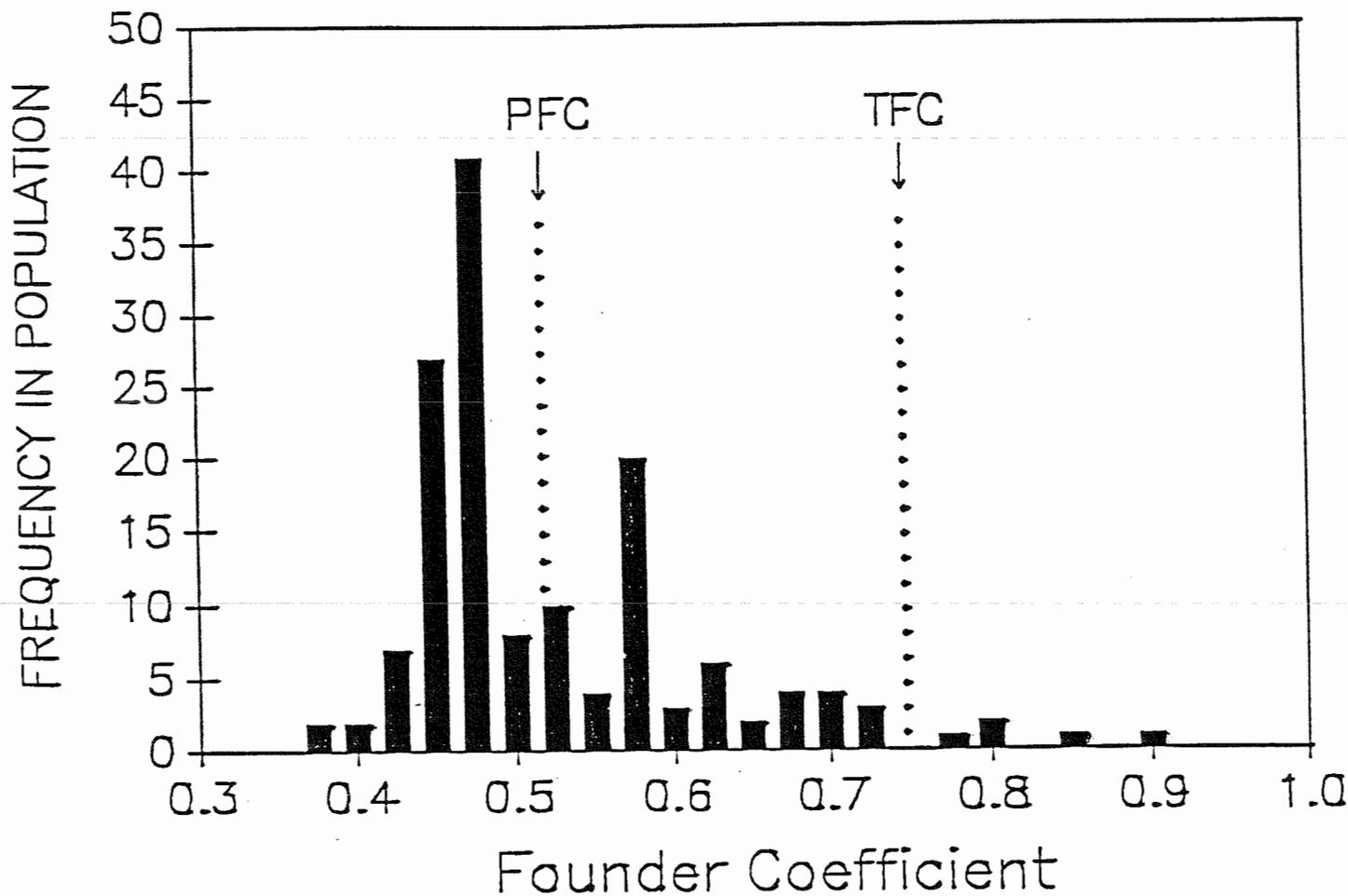


Figure 2. Distribution of founder coefficients in Przewalski's horses. The founder coefficient is a weighted average of the individual founder contributions weighted by the population founder contributions standardized to range between 0 and 1. Individuals with high coefficients are descendants of under-represented founders.

The "PFC" indicated the founder coefficient an individual would have if its founder contribution was identical to the current overall population founder contribution (coeff. of PFC = .53). Individuals with coefficients greater than the "PFC" value (greater than .53) would contribute to moving the population founder contribution towards the Target Founder Contribution ("TFC").

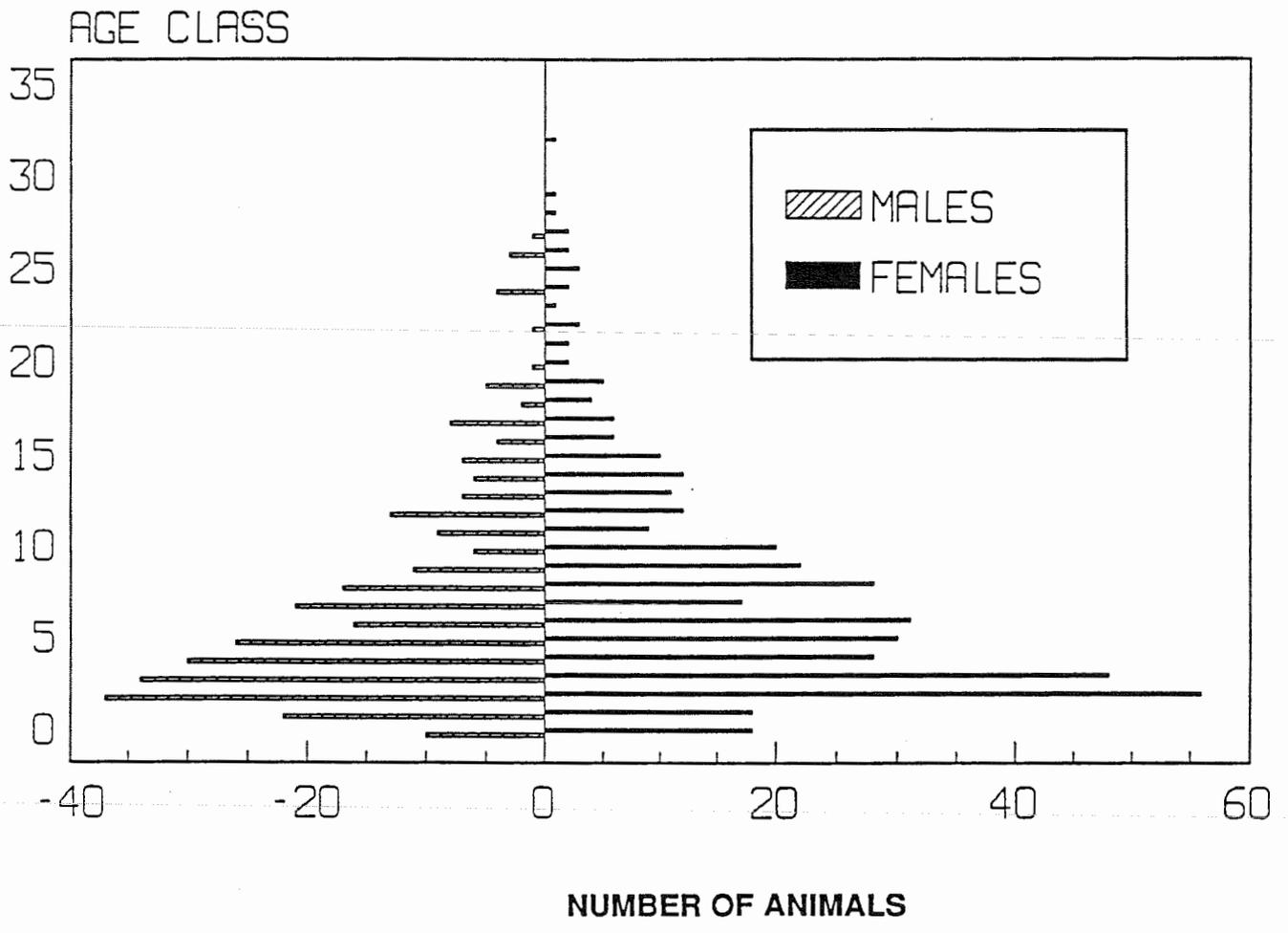


Figure 3. The age structure of Przewalski's horses for the world population by sex.

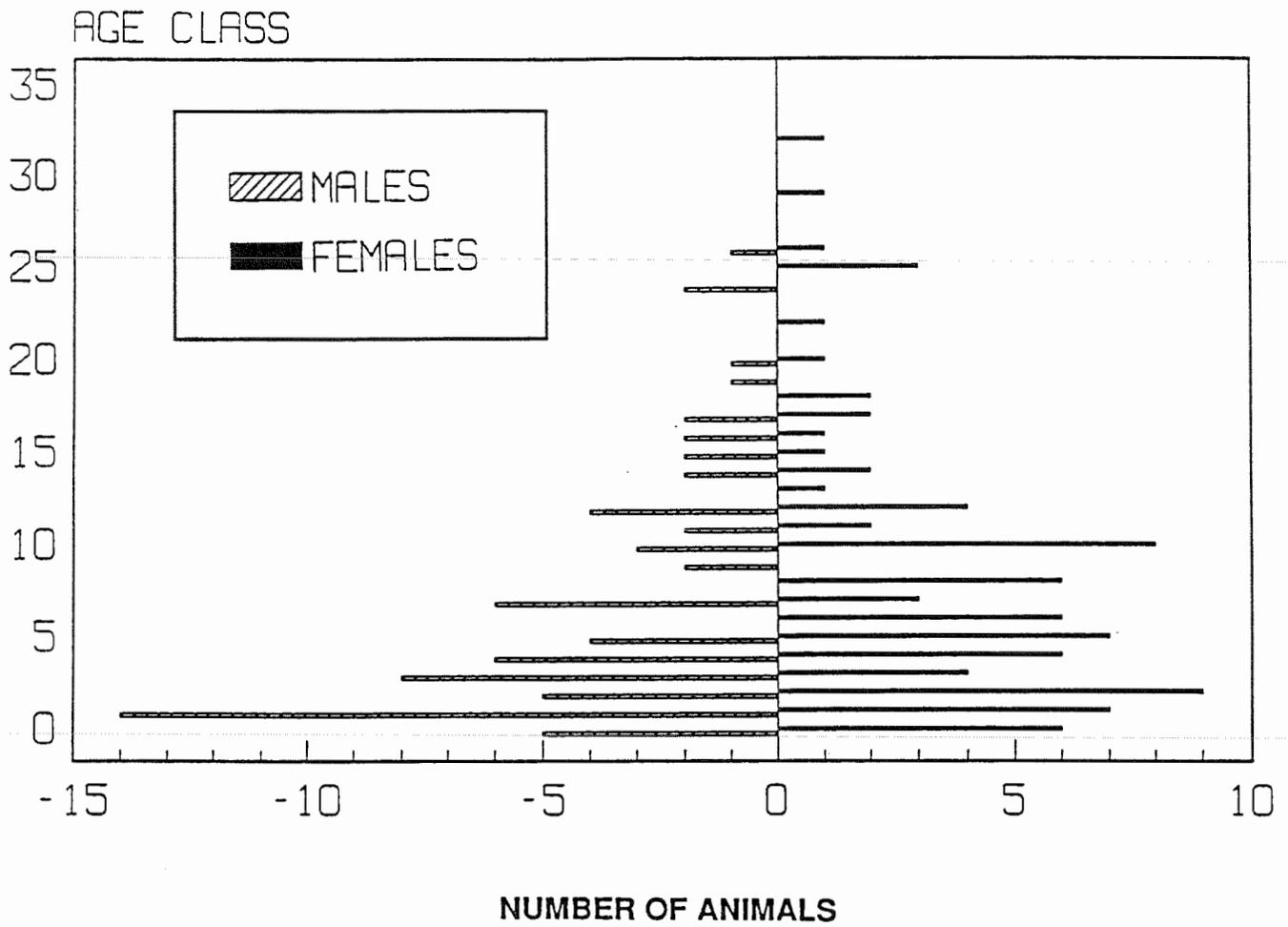


Figure 4. The age structure for male and female Przewalski's horses in the SSP population by sex.

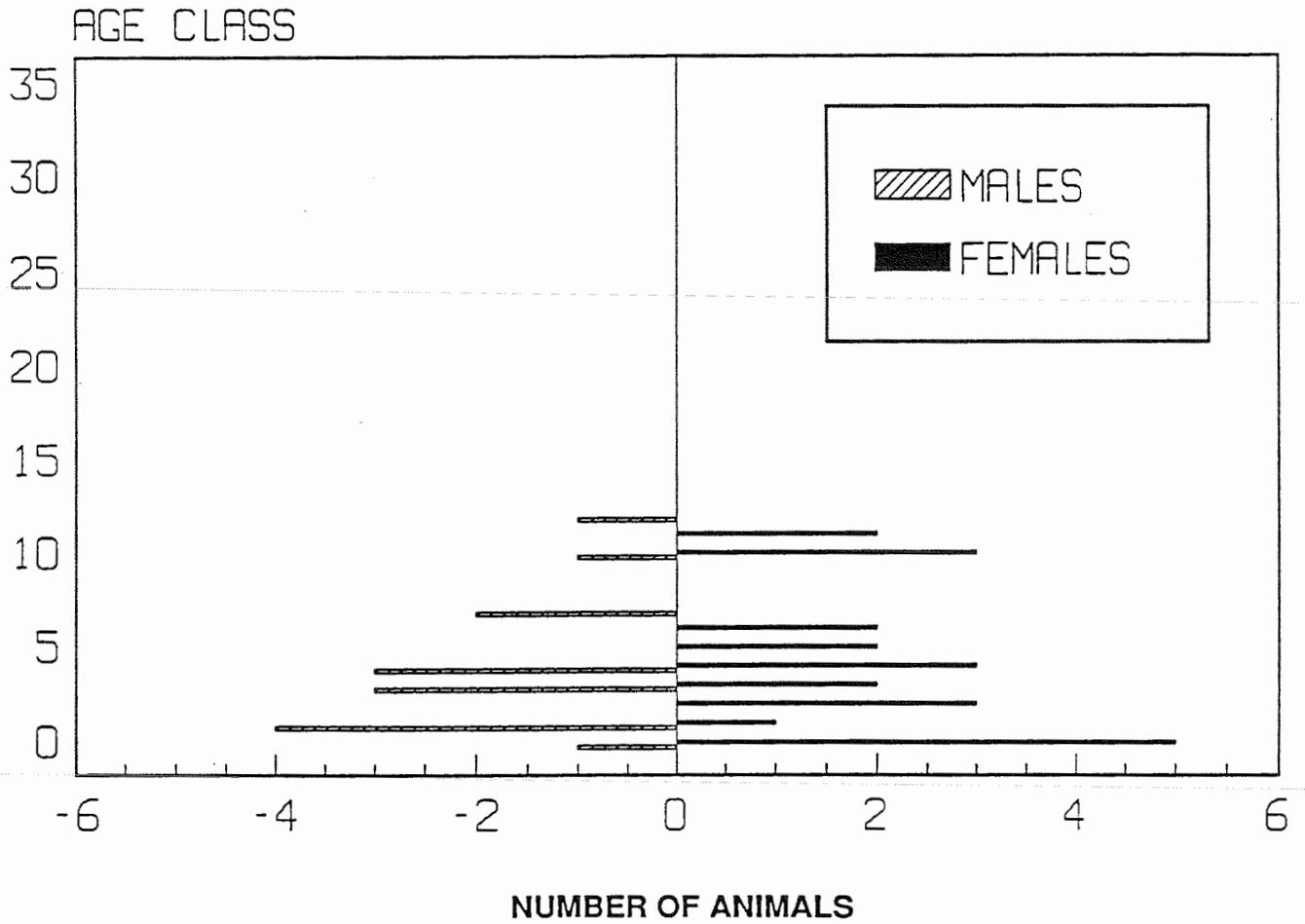


Figure 5. The age structure for male and female Przewalski's horses in the subset of the SSP population possessing genetic contribution from the Mongolian domestic mare as depicted in the International Studbook.

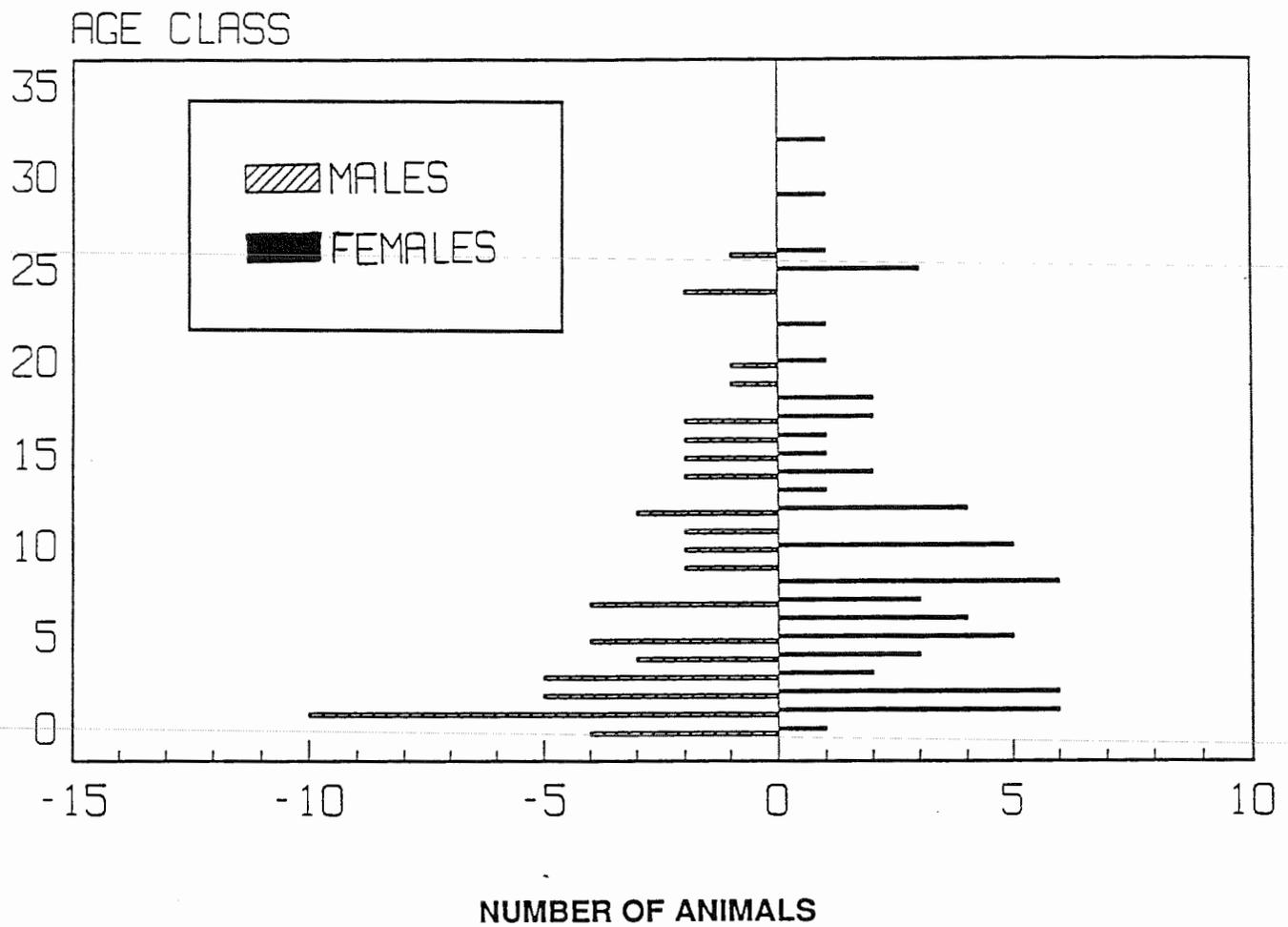


Figure 6. The age structure for male and female Przewalski's horses in the subset of the SSP population lacking genetic contribution from the Mongolian domestic mare as depicted in the International Studbook.

P. Horse Survivorship

World Since 1975

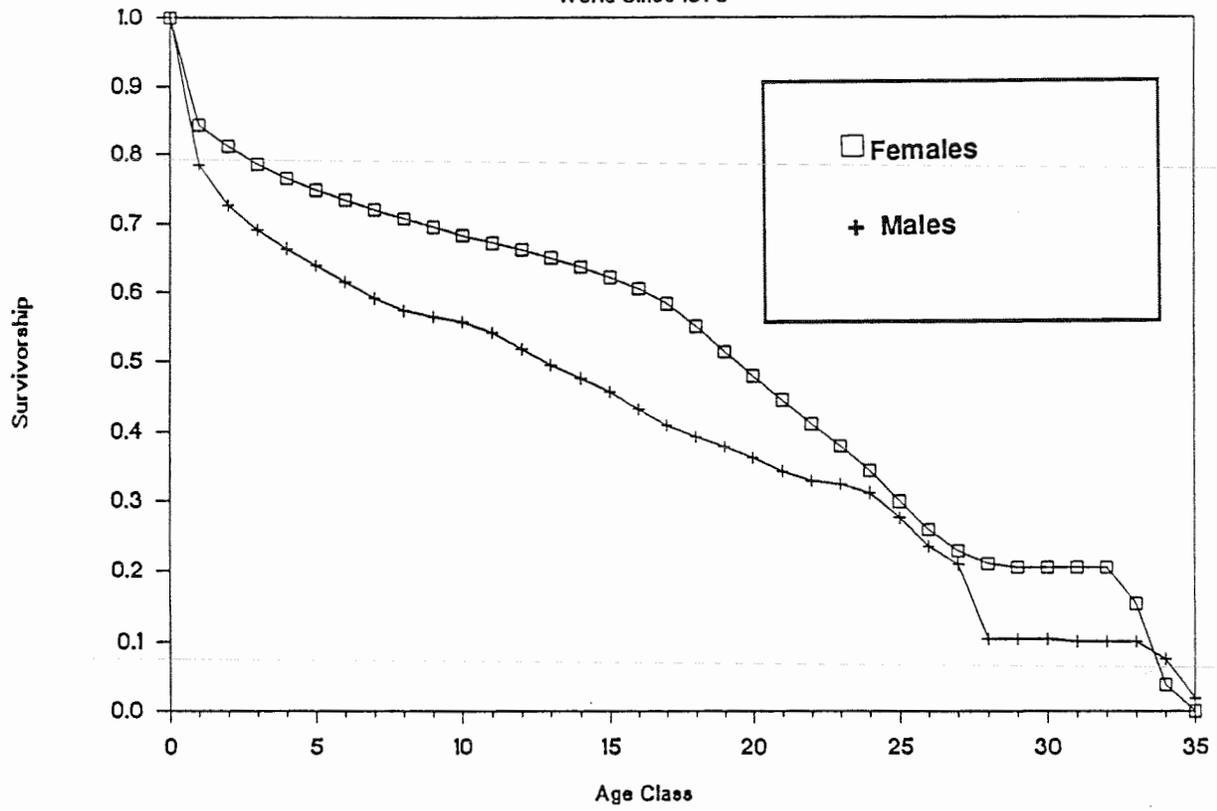


Figure 7a. Age-specific survivorships for Przewalski's horse of each sex.

P. Horse Female Fertility rates:

World Since 1975

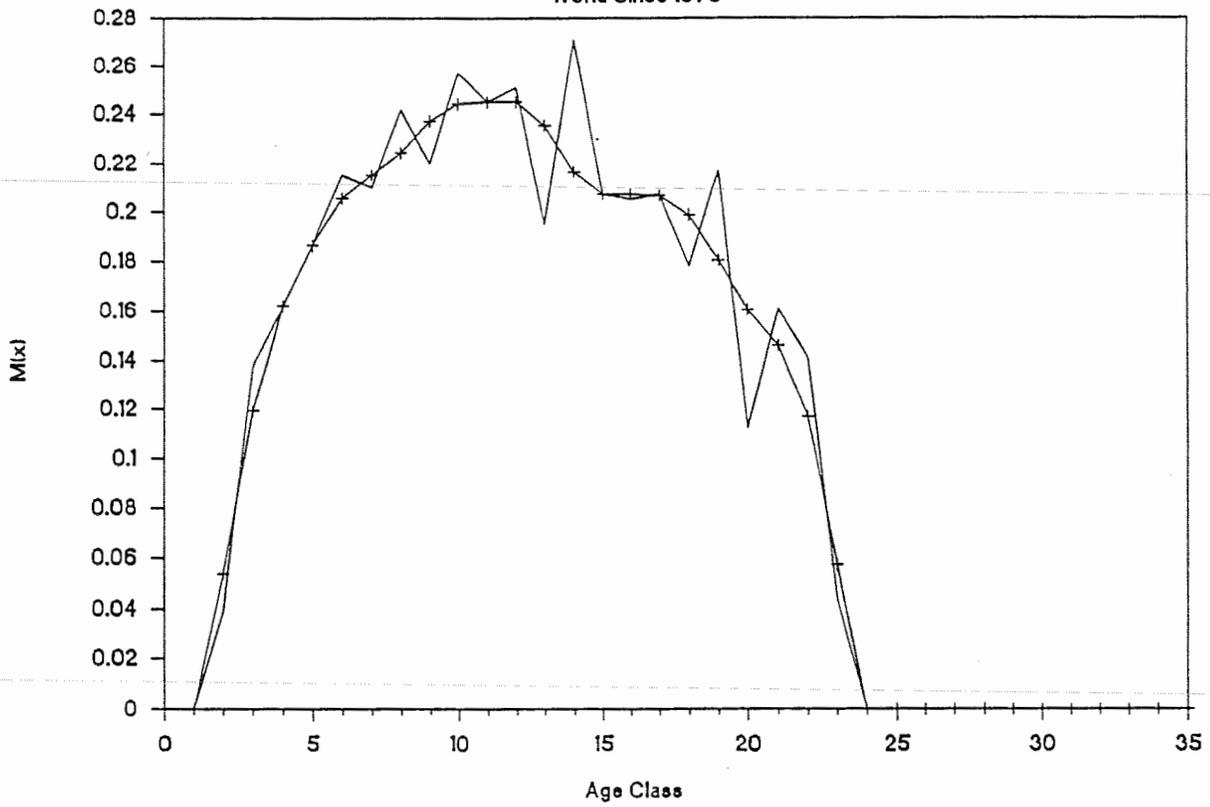


Figure 7b. Female fertilities for the world population.

P. Horse Male Fertility rates:

World Since 1975

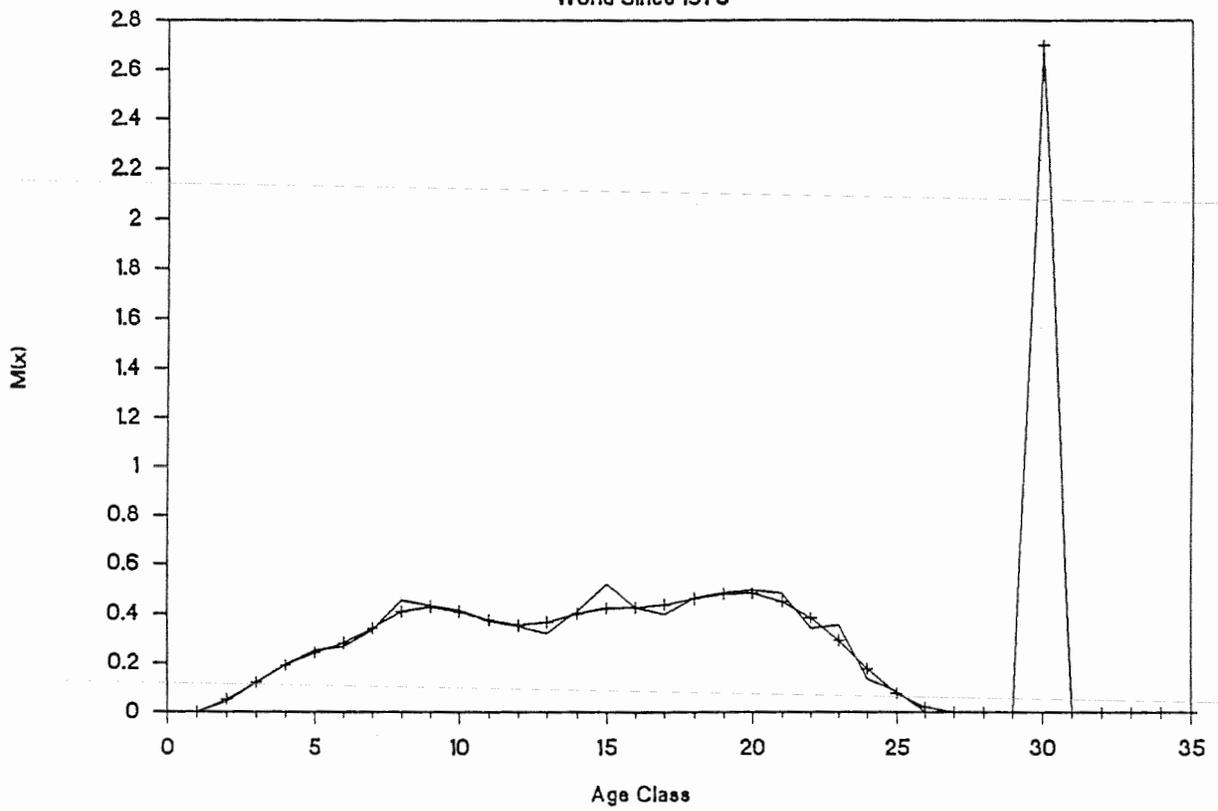


Figure 7c. Male fertilities for the world population.

P. Horse Survivorship

USA Population Since 1975

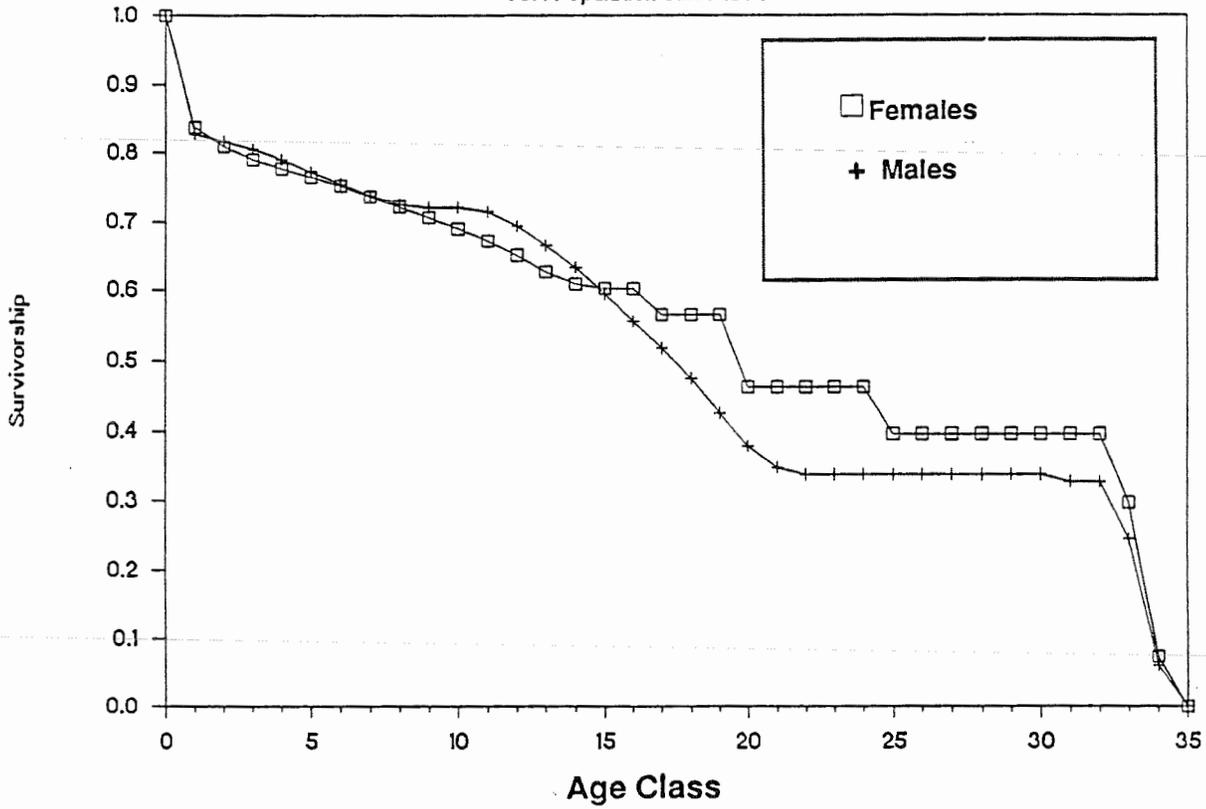


Figure 8a. Age-specific survivorships for Przewalski's horse of each sex for the SSP population.

P. Horse Female Fertility rates: USA Since 1975

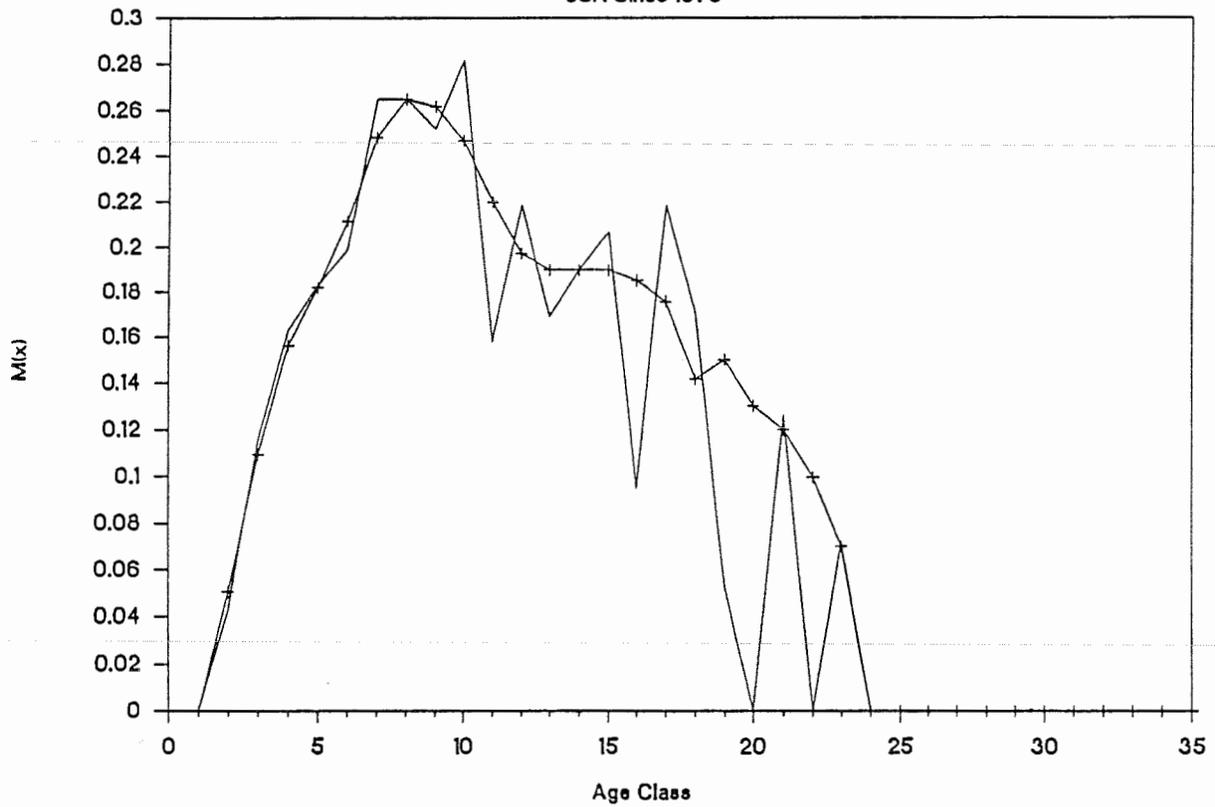


Figure 8b. Female fertilities for the SSP population.

P. Horse Male Fertility rates:

USA Since 1975

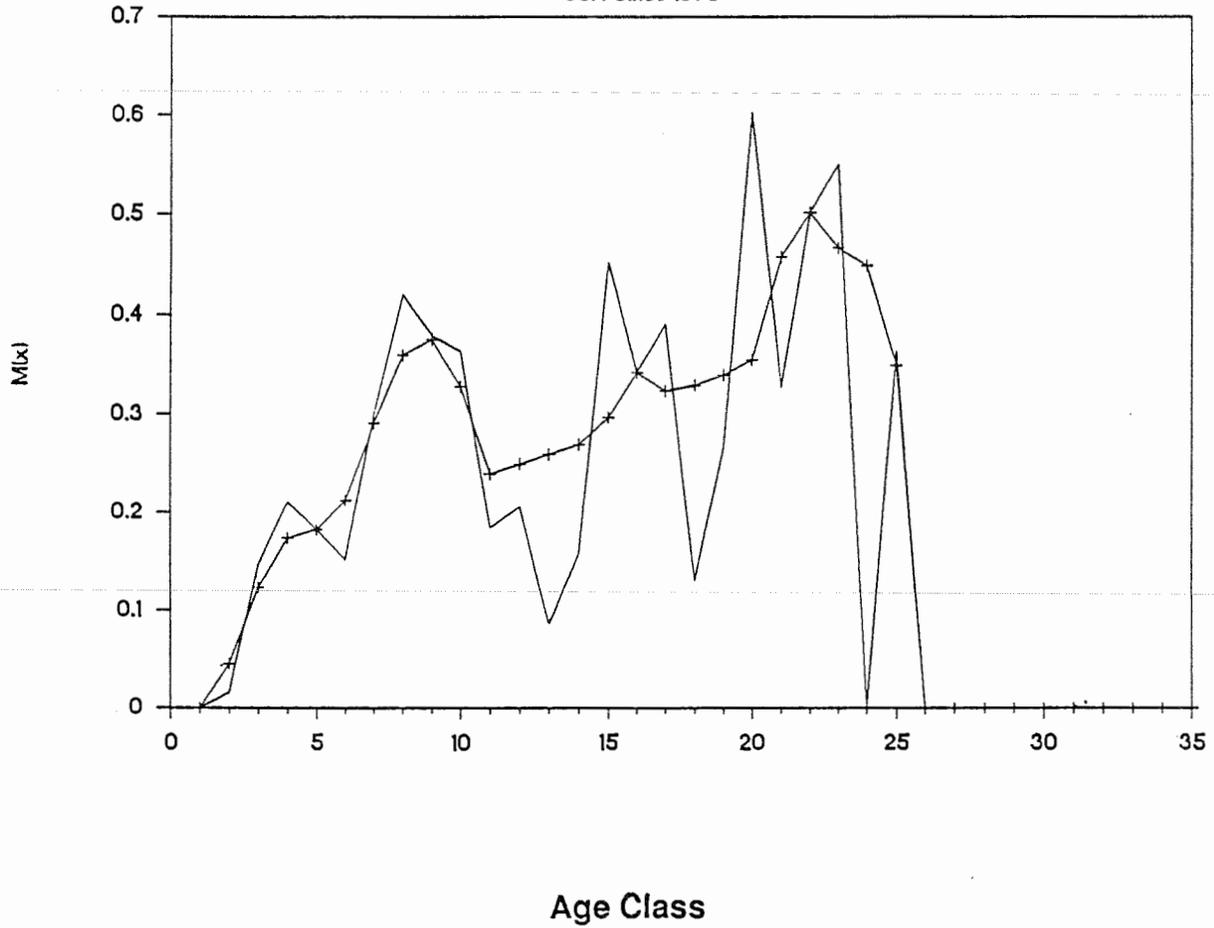


Figure 8c. Male fertilities for the SSP population.

P. Horse Survivorship

USA Domestic Line Since 1975

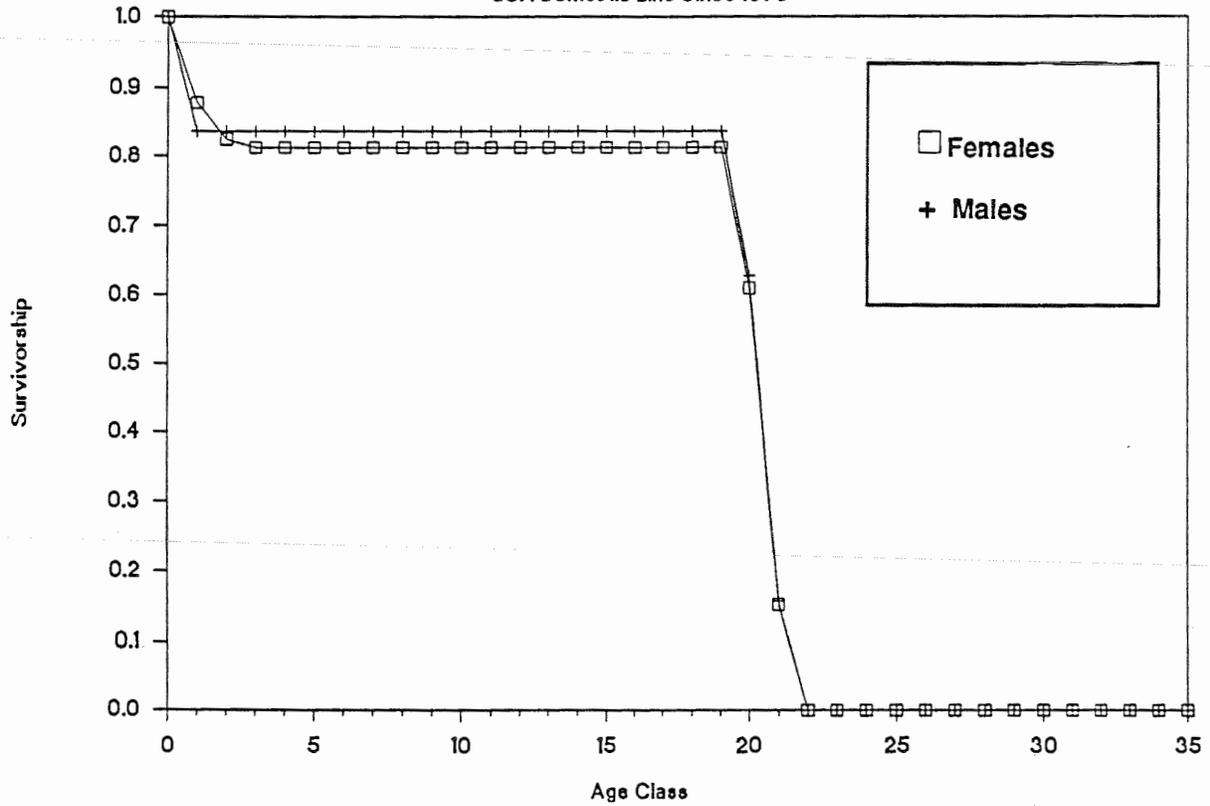


Figure 9a. Age-specific survivorships for Przewalski's horse of each sex for the subset of the SSP population possessing genetic contribution from the Mongolian domestic mare as depicted in the International Studbook.

P. Horse Female Fertility rates:

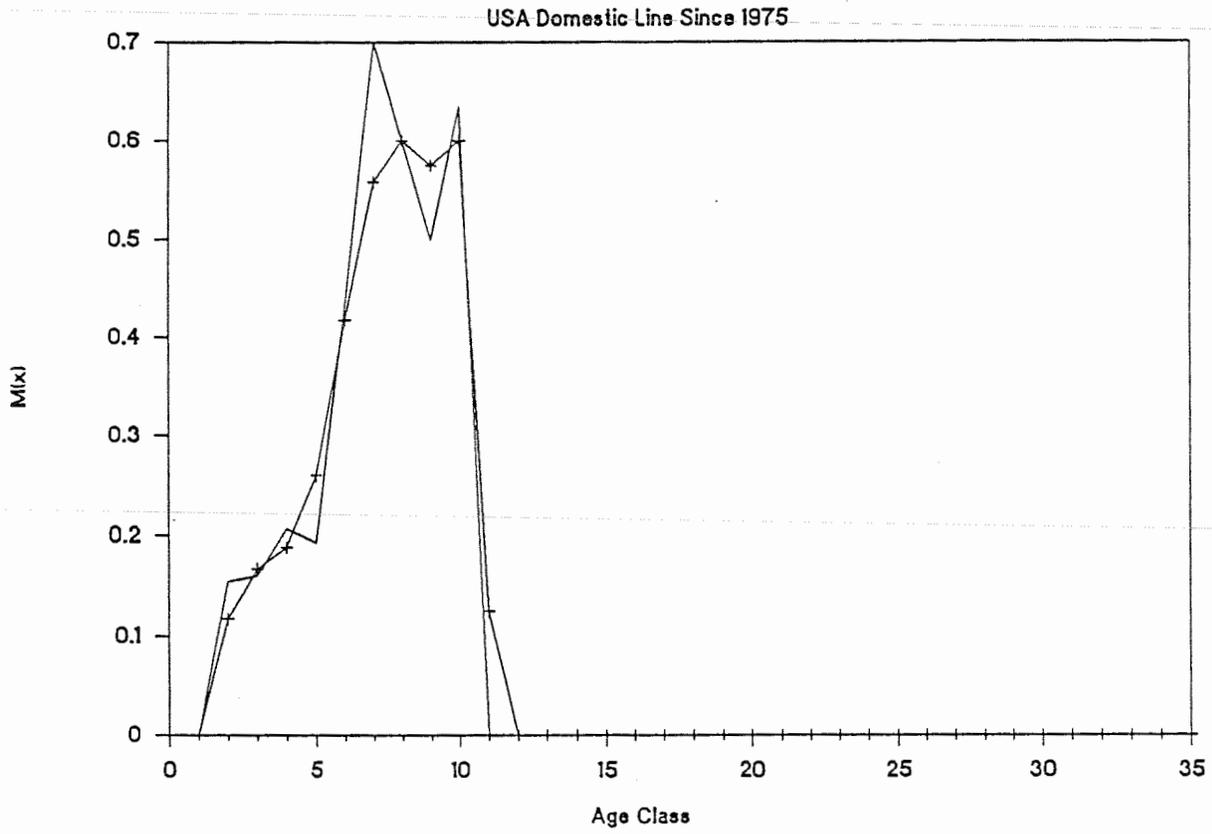


Figure 9b. Female fertilities for the subset of the SSP population possessing genetic contribution from the Mongolian domestic mare as depicted in the International Studbook.

P. Horses Male Fertility rates:

USE Domestic Line Since 1975

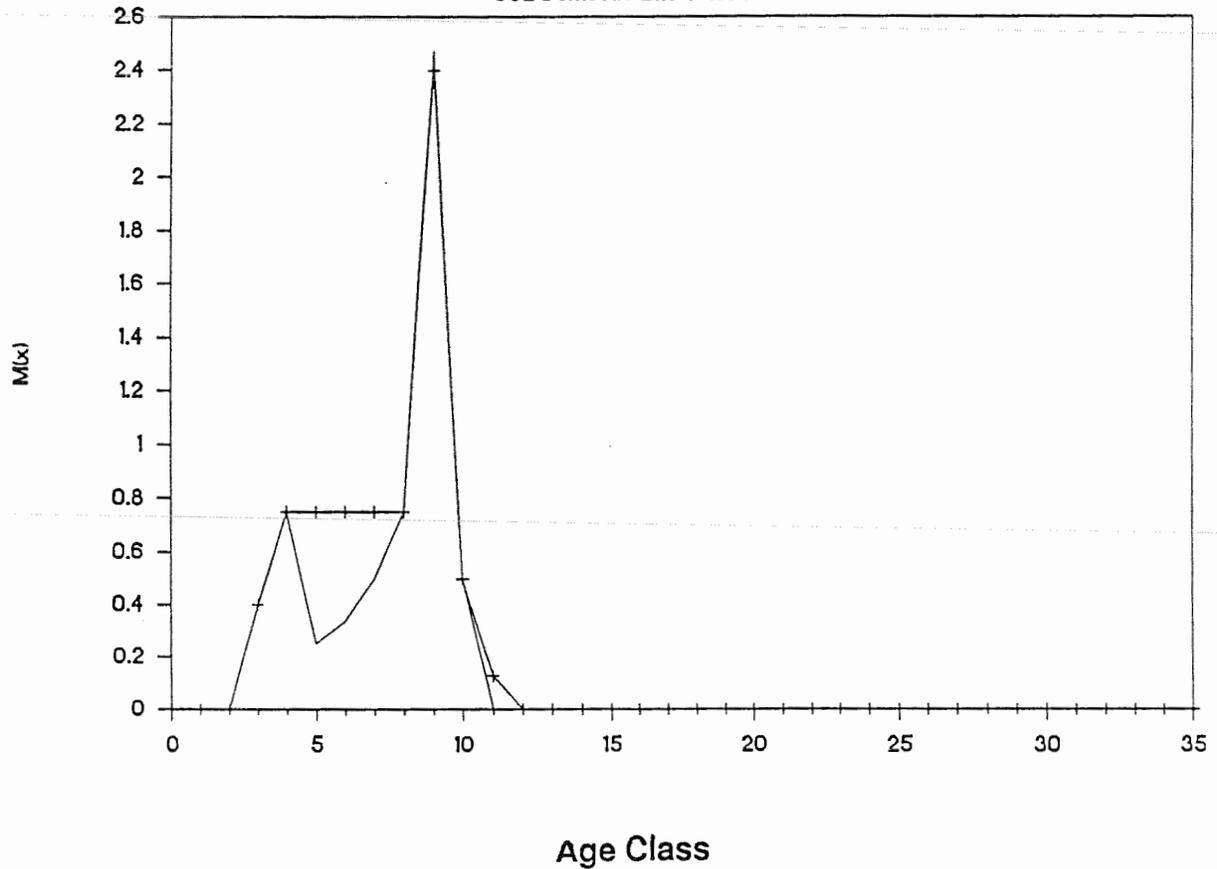


Figure 9c. Male fertilities for the subset of the SSP population possessing genetic contribution from the Mongolian domestic mare as depicted in the International Studbook.

P. Horse Survivorship

USA Pure Line Since 1975

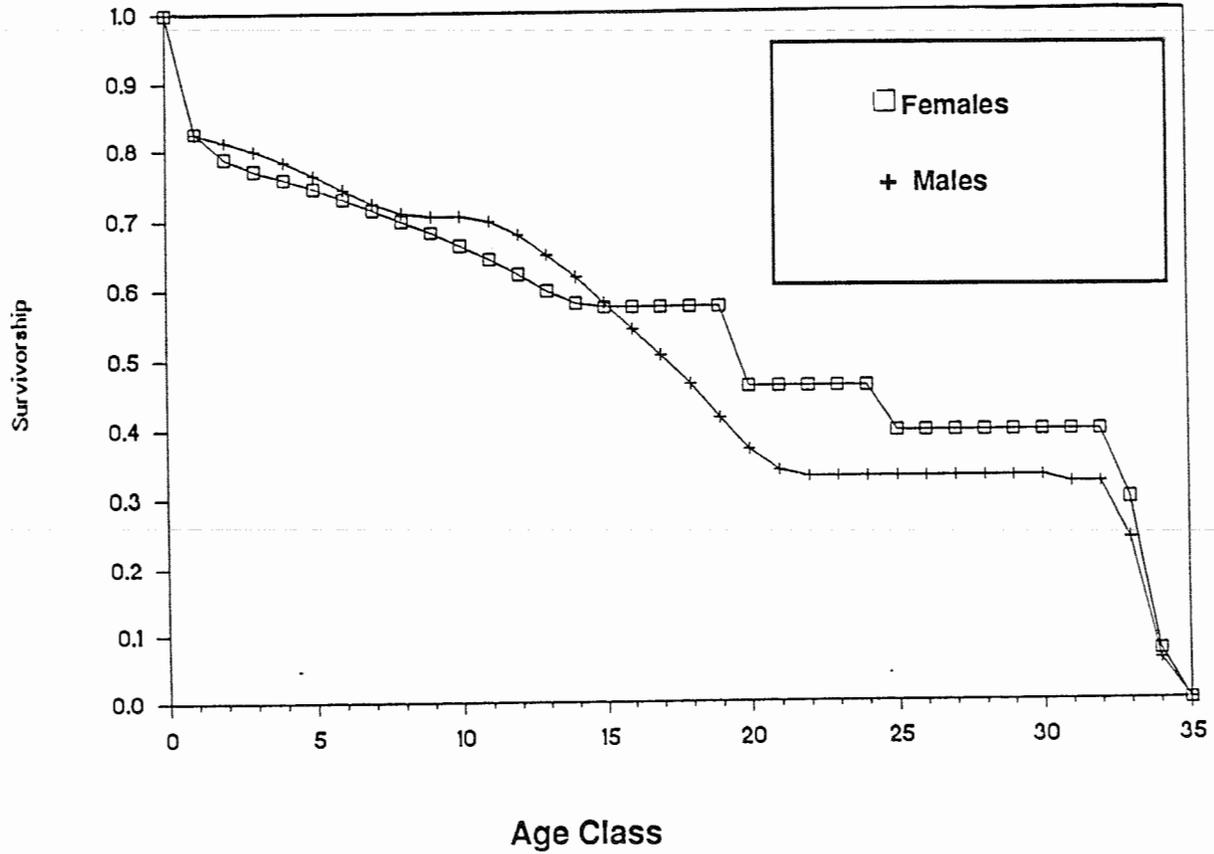


Figure 10a. Age-specific survivorships for Przewalski's horse of each sex for the subset of the SSP population possessing genetic contribution from the Mongolian domestic mare as depicted in the International Studbook.

P. Horse Female Fertility rates:

USA Pure Line Since 1975

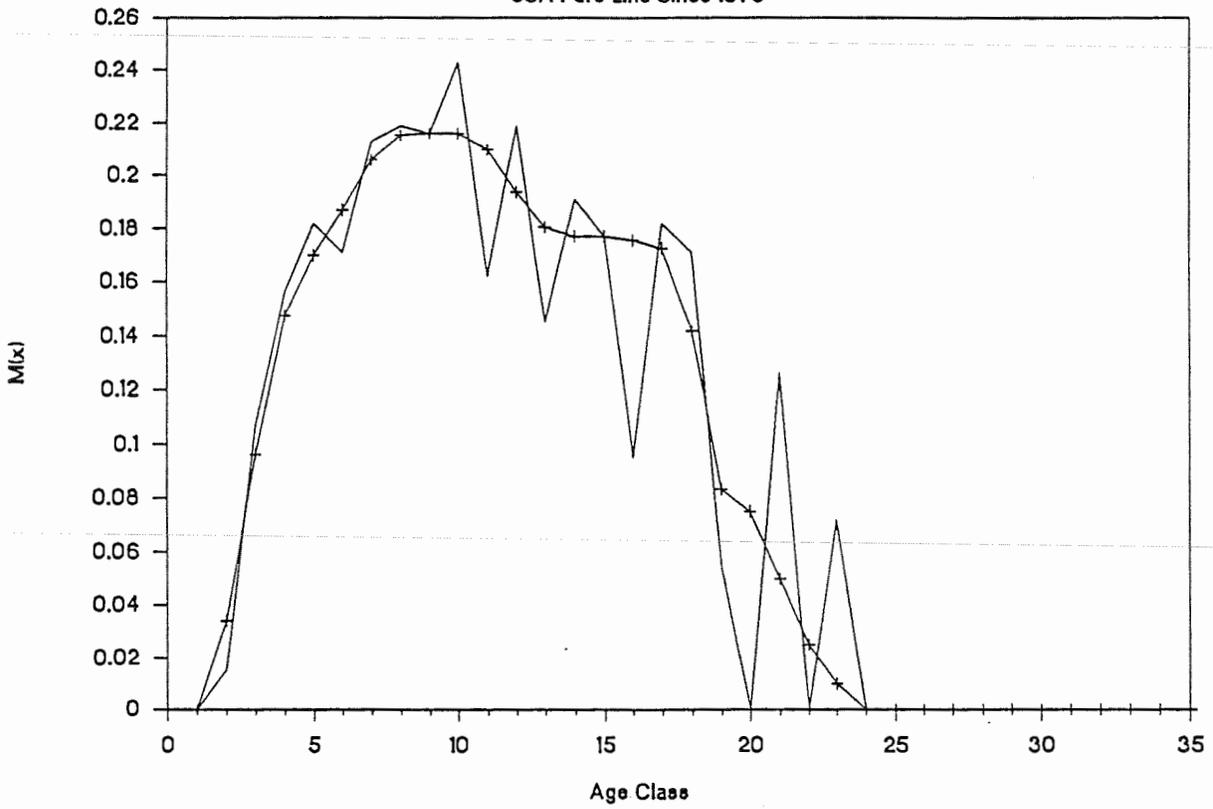


Figure 10b. Female fertilities for the subset of the SSP population possessing genetic contribution from the Mongolian domestic mare as depicted in the International Studbook.

P. Horse Male Fertility rates:

USA Pure Line Since 1975



Figure 10c. Male fertilities for the subset of the SSP population possessing genetic contribution from the Mongolian domestic mare as depicted in the International Studbook.

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Appendix 1

Census and Recommendations by Location

Criteria Used to Formulate Recommendations

The masterplan working group designated some individuals as surplus to the needs of the SSP. These individuals were all males and can be removed from the SSP population in any way that is consistent with AAZPA guidelines for management of surplus animals. Animals designated surplus should not reproduce again within SSP member institutions. Surplus individuals are derived from over-represented founders, have already provided their share of offspring, are too old to reproduce, or have a combination of these factors.

Some institutions must transfer animals from their facilities because of space considerations. These excess animals should ideally be placed in institutions that will participate in the SSP management program by signing memoranda of participation.

All females should be bred in the coming year.

SSP Przewalski's Horses by Location

CALGARY

STUD BOOK	SEX	SIRE	DAM	DATE OF BIRTH	LIVING OFFSPR	LIVING		FNDR COEF	F O U N D E R S												
						OFFSPR REPRO	LIVING SIBS		212	39	211	40	1	231	52	5	18	17	11	DOM	12
1085	M	568	608	820802	0.0.0	.439	.398	.145	.133	.121	.062	.000	.031	.031	.039	.039	.000	.000	.000
1094	F	685	722	821011	0.0.0	.451	.375	.172	.125	.141	.062	.000	.031	.031	.031	.031	.000	.000	.000
1180	F	606	545	830821	1.0.0	.551	.293	.121	.098	.105	.031	.219	.016	.016	.051	.051	.000	.000	.000
1199	M	368	697	840410	2.1.0	.568	.281	.109	.094	.094	.094	.000	.047	.047	.039	.039	.078	.039	.039
1219	M	368	694	840508	1.1.0	.568	.281	.109	.094	.094	.094	.000	.047	.047	.039	.039	.078	.039	.039
1260	F	368	700	840626	2.0.0	.505	.340	.098	.113	.082	.125	.031	.062	.062	.027	.027	.016	.008	.008
1272	F	606	722	840719	0.0.0	.551	.293	.121	.098	.105	.031	.219	.016	.016	.051	.051	.000	.000	.000

Calgary

Calgary Zoo
P.O. Box 3036
Station B
Calgary, Alberta
CANADA T2M 4R8

Stallion #1408, San Diego 43, "Heran", born 13.III.86 to be received from San Diego Wild Animal Park. Will be used as herd stallion for 1989.

SSP Przewalski's Horses by Location

CATSKILL

STUD BOOK	SEX	SIRE	DAM	DATE OF BIRTH	LIVING OFFSPR	LIVING		FNDR COEF	F O U N D E R S												
						OFFSPR REPRO	LIVING SIBS		212	39	211	40	1	231	52	5	18	17	11	DOM	12
168	F	154	151	550620	0.2.0	0.2.0	0.0.0	.447	.375	.203	.125	.172	.000	.000	.000	.000	.062	.062	.000	.000	.000
228	F	157	151	580404	1.1.0	1.1.0	0.0.0	.447	.375	.203	.125	.172	.000	.000	.000	.000	.062	.062	.000	.000	.000
267	F	154	162	610711	1.4.0	1.4.0	0.1.0	.370	.469	.172	.156	.141	.000	.000	.000	.000	.031	.031	.000	.000	.000
277	F	150	151	620627	2.1.0	1.0.0	0.0.0	.483	.375	.062	.125	.062	.125	.000	.062	.062	.062	.062	.000	.000	.000
278	F	154	162	620629	2.2.0	1.1.0	0.1.0	.370	.469	.172	.156	.141	.000	.000	.000	.000	.031	.031	.000	.000	.000
392	M	150	277	680530	0.1.0	.487	.375	.031	.125	.031	.188	.000	.094	.094	.031	.031	.000	.000	.000
408	F	150	267	690512	1.1.0	0.1.0	0.2.0	.430	.422	.086	.141	.070	.125	.000	.062	.062	.016	.016	.000	.000	.000
470	M	150	278	700521	0.2.0	0.0.0	0.0.0	.430	.422	.086	.141	.070	.125	.000	.062	.062	.016	.016	.000	.000	.000
535	F	150	277	720830	1.0.0	.487	.375	.031	.125	.031	.188	.000	.094	.094	.031	.031	.000	.000	.000
566	M	341	408	730811	0.1.0	.441	.398	.129	.133	.105	.094	.000	.047	.047	.023	.023	.000	.000	.000
736	F	341	278	770831	0.1.0	0.0.0	1.0.0	.411	.422	.172	.141	.141	.031	.000	.016	.016	.031	.031	.000	.000	.000
917	F	470	275	800614	0.0.0	.441	.398	.129	.133	.105	.094	.000	.047	.047	.023	.023	.000	.000	.000
921	F	505	278	800620	0.0.0	.382	.445	.199	.148	.160	.000	.000	.000	.000	.023	.023	.000	.000	.000
9109	F	470	736	870808	0.0.0	.420	.422	.129	.141	.105	.780	.000	.039	.039	.023	.023	.000	.000	.000

Catskill

*Catskill Game Farm
R.D. 1, Box 133
Catskill, NY 12414*

Continue breeding efforts.

A stallion with representation from #231 should be considered for replacement of Catskill-bred herd stallion.

SSP Przewalski's Horses by Location

WAGON MOUND

STUD		SIRE	DAM	DATE OF BIRTH	LIVING OFFSPR	LIVING REPRO	LIVING SIBS	FNDR COEF	F O U N D E R S												
BOOK	SEX								212	39	211	40	1	231	52	5	18	17	11	DOM	12
1179	F	753	713	830819	2.0.0	.459	.375	.141	.125	.117	.086	.000	.043	.043	.035	.035	.000	.000	.000
1306	M	685	618	850207	0.1.0	.446	.387	.150	.129	.123	.078	.000	.039	.039	.027	.027	.000	.000	.000
1311	M	685	608	850409	0.1.0	.431	.398	.172	.133	.141	.047	.000	.023	.023	.031	.031	.000	.000	.000

Canyon Colorado Equid Sanctuary

*Wagon Mound, New Mexico
P.O. Box 661
Colorado Springs, CO 80901*

Recommendation is to increase number of horses, holding at least two herds of mares. Recommend that breeding of both sub-populations take place at this spacious facility. Recommend transfer of following mares to the Equid Sanctuary:

- #1310, Minn. 21, "Yelena", born 28.III.85 at Minnesota
- #1332, Minn. 22, "Ipina", born 9.V.85 at Minnesota
- #1515, Minn. 29, born 17.IX.87 at Minnesota
- #1287, Minn. 20, "Maggie", born 9.IX.84 at Minnesota
(currently at Topeka)
- San Diego 55, "Betwa", born 21.XI.87 at San Diego
(studbook number pending)
- San Diego 57, "Borkana", born 31.XII.87 at San Diego
(studbook number pending)

Recommend transfer of the following stallions to the Equid Sanctuary:

- #886, Minn. 1, "JT" born 2.V.80 at Minnesota
- Denver 9, born 11.VII.87 at Denver

Recommend that two breeding groups be established.

Group 1

- Herd stallion: either #1306, Lukas or #1311 Roxas
(Use whichever male is currently in with Bonnie)
- Mares: #1179, "Bonnie"
San Diego 55, "Betwa"
San Diego 57, "Borkana"

Group 2

- Herd stallion: #886. Minn.1, "JT"
 - Mares: #1310, Minn. 21, "Yelena"
#1332, Minn. 22, "Ipina"
Minn. 29, born 17.IX.87 at Minnesota
(studbook number pending)"
#1287, Minn. 20, "Maggie",
-

SSP Przewalski's Horses by Location

CHICAGO

STUD BOOK	SEX	SIRE	DAM	DATE OF BIRTH	LIVING OFFSPR	LIVING OFFSPR REPRO	LIVING SIBS	FNDR COEF	F O U N D E R S													
									212	39	211	40	1	231	52	5	18	17	11	DOM	12	
BROOKFIELD ZOO																						
526	M	368	366	720527	0.0.0	.469	.375	.102	.125	.086	.125	.000	.062	.062	.031	.031	.000	.000	.000	
BELL RANCH																						
1395	M	688	668	850902	0.2.0	.611	.246	.100	.082	.088	.078	.000	.039	.039	.047	.047	.117	.059	.059	
1400	M	688	667	851010	0.1.0	.606	.246	.107	.082	.096	.078	.000	.039	.039	.055	.055	.102	.051	.051	
1409	M	368	697	860325	2.1.0	.568	.281	.109	.094	.094	.094	.000	.047	.047	.039	.039	.078	.039	.039	
1451	M	368	700	860527	1.1.0	.505	.340	.098	.113	.082	.125	.031	.062	.062	.027	.027	.016	.008	.008	

Chicago

*Chicago Zoological Park
(Brookfield Zoo)
3300 Golf Road
Brookfield, IL 60513*

Incorporate Bell Ranch plan into SSP plan.

SSP Przewalski's Horses by Location

DENVER

STUD BOOK	SEX	SIRE	DAM	DATE OF BIRTH	LIVING OFFSPR	LIVING OFFSPR REPRO	LIVING SIBS	FNDR COEF	F O U N D E R S												
									212	39	211	40	1	231	52	5	18	17	11	DOM	12
639	F	469	504	750708	3.0.0	0.0.0	0.3.0	.451	.375	.172	.125	.141	.062	.000	.031	.031	.031	.031	.000	.000	.000
713	F	469	504	770602	2.2.0	0.1.0	0.3.0	.451	.375	.172	.125	.141	.062	.000	.031	.031	.031	.031	.000	.000	.000
753	M	568	549	780508	5.1.0	0.0.0	1.0.0	.468	.375	.109	.125	.094	.109	.000	.055	.055	.039	.039	.000	.000	.000
1346	M	753	713	850524	1.1.0	.459	.375	.141	.125	.117	.086	.000	.043	.043	.035	.035	.000	.000	.000
1495	M	753	713	860707	1.1.0	.459	.375	.141	.125	.117	.086	.000	.043	.043	.035	.035	.000	.000	.000
9112	M	753	639	870711	2.0.0	.459	.375	.141	.125	.117	.086	.000	.043	.043	.035	.035	.000	.000	.000

Denver

*Denver Zoological Gardens
City Park
Denver, CO 80205*

Recommend transfer of stallion #1346, Denver 6, "Roscoe" to Brownesville

Recommend transfer of stallion #1481, Denver 7, "Bogart" to PRC

Recommend transfer of stallion #1495, Denver 8, "Gino" to EEP

Recommend transfer of stallion Denver 9, born 11.VII.87 to Canyon Colorado Equid Sanctuary

Breeding Group: stallion #753, Topeka 1, "Rococo"; Mares: # 639, #713

SSP Przewalski's Horses by Location

FRONT ROYAL

STUD BOOK	SEX	SIRE	DAM	DATE OF BIRTH	LIVING OFFSPR	LIVING OFFSPR REPRO	LIVING SIBS	FNDR COEF	F O U N D E R S												
									212	39	211	40	1	231	52	5	18	17	11	DOM	12
718	M	293	400	770611	1. 1. 0	0. 1. 0	0. 1. 0	.629	.234	.047	.078	.047	.125	.125	.062	.062	.047	.047	.062	.031	.031
948	F	688	697	810404	0. 2. 0	0. 1. 0	0. 1. 0	.563	.293	.088	.098	.076	.109	.000	.055	.055	.035	.035	.078	.039	.039
952	F	688	694	810418	0. 1. 0	0. 1. 0	0. 1. 0	.563	.293	.088	.098	.076	.109	.000	.055	.055	.035	.035	.078	.039	.039
1028	F	688	694	820411	0. 1. 0	.563	.293	.088	.098	.076	.109	.000	.055	.055	.035	.035	.078	.039	.039
1035	F	688	697	820423	0. 1. 0	0. 0. 0	0. 1. 0	.563	.293	.088	.098	.076	.109	.000	.055	.055	.035	.035	.078	.039	.039
1065	M	568	822	920609	1. 2. 0	0. 0. 0	2. 1. 0	.454	.387	.123	.129	.104	.094	.000	.047	.047	.033	.033	.000	.000	.000
1125	F	368	948	830515	0. 1. 0	0. 0. 0	0. 1. 0	.507	.334	.130	.111	.108	.086	.000	.043	.043	.033	.033	.039	.020	.020
1155	F	368	952	830620	1. 0. 0	0. 0. 0	0. 0. 0	.507	.334	.130	.111	.108	.086	.000	.043	.043	.033	.033	.039	.020	.020
1165	M	753	639	830708	2. 0. 0	.459	.375	.141	.125	.117	.086	.000	.043	.043	.035	.035	.000	.000	.000
1240	F	368	948	840527	0. 1. 0	.507	.334	.130	.111	.108	.086	.000	.043	.043	.033	.033	.039	.020	.020
1275	M	293	961	840730	0. 0. 0	.466	.387	.064	.129	.053	.172	.000	.086	.086	.012	.012	.000	.000	.000
151	F	1065	1125	860825	0. 0. 0	.480	.360	.126	.120	.106	.090	.000	.045	.045	.034	.034	.020	.010	.010
9201	F	1065	1035	870813	0. 0. 0	.508	.340	.105	.113	.090	.102	.000	.051	.051	.035	.035	.039	.020	.020
9202	M	1065	1155	871015	0. 0. 0	.480	.360	.126	.120	.106	.090	.000	.045	.045	.034	.034	.020	.010	.010

Front Royal (NRP/CRC)

*National Zoological Park
Conservation and Research Center
Front Royal VA 22630*

Recommend transfer of stallion #615, London 30, "Kuporovitch" from Minnesota.

Composition of breeding groups for 1988:

Some mares are already in foal. The mares who are still open will be pooled and placed with stallion # 718, Marwell 28, "Janus" who is important because of his contributions from #231, Orlitza III through #285, Askania 3, "Bars".

Composition of breeding groups for 1989:

Group 1

Herd stallion: #615, London 30, "Kuporovitch"

Mares: #1085

#1155

#1125

2 foals

Group 2

Herd Stallion: #718, Marwell 28, "Janus"

Mares: #1028

#948

#952

#1240

#1510

These males are designated surplus:

#1275, San Diego 40, Belek

#1165, Denver 4, Bosco

#1065, Topeka 5, Bektair

Recommend transfer of stallion #1065, Topeka 5, Bektair to PRC

SSP Przewalski's Horses by Location

MEMPHIS

STUD BOOK	SEX	SIRE	DAM	DATE OF BIRTH	LIVING OFFSPR	LIVING		FNDR COEF	F O U N D E R S												
						OFFSPR REPRO	LIVING SIBS		212	39	211	40	1	231	52	5	18	17	11	DOM	12
608	F	341	267	740926	2.1.0	0.0.0	0.0.0	.411	.422	.172	.141	.141	.031	.000	.016	.016	.031	.031	.000	.000	.000
618	F	341	408	750515	1.1.0	0.0.0	1.0.0	.441	.398	.129	.133	.105	.094	.000	.047	.047	.023	.023	.000	.000	.000
685	M	469	406	760707	3.5.0	0.2.0	0.1.0	.451	.375	.172	.125	.141	.062	.000	.031	.031	.031	.031	.000	.000	.000
9114	F	685	608	860517	1.0.0	.431	.398	.172	.133	.141	.047	.000	.023	.023	.031	.031	.000	.000	.000
9115	F	685	618	860612	1.0.0	.446	.387	.150	.129	.123	.078	.000	.039	.039	.027	.027	.000	.000	.000

Memphis

Memphis Zoological Park
2000 Galloway Avenue
Memphis, TN 38122

Genetic input from #231 (without genes from #11, #12 and the Mongolian domestic mare) is needed, probably best achieved through stallion replacement.

SSP Przewalski's Horses by Location

MINNESOTA

STUD BOOK	SEX	SIRE	DAM	DATE OF BIRTH	LIVING OFFSPR	LIVING		FNDR COEF	F O U N D E R S												
						OFFSPR REPRO	LIVING SIBS		212	39	211	40	1	231	52	5	18	17	11	DOM	12
368 M		171	228	670509	9. 6. 0	0. 4. 0	0. 1. 0	.451	.375	.172	.125	.141	.062	.000	.031	.031	.031	.031	.000	.000	.000
505 M		157	267	710622	0. 1. 0	0. 0. 0	0. 0. 0	.395	.422	.227	.141	.180	.000	.000	.000	.000	.016	.016	.000	.000	.000
615 M		306	389	750510	2. 0. 0	0. 0. 0	0. 0. 0	.878	.000	.094	.000	.094	.000	.000	.000	.000	.094	.094	.312	.156	.156
626 M		381	380	750602	0. 0. 0	.441	.398	.129	.133	.105	.094	.000	.047	.047	.023	.023	.000	.000	.000
667 F		517	286	760522	2. 1. 0	0. 0. 0	0. 0. 0	.772	.094	.086	.031	.086	.062	.000	.031	.031	.086	.086	.203	.102	.102
668 F		517	258	760523	2. 3. 0	0. 1. 0	0. 0. 0	.781	.094	.070	.031	.070	.062	.000	.031	.031	.070	.070	.234	.117	.117
688 M		381	373	760731	3. 9. 0	0. 3. 0	0. 1. 0	.441	.398	.129	.133	.105	.094	.000	.047	.047	.023	.023	.000	.000	.000
694 F		293	234	770405	2. 3. 0	0. 2. 0	0. 0. 0	.684	.188	.047	.062	.047	.125	.000	.062	.062	.047	.047	.156	.078	.078
697 F		293	393	770417	3. 3. 0	0. 3. 0	0. 0. 0	.684	.188	.047	.062	.047	.125	.000	.062	.062	.047	.047	.156	.078	.078
700 F		293	529	770427	4. 1. 0	0. 0. 0	0. 0. 0	.560	.305	.023	.102	.023	.188	.062	.094	.094	.023	.023	.031	.016	.016
886 M		615	668	800502	0. 0. 0	.830	.047	.082	.016	.082	.031	.000	.016	.016	.082	.082	.273	.137	.137
909 M		615	700	800601	0. 0. 0	.719	.152	.059	.051	.059	.094	.031	.047	.047	.059	.059	.172	.086	.086
1109 M		368	697	830411	2. 1. 0	.568	.281	.109	.094	.094	.094	.000	.047	.047	.039	.039	.078	.039	.039
1111 M		368	694	830422	1. 1. 0	.568	.281	.109	.094	.094	.094	.000	.047	.047	.039	.039	.078	.039	.039
1164 M		368	700	830707	0. 0. 0	.505	.340	.098	.113	.082	.125	.031	.062	.062	.027	.027	.016	.008	.008
1167 F		718	668	830710	1. 0. 0	0. 0. 0	3. 0. 0	.705	.164	.059	.055	.059	.094	.062	.047	.047	.059	.059	.148	.074	.074
1185 M		718	667	830916	2. 0. 0	.700	.164	.066	.055	.066	.094	.062	.047	.047	.066	.066	.133	.066	.066
1310 F		368	697	850328	0. 1. 0	0. 0. 0	1. 1. 0	.568	.281	.109	.094	.094	.094	.000	.047	.047	.039	.039	.078	.039	.039
1332 F		368	694	850509	0. 1. 0	0. 0. 0	1. 0. 0	.568	.281	.109	.094	.094	.094	.000	.047	.047	.039	.039	.078	.039	.039
1514 F		688	668	860912	0. 0. 0	.611	.246	.100	.082	.088	.078	.000	.039	.039	.047	.047	.117	.059	.059
1515 F		688	667	860917	0. 0. 0	.606	.246	.107	.082	.096	.078	.000	.039	.039	.055	.055	.102	.051	.051
9122 F		688	1310	870522	0. 0. 0	.504	.340	.119	.113	.100	.094	.000	.047	.047	.031	.031	.039	.020	.020
9123 M		688	700	870601	0. 0. 0	.500	.352	.076	.117	.064	.141	.031	.070	.070	.023	.023	.016	.008	.008
9124 F		688	1332	870622	0. 0. 0	.504	.340	.119	.113	.100	.094	.000	.047	.047	.031	.031	.039	.020	.020
9125 M		368	1167	870702	0. 0. 0	.578	.270	.115	.090	.100	.078	.031	.039	.039	.045	.045	.074	.037	.037

SSP Przewalski's Horses by Location

NEW YORK

STUD BOOK	SEX	SIRE	DAM	DATE OF BIRTH	LIVING OFFSPR	LIVING REPRO	LIVING SIBS	FNDR COEF	F O U N D E R S												
									212	39	211	40	1	231	52	5	18	17	11	DOM	12
380	F	150	267	670618	2. 2. 0	0. 1. 0	0. 2. 0	.430	.422	.086	.141	.070	.125	.000	.062	.062	.016	.016	.000	.000	.000
498	F	171	168	710604	1. 3. 0	0. 2. 0	0. 1. 0	.451	.375	.172	.125	.141	.062	.000	.031	.031	.031	.031	.000	.000	.000
545	F	171	168	730506	1. 2. 0	0. 1. 0	0. 1. 0	.451	.375	.172	.125	.141	.062	.000	.031	.031	.031	.031	.000	.000	.000
722	F	381	498	770619	0. 2. 0	0. 0. 0	0. 0. 0	.451	.375	.172	.125	.141	.062	.000	.031	.031	.031	.031	.000	.000	.000
831	F	259	490	790523	2. 0. 0	0. 0. 0	0. 0. 0	.651	.211	.070	.070	.070	.000	.438	.000	.000	.070	.070	.000	.000	.000
933	F	533	545	800713	1. 0. 0	0. 0. 0	0. 0. 0	.423	.398	.199	.133	.160	.031	.000	.016	.016	.023	.023	.000	.000	.000
988	F	638	380	810604	0. 1. 0	0. 0. 0	0. 0. 0	.436	.410	.107	.137	.088	.109	.000	.055	.055	.020	.020	.000	.000	.000
942	M	533	498	811001	0. 1. 0	.423	.398	.199	.133	.160	.031	.000	.016	.016	.023	.023	.000	.000	.000
1063	F	533	498	820606	0. 1. 0	0. 0. 0	1. 0. 0	.423	.398	.199	.133	.160	.031	.000	.016	.016	.023	.023	.000	.000	.000
1124	M	411	754	830514	0. 0. 0	.437	.375	.211	.125	.164	.062	.000	.031	.031	.000	.000	.000	.000	.000
1291	F	606	380	841022	0. 0. 0	.541	.316	.078	.105	.070	.062	.219	.031	.031	.043	.043	.000	.000	.000
1315	F	887	945	850422	1. 0. 0	.457	.381	.130	.127	.108	.094	.000	.047	.047	.033	.033	.000	.000	.000
1361	M	606	831	850606	1. 0. 0	.651	.211	.070	.070	.070	.000	.438	.000	.000	.070	.070	.000	.000	.000
1363	F	606	988	850609	0. 0. 0	.543	.311	.089	.104	.079	.055	.219	.027	.027	.045	.045	.000	.000	.000
1393	F	606	1063	850815	0. 0. 0	.537	.305	.135	.102	.115	.016	.219	.008	.008	.047	.047	.000	.000	.000
1398	F	606	498	850912	0. 0. 0	.551	.293	.121	.098	.105	.031	.219	.016	.016	.051	.051	.000	.000	.000
1403	M	606	545	851219	0. 1. 0	.551	.293	.121	.098	.105	.031	.219	.016	.016	.051	.051	.000	.000	.000

New York

Bronx Zoo
185th St. & Southern Blvd.
Bronx NY 10460

Composition of breeding groups for 1988/1989:

Group 1

Herd stallion: #701, Memphis 1, Rousseau

Mares: #831
#1291
#1363
#1393
#1398

Group 2

Herd stallion: #1124, Hell. 92, Sirtaki

Mares: #380
#498
#545
#722
#933
#988
#1063
#1315

Transfer stallion #1403, New York 47, Vagabond to Toronto

SSP Przewalski's Horses by Location

SAN DIEGO

STUD BOOK	SEX	SIRE	DAM	DATE OF BIRTH	LIVING OFFSPR	LIVING OFFSPR REPRO	LIVING SIBS	FNDR COEF	F O U N D E R S												
									212	39	211	40	1	231	52	5	18	17	11	DOM	12
879	M	638	480	800420	0.0.0	.436	.410	.107	.137	.088	.109	.000	.055	.055	.020	.020	.000	.000	.000
945	F	685	712	810218	1.1.0	0.0.0	0.0.0	.446	.387	.150	.129	.123	.078	.000	.039	.039	.027	.027	.000	.000	.000
964	F	685	713	810509	1.0.0	0.0.0	0.0.0	.451	.375	.172	.125	.141	.062	.000	.031	.031	.031	.031	.000	.000	.000
1064	F	568	841	820608	1.0.0	0.0.0	1.2.0	.459	.375	.145	.125	.121	.078	.000	.039	.039	.039	.039	.000	.000	.000
1481	M	753	639	860616	2.0.0	.459	.375	.141	.125	.117	.086	.000	.043	.043	.035	.035	.000	.000	.000

San Diego Zoo

San Diego Zoo
P.O. Box 551
San Diego CA 92112

Composition of breeding group for 1988/1989:

Herd stallion: #1210, New York 36, Viktor (now at SDWAP)

Mares: #945

#964

#1064

Stallion #879, San Diego 29, Rogmar, is surplus.

SSP Przewalski's Horses by Location

SAN PASQUAL

STUD BOOK	SEX	SIRE	DAM	DATE OF BIRTH	LIVING OFFSPR	LIVING		FNDR COEF	F O U N D E R S												
						OFFSPR	SIBS		212	39	211	40	1	231	52	5	18	17	11	DOM	12
293 M	150	149	630623	7. 6. 0	1. 3. 0	0. 0. 0	.491	.375	.000	.125	.000	.250	.000	.125	.125	.000	.000	.000	.000	.000	.000
339 F	171	228	650627	1. 1. 0	0. 1. 0	1. 0. 0	.451	.375	.172	.125	.141	.062	.000	.031	.031	.031	.031	.000	.000	.000	.000
406 F	320	339	690408	2. 1. 0	1. 1. 0	0. 0. 0	.451	.375	.172	.125	.141	.062	.000	.031	.031	.031	.031	.000	.000	.000	.000
458 F	320	319	700210	1. 3. 0	1. 3. 0	0. 0. 0	.430	.422	.086	.141	.070	.125	.000	.062	.062	.016	.016	.000	.000	.000	.000
480 F	150	267	700616	1. 0. 0	0. 0. 0	0. 2. 0	.430	.422	.086	.141	.070	.125	.000	.062	.062	.016	.016	.000	.000	.000	.000
568 M	341	277	730820	8. 6. 0	2. 1. 0	0. 0. 0	.467	.375	.117	.125	.102	.094	.000	.047	.047	.047	.047	.000	.000	.000	.000
712 F	469	458	770531	1. 1. 0	0. 1. 0	1. 2. 0	.441	.398	.129	.133	.105	.094	.000	.047	.047	.023	.023	.000	.000	.000	.000
737 F	473	268	770901	2. 0. 0	0. 0. 0	0. 0. 0	.471	.375	.086	.125	.070	.156	.000	.078	.078	.016	.016	.000	.000	.000	.000
826 F	259	548	790522	3. 1. 0	0. 0. 0	0. 0. 0	.676	.188	.062	.062	.062	.000	.500	.000	.000	.062	.062	.000	.000	.000	.000
961 F	469	458	810505	1. 1. 0	0. 0. 0	1. 2. 0	.441	.398	.129	.133	.105	.094	.000	.047	.047	.023	.023	.000	.000	.000	.000
1021 F	469	406	811213	0. 1. 0	0. 0. 0	1. 0. 0	.451	.375	.172	.125	.141	.062	.000	.031	.031	.031	.031	.000	.000	.000	.000
1071 F	469	504	820622	0. 1. 0	0. 0. 0	0. 3. 0	.451	.375	.172	.125	.141	.062	.000	.031	.031	.031	.031	.000	.000	.000	.000
1192 M	293	826	840228	0. 1. 0	.583	.281	.031	.094	.031	.125	.250	.062	.062	.031	.031	.000	.000	.000	.000
1205 M	606	933	840423	0. 0. 0	.537	.305	.135	.102	.115	.016	.219	.008	.008	.047	.047	.000	.000	.000	.000
1210 M	606	831	840429	1. 0. 0	.651	.211	.070	.070	.070	.000	.438	.000	.000	.070	.070	.000	.000	.000	.000
1312 F	293	826	850410	1. 0. 0	.583	.281	.031	.094	.031	.125	.250	.062	.062	.031	.031	.000	.000	.000	.000
1408 M	293	737	860317	1. 0. 0	.481	.375	.043	.125	.035	.203	.000	.102	.102	.008	.008	.000	.000	.000	.000
1425 M	887	945	860507	0. 1. 0	.457	.381	.130	.127	.108	.094	.000	.047	.047	.033	.033	.000	.000	.000	.000
1429 M	887	964	860509	0. 0. 0	.459	.375	.141	.125	.117	.086	.000	.043	.043	.035	.035	.000	.000	.000	.000
1444 F	606	1071	860519	0. 0. 0	.551	.293	.121	.098	.105	.031	.219	.016	.016	.051	.051	.000	.000	.000	.000
1465 M	606	1064	860603	0. 0. 0	.555	.293	.107	.098	.096	.039	.219	.020	.020	.055	.055	.000	.000	.000	.000
1483 M	606	406	860618	0. 0. 0	.551	.293	.121	.098	.105	.031	.219	.016	.016	.051	.051	.000	.000	.000	.000
1492 M	606	826	860630	0. 0. 0	.664	.199	.066	.066	.066	.000	.469	.000	.000	.066	.066	.000	.000	.000	.000
9138 M	293	712	870211	0. 0. 0	.466	.387	.064	.129	.053	.172	.000	.086	.086	.012	.012	.000	.000	.000	.000
9139 M	293	339	870326	0. 0. 0	.471	.375	.086	.125	.070	.156	.000	.078	.078	.016	.016	.000	.000	.000	.000
9140 M	293	737	870410	1. 0. 0	.481	.375	.043	.125	.035	.203	.000	.102	.102	.008	.008	.000	.000	.000	.000
9203 F	568	961	871121	0. 0. 0	.454	.387	.123	.129	.104	.094	.000	.047	.047	.035	.035	.000	.000	.000	.000
9204 M	568	826	871124	0. 0. 0	.572	.281	.090	.094	.082	.047	.250	.023	.023	.055	.055	.000	.000	.000	.000
9205 F	568	1021	871231	0. 0. 0	.459	.375	.145	.125	.121	.078	.000	.039	.039	.039	.039	.000	.000	.000	.000

San Pasqual

*San Diego Wild Animal Park
15500 San Pasqual Valley Rd.
Escondido CA 92027*

These males are designated surplus:

#568 Cats. 61, Rolmar
San Diego 52, Belden, born 11.II.87, (studbook # pending)
San Diego 53, Bowen, born 26.III.87, (studbook # pending)
San Diego 58, Vaton, born 16.I.88

Transfer stallion #1408, San Diego 43, "Heran", born 13.III.86 to Calgary

Transfer to the Canyon Colorado Equid Sanctuary the following mares:

San Diego 55, "Betwa", born 21.XI.87 at San Diego
(studbook number pending)
San Diego 57, "Borkana", born 31.XII.87 at San Diego
(studbook number pending)

Transfer the stallion #1205, New York 35, Virgil to Minnesota.

Transfer these stallions to the EEP

#1429, San Diego 45, Bochin
#1483, San Diego 50, Bolon

Composition of breeding groups for 1988/1989:

Group 1

Herd stallion: #1192, San Diego 38, Vasiliy

Mares: #406
#826
#1021
#1071
#1312
#1444

Group 2

Herd stallion: #293, Cats. 17, Basil

Mares: #339
#458
#480
#712
#737
#961

SSP Przewalski's Horses by Location

TOPEKA

STUD BOOK	SEX	SIRE	DAM	DATE OF BIRTH	LIVING OFFSPR	LIVING OFFSPR REPRO	LIVING SIBS	FNDR COEF	F O U N D E R S												
									212	39	211	40	1	231	52	5	18	17	11	DOM	12
616	M	341	278	750512	0. 1. 0	.411	.422	.172	.141	.141	.031	.000	.016	.016	.031	.031	.000	.000	.000
635	F	381	373	750702	1. 0. 0	.441	.398	.129	.133	.105	.094	.000	.047	.047	.023	.023	.000	.000	.000
822	F	469	458	790519	3. 1. 0	1. 0. 0	1. 2. 0	.441	.398	.129	.133	.105	.094	.000	.047	.047	.023	.023	.000	.000	.000
841	F	469	504	790606	1. 3. 0	0. 1. 0	0. 3. 0	.451	.375	.172	.125	.141	.062	.000	.031	.031	.031	.031	.000	.000	.000
1084	M	685	380	820731	0. 0. 0	.441	.398	.129	.133	.105	.094	.000	.047	.047	.023	.023	.000	.000	.000
1130	M	568	549	830518	1. 0. 0	.468	.375	.109	.125	.094	.109	.000	.055	.055	.039	.039	.000	.000	.000
1232	F	568	841	840517	1. 2. 0	.459	.375	.145	.125	.121	.078	.000	.039	.039	.039	.039	.000	.000	.000
1249	M	568	822	840607	2. 1. 0	.454	.387	.123	.129	.104	.094	.000	.047	.047	.035	.035	.000	.000	.000
1287	F	688	668	840909	1. 1. 0	.611	.246	.100	.082	.088	.078	.000	.039	.039	.047	.047	.117	.059	.059
1364	M	568	822	850609	2. 1. 0	.454	.387	.123	.129	.104	.094	.000	.047	.047	.035	.035	.000	.000	.000
1370	F	568	841	850614	1. 2. 0	.459	.375	.145	.125	.121	.078	.000	.039	.039	.039	.039	.000	.000	.000
1458	F	568	822	860530	3. 0. 0	.454	.387	.123	.129	.104	.094	.000	.047	.047	.035	.035	.000	.000	.000
1472	M	568	841	860609	0. 3. 0	.459	.375	.145	.125	.121	.078	.000	.039	.039	.039	.039	.000	.000	.000

Topeka

Topeka Zoological Park
635 Gage Blvd.
Topeka KS 66606

These males are designated surplus:

#1249, Topeka 10, Bryansk

#1364, Topeka 11, Bevin

Transfer mare #1287, Minn.20, Maggie, to Canyon Colorado Equid Sanctuary

Composition of breeding group for 1988:

Herd stallion: #368, Cats. 35, Bonhold

Mares: #635
#822
#841
#1232
#1370
#1458

In order to correct for founder representation bias, a replacement stallion should be arranged for 1989. (suggest #1210, New York 36, Viktor [at SDZoo]).

SSP Przewalski's Horses by Location

TORONTO

STUD BOOK	SEX	SIRE	DAM	DATE OF BIRTH	LIVING OFFSPR	LIVING OFFSPR REPRO	LIVING SIBS	FNDR COEF	F O U N D E R S												
									212	39	211	40	1	231	52	5	18	17	11	DOM	12
638 M		469	458	750708	1.2.0	0.1.0	0.3.0	.441	.398	.129	.133	.105	.094	.000	.047	.047	.023	.023	.000	.000	.000
1144 F		293	508	830604	0.0.0	.680	.188	.055	.062	.055	.125	.000	.062	.062	.055	.055	.141	.070	.070
1166 F		293	400	830710	1.0.0	.629	.234	.047	.078	.047	.125	.125	.062	.062	.047	.047	.062	.031	.031
1174 F		517	530	830727	0.1.0	0.0.0	0.0.0	.781	.094	.070	.031	.070	.062	.000	.031	.031	.070	.070	.234	.117	.117
9126 F		638	1174	870528	0.0.0	.611	.246	.100	.082	.088	.078	.000	.039	.039	.047	.047	.117	.059	.059

Toronto

*Metropolitan Toronto Zoo
Box 280
West Hill, Toronto, Ontario
CANADA M1E 4R5*

Recommend transfer of stallion #638, San Diego 10 to Australian Species Management Group.

Receive stallion #1403, New York 47, Vagabond from Bronx Zoo.

Male foal, Toronto 2, born 13.X.87 to be kept available for future breeding.

Appendix 2

Pairwise Inbreeding Coefficients

	MALES														
FEMALES	293	298	368	392	470	496	505	526	566	568	615	616	626	685	688
168	0.156	0.275	0.275	0.203	0.246	0.239	0.297	0.239	0.334	0.336	0.047	0.379	0.334	0.312	0.334
228	0.156	0.400	0.400	0.203	0.225	0.302	0.318	0.302	0.239	0.252	0.047	0.273	0.239	0.364	0.239
267	0.195	0.289	0.289	0.221	0.305	0.255	0.457	0.255	0.360	0.278	0.029	0.362	0.360	0.294	0.308
268	0.402	0.218	0.218	0.341	0.299	0.279	0.176	0.279	0.258	0.249	0.000	0.207	0.258	0.218	0.258
277	0.279	0.226	0.226	0.453	0.287	0.339	0.209	0.339	0.256	0.402	0.035	0.236	0.256	0.226	0.256
278	0.195	0.289	0.289	0.221	0.410	0.255	0.352	0.255	0.308	0.278	0.029	0.468	0.308	0.294	0.360
339	0.218	0.396	0.396	0.209	0.241	0.303	0.291	0.303	0.288	0.280	0.029	0.312	0.288	0.433	0.288
380	0.299	0.241	0.241	0.317	0.326	0.279	0.316	0.279	0.315	0.270	0.015	0.278	0.425	0.244	0.289
406	0.218	0.365	0.365	0.209	0.247	0.287	0.286	0.287	0.311	0.301	0.029	0.338	0.311	0.516	0.311
408	0.299	0.241	0.241	0.317	0.326	0.279	0.316	0.279	0.425	0.270	0.015	0.278	0.315	0.244	0.289
458	0.299	0.285	0.285	0.281	0.288	0.283	0.250	0.283	0.307	0.295	0.015	0.302	0.307	0.321	0.307
480	0.299	0.241	0.241	0.317	0.326	0.279	0.316	0.279	0.315	0.270	0.015	0.278	0.315	0.244	0.289
498	0.218	0.334	0.334	0.209	0.252	0.272	0.280	0.272	0.335	0.322	0.029	0.364	0.335	0.355	0.335
535	0.341	0.209	0.209	0.434	0.317	0.322	0.192	0.322	0.263	0.331	0.018	0.215	0.263	0.209	0.263
545	0.218	0.334	0.334	0.209	0.252	0.272	0.280	0.272	0.335	0.322	0.029	0.364	0.335	0.355	0.335
569	0.218	0.365	0.365	0.209	0.247	0.287	0.286	0.287	0.311	0.301	0.029	0.338	0.311	0.420	0.311
608	0.207	0.312	0.312	0.215	0.278	0.263	0.369	0.263	0.399	0.352	0.029	0.415	0.348	0.325	0.321
618	0.258	0.288	0.288	0.263	0.289	0.276	0.298	0.276	0.432	0.347	0.022	0.373	0.325	0.299	0.312
635	0.258	0.288	0.288	0.263	0.315	0.276	0.272	0.276	0.312	0.295	0.022	0.348	0.364	0.299	0.432
639	0.218	0.381	0.381	0.209	0.244	0.295	0.288	0.295	0.299	0.290	0.029	0.325	0.299	0.452	0.299
667	0.163	0.081	0.081	0.101	0.088	0.091	0.068	0.091	0.085	0.092	0.260	0.078	0.085	0.081	0.085
668	0.163	0.076	0.076	0.098	0.086	0.087	0.064	0.087	0.081	0.086	0.333	0.074	0.081	0.076	0.081
694	0.326	0.124	0.124	0.179	0.157	0.151	0.101	0.151	0.140	0.140	0.195	0.118	0.140	0.124	0.140
697	0.326	0.124	0.124	0.179	0.157	0.151	0.101	0.151	0.140	0.140	0.183	0.118	0.140	0.124	0.140
700	0.499	0.181	0.181	0.271	0.239	0.226	0.150	0.226	0.210	0.206	0.046	0.174	0.210	0.181	0.210
712	0.258	0.341	0.341	0.245	0.265	0.293	0.271	0.293	0.297	0.287	0.022	0.307	0.297	0.403	0.297
713	0.218	0.381	0.381	0.209	0.244	0.295	0.288	0.295	0.299	0.290	0.029	0.325	0.299	0.452	0.299
722	0.218	0.334	0.334	0.209	0.252	0.272	0.280	0.272	0.335	0.322	0.029	0.364	0.387	0.355	0.387
736	0.207	0.312	0.312	0.215	0.331	0.263	0.316	0.263	0.373	0.352	0.029	0.468	0.321	0.325	0.348
737	0.310	0.292	0.292	0.275	0.273	0.283	0.231	0.283	0.285	0.275	0.015	0.272	0.285	0.319	0.285
822	0.258	0.341	0.341	0.245	0.265	0.293	0.271	0.293	0.297	0.287	0.022	0.307	0.297	0.403	0.297
826	0.078	0.105	0.105	0.098	0.102	0.102	0.109	0.102	0.104	0.111	0.035	0.115	0.104	0.105	0.104
830	0.049	0.095	0.095	0.069	0.088	0.082	0.109	0.082	0.094	0.095	0.312	0.114	0.094	0.097	0.094
831	0.088	0.119	0.119	0.110	0.114	0.114	0.123	0.114	0.116	0.125	0.040	0.130	0.116	0.119	0.116
841	0.218	0.381	0.381	0.209	0.244	0.295	0.288	0.295	0.299	0.290	0.029	0.325	0.299	0.452	0.299
917	0.258	0.319	0.319	0.263	0.419	0.291	0.277	0.291	0.288	0.275	0.022	0.321	0.288	0.312	0.302
921	0.186	0.290	0.290	0.207	0.337	0.248	0.498	0.248	0.303	0.261	0.028	0.392	0.303	0.291	0.316
933	0.197	0.313	0.313	0.201	0.284	0.257	0.327	0.257	0.303	0.283	0.028	0.366	0.303	0.322	0.317
945	0.238	0.361	0.361	0.227	0.254	0.294	0.279	0.294	0.298	0.289	0.026	0.316	0.298	0.543	0.298
948	0.292	0.206	0.206	0.221	0.236	0.213	0.187	0.213	0.226	0.218	0.102	0.233	0.252	0.211	0.383
952	0.292	0.206	0.206	0.221	0.236	0.213	0.187	0.213	0.226	0.218	0.109	0.233	0.252	0.211	0.383
961	0.258	0.341	0.341	0.245	0.265	0.293	0.271	0.293	0.297	0.287	0.022	0.307	0.297	0.403	0.297
964	0.218	0.381	0.381	0.209	0.244	0.295	0.288	0.295	0.299	0.290	0.029	0.325	0.299	0.567	0.299
988	0.279	0.291	0.291	0.281	0.295	0.286	0.293	0.286	0.306	0.278	0.018	0.293	0.361	0.323	0.293
1021	0.218	0.381	0.381	0.209	0.244	0.295	0.288	0.295	0.299	0.290	0.029	0.325	0.299	0.500	0.299
1028	0.292	0.206	0.206	0.221	0.236	0.213	0.187	0.213	0.226	0.218	0.109	0.233	0.252	0.211	0.383
1035	0.292	0.206	0.206	0.221	0.236	0.213	0.187	0.213	0.226	0.218	0.102	0.233	0.252	0.211	0.383
1063	0.197	0.313	0.313	0.201	0.284	0.257	0.327	0.257	0.303	0.283	0.028	0.366	0.303	0.322	0.317

	MALES														
FEMALES	293	298	368	392	470	496	505	526	566	568	615	616	626	685	688
1064	0.233	0.330	0.330	0.270	0.257	0.300	0.266	0.300	0.323	0.452	0.031	0.338	0.298	0.371	0.298
1071	0.218	0.381	0.381	0.209	0.244	0.295	0.288	0.295	0.299	0.290	0.029	0.325	0.299	0.452	0.299
1125	0.255	0.301	0.405	0.215	0.239	0.310	0.239	0.310	0.257	0.249	0.066	0.272	0.270	0.296	0.335
1155	0.255	0.301	0.405	0.215	0.239	0.310	0.239	0.310	0.257	0.249	0.069	0.272	0.270	0.296	0.335
1167	0.254	0.111	0.111	0.150	0.133	0.130	0.094	0.130	0.122	0.125	0.213	0.108	0.122	0.111	0.122
1179	0.241	0.336	0.362	0.268	0.259	0.329	0.266	0.329	0.305	0.375	0.029	0.316	0.293	0.372	0.293
1232	0.233	0.330	0.330	0.270	0.257	0.300	0.266	0.300	0.323	0.452	0.031	0.338	0.298	0.371	0.298
1240	0.255	0.301	0.405	0.215	0.239	0.310	0.239	0.310	0.257	0.249	0.066	0.272	0.270	0.296	0.335
1287	0.211	0.182	0.182	0.181	0.201	0.181	0.168	0.181	0.197	0.191	0.178	0.211	0.222	0.188	0.354
1291	0.193	0.180	0.180	0.214	0.220	0.197	0.220	0.197	0.216	0.197	0.027	0.204	0.271	0.181	0.203
1310	0.272	0.260	0.364	0.194	0.199	0.279	0.196	0.279	0.214	0.210	0.106	0.215	0.214	0.252	0.214
1312	0.365	0.162	0.162	0.219	0.200	0.190	0.143	0.190	0.181	0.180	0.018	0.161	0.181	0.162	0.181
1315	0.251	0.326	0.352	0.277	0.264	0.329	0.261	0.329	0.305	0.374	0.027	0.312	0.292	0.418	0.292
1332	0.272	0.260	0.364	0.194	0.199	0.279	0.196	0.279	0.214	0.210	0.112	0.215	0.214	0.252	0.214
1363	0.183	0.205	0.205	0.196	0.205	0.200	0.208	0.200	0.211	0.202	0.029	0.211	0.239	0.221	0.205
1370	0.233	0.330	0.330	0.270	0.257	0.300	0.266	0.300	0.323	0.452	0.031	0.338	0.298	0.371	0.298
1388	0.078	0.133	0.133	0.100	0.130	0.117	0.155	0.117	0.136	0.131	0.236	0.161	0.136	0.135	0.136
1393	0.142	0.216	0.216	0.155	0.199	0.185	0.225	0.185	0.210	0.204	0.034	0.248	0.210	0.220	0.217
1398	0.153	0.226	0.226	0.160	0.183	0.193	0.202	0.193	0.226	0.224	0.034	0.247	0.226	0.237	0.226
9114	0.212	0.346	0.346	0.212	0.261	0.279	0.328	0.279	0.349	0.321	0.029	0.370	0.324	0.504	0.310
9132	0.153	0.250	0.250	0.160	0.179	0.205	0.206	0.205	0.208	0.208	0.034	0.227	0.208	0.285	0.208
9133	0.173	0.230	0.230	0.177	0.189	0.204	0.197	0.204	0.207	0.206	0.031	0.218	0.207	0.261	0.207
9127	0.253	0.310	0.310	0.288	0.267	0.299	0.258	0.299	0.322	0.450	0.027	0.329	0.297	0.346	0.297
9115	0.238	0.334	0.334	0.236	0.266	0.285	0.293	0.285	0.366	0.319	0.026	0.349	0.312	0.491	0.306
9113	0.254	0.306	0.357	0.252	0.253	0.305	0.248	0.305	0.290	0.349	0.046	0.301	0.283	0.321	0.316
9119	0.211	0.182	0.182	0.181	0.201	0.181	0.168	0.181	0.197	0.191	0.178	0.211	0.222	0.188	0.354
9120	0.211	0.184	0.184	0.182	0.202	0.183	0.170	0.183	0.198	0.194	0.141	0.213	0.224	0.190	0.355
9122	0.265	0.274	0.326	0.229	0.257	0.277	0.234	0.277	0.263	0.253	0.064	0.281	0.289	0.276	0.420
9124	0.265	0.274	0.326	0.229	0.257	0.277	0.234	0.277	0.263	0.253	0.067	0.281	0.289	0.276	0.420
9125	0.236	0.254	0.357	0.180	0.187	0.268	0.192	0.268	0.205	0.202	0.121	0.210	0.205	0.246	0.205
9109	0.253	0.276	0.276	0.266	0.464	0.271	0.290	0.271	0.331	0.311	0.022	0.399	0.305	0.284	0.332

	MALES														
EMALES	701	718	753	868	869	879	886	909	942	1070	1084	1110	1110	1124	1130
168	0.338	0.125	0.288	0.205	0.292	0.269	0.061	0.094	0.359	0.314	0.28	0.188	0.188	0.275	0.288
228	0.296	0.125	0.277	0.184	0.313	0.269	0.061	0.094	0.286	0.282	0.29	0.251	0.251	0.232	0.277
267	0.410	0.139	0.267	0.236	0.283	0.347	0.050	0.098	0.331	0.281	0.35	0.201	0.201	0.309	0.267
268	0.191	0.221	0.264	0.107	0.258	0.279	0.050	0.156	0.197	0.253	0.26	0.209	0.209	0.218	0.264
277	0.222	0.181	0.371	0.154	0.244	0.266	0.066	0.133	0.217	0.323	0.26	0.191	0.191	0.211	0.371
278	0.410	0.139	0.267	0.236	0.283	0.294	0.050	0.098	0.384	0.281	0.300	0.201	0.201	0.309	0.267
339	0.301	0.145	0.291	0.171	0.341	0.291	0.053	0.105	0.313	0.310	0.337	0.260	0.260	0.257	0.291
380	0.297	0.180	0.274	0.172	0.265	0.322	0.050	0.127	0.258	0.267	0.421	0.199	0.199	0.275	0.274
406	0.312	0.145	0.294	0.177	0.361	0.304	0.053	0.105	0.331	0.331	0.381	0.244	0.244	0.268	0.294
408	0.297	0.180	0.274	0.172	0.265	0.322	0.050	0.127	0.258	0.267	0.311	0.199	0.199	0.275	0.274
458	0.276	0.180	0.289	0.158	0.451	0.370	0.050	0.127	0.288	0.373	0.305	0.221	0.221	0.263	0.289
480	0.297	0.180	0.274	0.172	0.265	0.431	0.050	0.127	0.258	0.267	0.311	0.199	0.199	0.275	0.274
498	0.322	0.145	0.297	0.182	0.330	0.291	0.053	0.105	0.453	0.326	0.303	0.229	0.229	0.279	0.297
535	0.204	0.201	0.326	0.131	0.245	0.281	0.058	0.144	0.201	0.288	0.263	0.194	0.194	0.227	0.326
545	0.322	0.145	0.297	0.182	0.330	0.291	0.053	0.105	0.349	0.326	0.303	0.229	0.229	0.279	0.297
569	0.312	0.145	0.294	0.177	0.361	0.304	0.053	0.105	0.331	0.331	0.333	0.244	0.244	0.268	0.294
608	0.486	0.142	0.308	0.209	0.307	0.319	0.051	0.102	0.340	0.329	0.328	0.215	0.215	0.294	0.308
618	0.336	0.162	0.311	0.177	0.297	0.306	0.052	0.116	0.303	0.322	0.307	0.214	0.214	0.277	0.311
635	0.310	0.162	0.286	0.177	0.297	0.293	0.052	0.116	0.317	0.297	0.294	0.214	0.214	0.277	0.286
639	0.307	0.145	0.293	0.174	0.403	0.323	0.053	0.105	0.322	0.346	0.348	0.252	0.252	0.263	0.293
667	0.073	0.165	0.091	0.138	0.085	0.086	0.279	0.212	0.075	0.088	0.085	0.167	0.146	0.071	0.091
668	0.069	0.156	0.087	0.146	0.081	0.083	0.463	0.246	0.070	0.084	0.081	0.167	0.153	0.068	0.087
694	0.109	0.219	0.146	0.133	0.140	0.148	0.212	0.234	0.112	0.140	0.140	0.189	0.312	0.118	0.146
697	0.109	0.222	0.146	0.126	0.140	0.148	0.220	0.228	0.112	0.140	0.140	0.312	0.189	0.118	0.146
700	0.162	0.330	0.216	0.117	0.210	0.225	0.103	0.360	0.166	0.208	0.210	0.228	0.227	0.177	0.216
712	0.289	0.162	0.290	0.165	0.448	0.356	0.052	0.116	0.300	0.367	0.334	0.240	0.240	0.260	0.290
713	0.307	0.145	0.293	0.174	0.403	0.353	0.053	0.105	0.322	0.346	0.348	0.252	0.252	0.263	0.293
722	0.322	0.145	0.297	0.182	0.330	0.291	0.053	0.105	0.401	0.326	0.303	0.229	0.229	0.279	0.297
736	0.392	0.142	0.308	0.209	0.307	0.293	0.051	0.102	0.366	0.329	0.302	0.215	0.215	0.294	0.308
737	0.251	0.183	0.279	0.142	0.310	0.291	0.052	0.131	0.264	0.292	0.296	0.227	0.227	0.243	0.279
822	0.289	0.162	0.290	0.165	0.448	0.356	0.052	0.116	0.300	0.465	0.334	0.240	0.240	0.260	0.290
826	0.112	0.113	0.106	0.110	0.104	0.103	0.041	0.065	0.107	0.107	0.104	0.081	0.081	0.09	0.106
830	0.111	0.104	0.089	0.272	0.088	0.088	0.279	0.194	0.105	0.092	0.092	0.129	0.136	0.091	0.089
831	0.126	0.120	0.120	0.120	0.116	0.115	0.046	0.072	0.121	0.121	0.116	0.091	0.091	0.101	0.12
841	0.307	0.145	0.293	0.174	0.403	0.323	0.053	0.105	0.322	0.346	0.348	0.252	0.252	0.263	0.293
917	0.299	0.162	0.283	0.171	0.303	0.293	0.052	0.116	0.298	0.289	0.298	0.229	0.229	0.266	0.283
921	0.390	0.131	0.255	0.219	0.277	0.294	0.048	0.093	0.355	0.269	0.301	0.198	0.198	0.303	0.255
933	0.347	0.135	0.270	0.192	0.300	0.279	0.049	0.097	0.406	0.292	0.290	0.212	0.212	0.288	0.270
945	0.298	0.154	0.291	0.169	0.425	0.340	0.052	0.111	0.311	0.357	0.398	0.246	0.246	0.261	0.291
948	0.210	0.192	0.216	0.152	0.219	0.221	0.136	0.172	0.214	0.218	0.217	0.263	0.202	0.197	0.216
952	0.210	0.190	0.216	0.155	0.219	0.221	0.132	0.175	0.214	0.218	0.217	0.202	0.263	0.197	0.216
961	0.289	0.162	0.290	0.165	0.448	0.356	0.052	0.116	0.300	0.367	0.334	0.240	0.240	0.260	0.290
964	0.307	0.145	0.293	0.174	0.403	0.323	0.053	0.105	0.322	0.346	0.406	0.252	0.252	0.263	0.293
988	0.293	0.171	0.282	0.168	0.405	0.388	0.051	0.122	0.279	0.317	0.377	0.220	0.220	0.268	0.282
1021	0.307	0.145	0.293	0.174	0.403	0.323	0.053	0.105	0.322	0.346	0.372	0.252	0.252	0.263	0.293
1028	0.210	0.190	0.216	0.155	0.219	0.221	0.132	0.175	0.214	0.218	0.217	0.202	0.263	0.197	0.216
1035	0.210	0.192	0.216	0.152	0.219	0.221	0.136	0.172	0.214	0.218	0.217	0.263	0.202	0.197	0.216
1063	0.347	0.135	0.270	0.192	0.300	0.279	0.049	0.097	0.458	0.292	0.290	0.212	0.212	0.288	0.270

	MALES														
FEMALES	701	718	753	868	869	879	886	909	942	1070	1084	1110	1110	1124	1130
1064	0.302	0.154	0.376	0.171	0.345	0.301	0.056	0.112	0.302	0.398	0.31	0.231	0.231	0.254	0.376
1071	0.307	0.145	0.293	0.174	0.403	0.323	0.053	0.105	0.322	0.346	0.35	0.252	0.252	0.263	0.293
1125	0.255	0.169	0.279	0.161	0.280	0.256	0.094	0.139	0.263	0.264	0.26	0.313	0.283	0.227	0.279
1155	0.255	0.168	0.279	0.163	0.280	0.256	0.092	0.140	0.263	0.264	0.26	0.283	0.313	0.227	0.279
1167	0.101	0.338	0.127	0.136	0.122	0.127	0.294	0.229	0.102	0.123	0.12	0.175	0.167	0.102	0.127
1179	0.291	0.156	0.473	0.167	0.346	0.303	0.055	0.114	0.296	0.361	0.03	0.248	0.248	0.253	0.375
1232	0.302	0.154	0.376	0.171	0.345	0.301	0.056	0.112	0.302	0.398	0.314	0.231	0.231	0.254	0.376
1240	0.255	0.169	0.279	0.161	0.280	0.256	0.094	0.139	0.263	0.264	0.264	0.313	0.283	0.227	0.279
1287	0.189	0.159	0.186	0.161	0.189	0.188	0.257	0.181	0.193	0.190	0.188	0.190	0.183	0.172	0.186
1291	0.212	0.150	0.197	0.146	0.191	0.219	0.048	0.099	0.189	0.194	0.269	0.145	0.145	0.188	0.197
1310	0.205	0.183	0.245	0.149	0.240	0.220	0.136	0.167	0.212	0.225	0.226	0.338	0.276	0.188	0.245
1312	0.152	0.229	0.185	0.109	0.181	0.191	0.061	0.157	0.152	0.180	0.181	0.177	0.177	0.154	0.185
1315	0.286	0.161	0.374	0.164	0.358	0.311	0.055	0.116	0.290	0.366	0.341	0.245	0.245	0.252	0.374
1332	0.205	0.182	0.245	0.152	0.240	0.220	0.132	0.170	0.212	0.225	0.226	0.276	0.338	0.188	0.245
1363	0.210	0.145	0.201	0.144	0.261	0.251	0.048	0.097	0.200	0.219	0.247	0.155	0.155	0.184	0.201
1370	0.302	0.154	0.376	0.171	0.345	0.301	0.056	0.112	0.302	0.398	0.314	0.231	0.231	0.254	0.376
1388	0.158	0.115	0.124	0.445	0.126	0.128	0.216	0.166	0.148	0.129	0.133	0.139	0.144	0.132	0.124
1393	0.236	0.127	0.195	0.156	0.208	0.197	0.047	0.084	0.289	0.206	0.203	0.152	0.152	0.194	0.195
1398	0.224	0.132	0.208	0.151	0.223	0.203	0.049	0.089	0.287	0.223	0.210	0.160	0.160	0.190	0.208
9114	0.396	0.143	0.300	0.191	0.355	0.321	0.052	0.104	0.331	0.338	0.396	0.233	0.233	0.278	0.300
9132	0.216	0.132	0.206	0.147	0.260	0.219	0.049	0.089	0.221	0.234	0.232	0.172	0.172	0.182	0.206
9133	0.207	0.141	0.205	0.142	0.282	0.236	0.049	0.094	0.211	0.244	0.225	0.166	0.166	0.181	0.205
9127	0.293	0.163	0.375	0.166	0.367	0.317	0.055	0.118	0.292	0.457	0.307	0.225	0.225	0.253	0.375
9115	0.321	0.154	0.302	0.175	0.350	0.315	0.052	0.111	0.313	0.334	0.385	0.233	0.233	0.270	0.302
9113	0.274	0.166	0.327	0.164	0.324	0.287	0.075	0.128	0.278	0.454	0.285	0.269	0.254	0.240	0.327
9119	0.189	0.159	0.186	0.161	0.189	0.188	0.257	0.181	0.193	0.190	0.188	0.190	0.183	0.172	0.186
9120	0.192	0.163	0.189	0.157	0.191	0.190	0.165	0.164	0.196	0.192	0.189	0.191	0.180	0.174	0.189
9122	0.258	0.173	0.265	0.163	0.269	0.256	0.094	0.142	0.265	0.261	0.260	0.276	0.245	0.232	0.265
9124	0.258	0.172	0.265	0.164	0.269	0.256	0.092	0.143	0.265	0.261	0.260	0.245	0.276	0.232	0.265
9125	0.201	0.242	0.235	0.154	0.231	0.209	0.173	0.167	0.207	0.217	0.216	0.269	0.267	0.180	0.235
9109	0.345	0.161	0.291	0.190	0.286	0.294	0.051	0.114	0.325	0.298	0.293	0.207	0.207	0.285	0.291

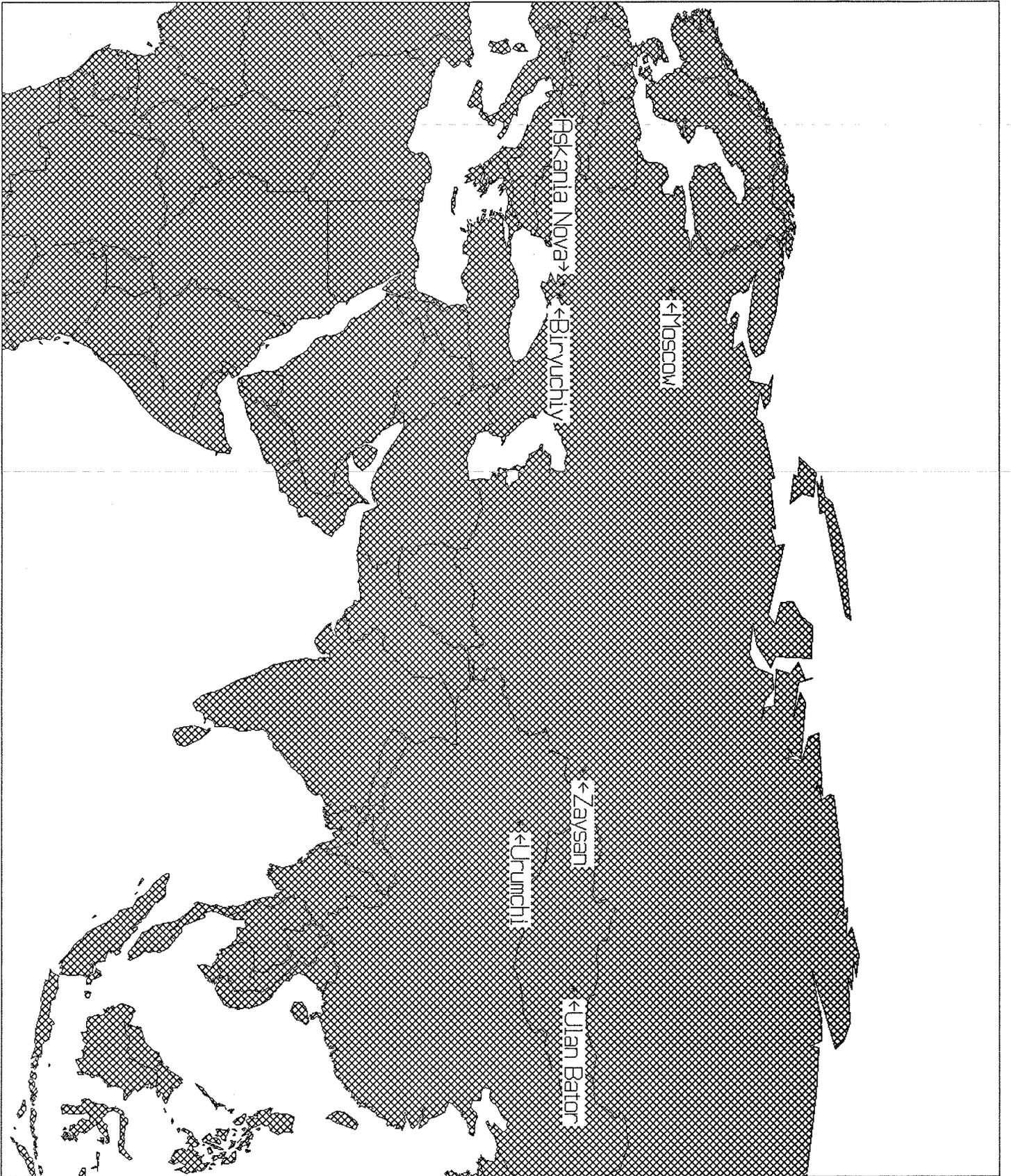
	MALES														
FEMALE	1400	1403	9129	9116	9130	9131	9118	9134	9110	9128	9136	9137	9111	9138	9139
168	0.208	0.281	0.204	0.188	0.295	0.300	0.208	0.232	0.300	0.324	0.245	0.133	0.300	0.224	0.216
228	0.161	0.197	0.199	0.251	0.307	0.320	0.271	0.224	0.320	0.308	0.234	0.133	0.320	0.234	0.278
267	0.192	0.226	0.221	0.201	0.278	0.281	0.228	0.214	0.281	0.286	0.220	0.133	0.281	0.239	0.242
268	0.179	0.153	0.419	0.209	0.251	0.241	0.265	0.161	0.241	0.233	0.153	0.083	0.241	0.330	0.310
277	0.179	0.179	0.266	0.191	0.303	0.298	0.228	0.223	0.298	0.314	0.179	0.125	0.298	0.262	0.252
278	0.218	0.226	0.221	0.201	0.278	0.281	0.228	0.214	0.281	0.286	0.220	0.133	0.281	0.239	0.242
339	0.184	0.226	0.281	0.260	0.339	0.362	0.289	0.237	0.362	0.356	0.294	0.112	0.362	0.279	0.411
380	0.189	0.183	0.286	0.199	0.264	0.259	0.240	0.185	0.259	0.257	0.180	0.108	0.259	0.282	0.270
406	0.196	0.247	0.282	0.244	0.366	0.381	0.273	0.239	0.357	0.360	0.393	0.112	0.357	0.290	0.343
408	0.189	0.183	0.286	0.199	0.264	0.259	0.240	0.185	0.259	0.257	0.180	0.108	0.259	0.282	0.270
458	0.198	0.220	0.313	0.221	0.337	0.305	0.262	0.211	0.305	0.308	0.236	0.108	0.305	0.375	0.292
480	0.189	0.183	0.286	0.199	0.264	0.259	0.240	0.185	0.259	0.257	0.180	0.108	0.259	0.282	0.270
498	0.208	0.268	0.257	0.229	0.320	0.326	0.258	0.229	0.326	0.338	0.247	0.112	0.326	0.274	0.276
535	0.182	0.160	0.308	0.194	0.277	0.268	0.240	0.190	0.268	0.270	0.160	0.104	0.268	0.293	0.275
545	0.208	0.372	0.257	0.229	0.320	0.326	0.258	0.229	0.326	0.338	0.247	0.112	0.326	0.274	0.276
569	0.196	0.247	0.282	0.244	0.342	0.357	0.273	0.239	0.357	0.360	0.296	0.112	0.357	0.290	0.343
608	0.200	0.247	0.239	0.215	0.312	0.316	0.243	0.234	0.316	0.338	0.234	0.122	0.316	0.257	0.259
618	0.198	0.226	0.272	0.214	0.305	0.305	0.249	0.220	0.305	0.323	0.214	0.110	0.305	0.278	0.273
635	0.258	0.226	0.272	0.214	0.292	0.293	0.249	0.207	0.293	0.298	0.214	0.110	0.293	0.278	0.273
639	0.190	0.237	0.268	0.252	0.360	0.384	0.281	0.257	0.488	0.395	0.269	0.112	0.396	0.310	0.325
667	0.337	0.070	0.127	0.167	0.087	0.086	0.123	0.072	0.086	0.086	0.070	0.055	0.086	0.124	0.122
668	0.190	0.064	0.126	0.167	0.083	0.082	0.118	0.066	0.082	0.081	0.064	0.049	0.082	0.122	0.120
694	0.175	0.094	0.244	0.189	0.139	0.135	0.198	0.098	0.135	0.132	0.094	0.060	0.135	0.233	0.225
697	0.197	0.094	0.244	0.312	0.139	0.135	0.199	0.098	0.135	0.132	0.094	0.060	0.135	0.233	0.225
700	0.187	0.143	0.373	0.228	0.206	0.199	0.427	0.149	0.199	0.194	0.143	0.100	0.199	0.355	0.340
712	0.191	0.223	0.284	0.240	0.406	0.346	0.275	0.231	0.346	0.345	0.239	0.110	0.346	0.450	0.299
713	0.190	0.237	0.268	0.252	0.360	0.430	0.281	0.257	0.396	0.395	0.269	0.112	0.488	0.310	0.325
722	0.234	0.268	0.257	0.229	0.320	0.326	0.258	0.229	0.326	0.338	0.247	0.112	0.326	0.274	0.276
736	0.213	0.247	0.239	0.215	0.312	0.316	0.243	0.234	0.316	0.338	0.234	0.122	0.316	0.257	0.259
737	0.188	0.200	0.459	0.227	0.297	0.299	0.269	0.200	0.299	0.297	0.225	0.098	0.299	0.310	0.327
822	0.191	0.223	0.284	0.240	0.358	0.346	0.275	0.231	0.346	0.345	0.239	0.110	0.346	0.353	0.299
826	0.078	0.236	0.085	0.081	0.105	0.106	0.101	0.238	0.106	0.108	0.236	0.527	0.106	0.091	0.092
830	0.152	0.084	0.061	0.129	0.091	0.093	0.086	0.081	0.093	0.096	0.082	0.063	0.093	0.069	0.072
831	0.087	0.270	0.096	0.091	0.119	0.119	0.111	0.272	0.119	0.122	0.270	0.395	0.119	0.102	0.103
841	0.190	0.237	0.268	0.252	0.360	0.384	0.281	0.303	0.396	0.486	0.269	0.112	0.396	0.310	0.325
917	0.193	0.205	0.270	0.229	0.295	0.298	0.265	0.205	0.298	0.294	0.211	0.110	0.298	0.280	0.289
921	0.194	0.214	0.212	0.198	0.270	0.273	0.224	0.204	0.273	0.276	0.212	0.125	0.273	0.231	0.238
933	0.196	0.287	0.230	0.212	0.290	0.296	0.239	0.212	0.296	0.302	0.226	0.114	0.296	0.249	0.255
945	0.191	0.230	0.276	0.246	0.496	0.388	0.278	0.238	0.359	0.358	0.278	0.111	0.359	0.380	0.312
948	0.276	0.160	0.258	0.263	0.215	0.214	0.224	0.152	0.214	0.215	0.154	0.085	0.214	0.256	0.249
952	0.265	0.160	0.258	0.202	0.215	0.214	0.223	0.152	0.214	0.215	0.154	0.085	0.214	0.256	0.249
961	0.191	0.223	0.284	0.240	0.358	0.346	0.275	0.231	0.346	0.345	0.239	0.110	0.346	0.353	0.299
964	0.190	0.237	0.268	0.252	0.389	0.509	0.281	0.251	0.384	0.383	0.293	0.112	0.430	0.310	0.325
988	0.190	0.203	0.285	0.220	0.311	0.303	0.258	0.208	0.303	0.301	0.210	0.109	0.303	0.317	0.285
1021	0.190	0.237	0.268	0.252	0.372	0.384	0.281	0.245	0.372	0.371	0.317	0.112	0.372	0.310	0.325
1028	0.265	0.160	0.258	0.202	0.215	0.214	0.223	0.152	0.214	0.215	0.154	0.085	0.214	0.256	0.249
1035	0.276	0.160	0.258	0.263	0.215	0.214	0.224	0.152	0.214	0.215	0.154	0.085	0.214	0.256	0.249
1063	0.196	0.235	0.230	0.212	0.290	0.296	0.239	0.212	0.296	0.302	0.226	0.114	0.296	0.249	0.255

	MALES														
FEMALES	1400	1403	9129	9116	9130	9131	9118	9134	9110	9128	9136	9137	9111	9138	9139
1064	0.192	0.230	0.265	0.231	0.367	0.380	0.262	0.384	0.386	0.469	0.241	0.115	0.386	0.289	0.295
1071	0.190	0.237	0.268	0.252	0.360	0.384	0.281	0.257	0.396	0.395	0.269	0.112	0.396	0.310	0.325
1125	0.230	0.193	0.256	0.313	0.284	0.288	0.308	0.188	0.288	0.273	0.198	0.099	0.288	0.267	0.278
1155	0.225	0.193	0.256	0.283	0.284	0.288	0.308	0.188	0.288	0.273	0.198	0.099	0.288	0.267	0.278
1167	0.176	0.098	0.195	0.175	0.122	0.119	0.178	0.102	0.119	0.118	0.098	0.083	0.119	0.188	0.183
1179	0.189	0.223	0.270	0.248	0.367	0.402	0.280	0.252	0.435	0.386	0.238	0.113	0.480	0.294	0.301
1232	0.192	0.230	0.265	0.231	0.367	0.380	0.262	0.295	0.386	0.469	0.241	0.115	0.386	0.289	0.295
1240	0.230	0.193	0.256	0.313	0.284	0.288	0.308	0.188	0.288	0.273	0.198	0.099	0.288	0.267	0.278
1287	0.272	0.145	0.199	0.190	0.187	0.187	0.184	0.137	0.187	0.189	0.139	0.079	0.187	0.200	0.196
1291	0.138	0.277	0.191	0.145	0.191	0.189	0.176	0.279	0.189	0.189	0.276	0.302	0.189	0.192	0.187
1310	0.191	0.160	0.249	0.338	0.245	0.248	0.296	0.161	0.248	0.231	0.168	0.086	0.248	0.256	0.266
1312	0.144	0.195	0.283	0.177	0.178	0.173	0.229	0.199	0.173	0.171	0.195	0.305	0.173	0.273	0.263
1315	0.190	0.219	0.274	0.245	0.484	0.430	0.279	0.243	0.367	0.367	0.243	0.112	0.367	0.329	0.295
1332	0.180	0.160	0.249	0.276	0.245	0.248	0.295	0.161	0.248	0.231	0.168	0.086	0.248	0.256	0.266
1363	0.139	0.288	0.190	0.155	0.215	0.211	0.185	0.291	0.211	0.211	0.291	0.303	0.211	0.210	0.194
1370	0.192	0.230	0.265	0.231	0.367	0.380	0.262	0.295	0.386	0.469	0.241	0.115	0.386	0.289	0.295
1388	0.155	0.117	0.093	0.139	0.127	0.130	0.115	0.113	0.130	0.133	0.115	0.089	0.130	0.102	0.106
1393	0.142	0.303	0.163	0.152	0.205	0.208	0.175	0.293	0.208	0.212	0.299	0.305	0.208	0.175	0.179
1398	0.148	0.320	0.176	0.160	0.219	0.223	0.184	0.301	0.223	0.230	0.310	0.304	0.223	0.288	0.190
9114	0.195	0.242	0.254	0.233	0.365	0.373	0.262	0.239	0.344	0.355	0.276	0.117	0.344	0.283	0.292
9132	0.139	0.304	0.182	0.172	0.239	0.252	0.196	0.315	0.258	0.259	0.320	0.304	0.258	0.206	0.214
9133	0.139	0.298	0.190	0.166	0.238	0.233	0.193	0.302	0.233	0.233	0.305	0.303	0.233	0.228	0.201
9127	0.192	0.223	0.273	0.225	0.366	0.361	0.259	0.260	0.361	0.398	0.226	0.114	0.361	0.310	0.282
9115	0.194	0.231	0.270	0.233	0.361	0.368	0.265	0.232	0.339	0.347	0.266	0.111	0.339	0.294	0.299
9113	0.211	0.208	0.265	0.269	0.325	0.324	0.284	0.224	0.324	0.335	0.212	0.106	0.324	0.289	0.280
9119	0.272	0.145	0.199	0.190	0.187	0.187	0.184	0.137	0.187	0.189	0.139	0.079	0.187	0.200	0.196
9120	0.346	0.148	0.199	0.191	0.190	0.189	0.186	0.140	0.189	0.192	0.142	0.082	0.189	0.201	0.198
9122	0.273	0.193	0.260	0.276	0.269	0.270	0.272	0.184	0.270	0.264	0.191	0.098	0.270	0.267	0.269
9124	0.268	0.193	0.260	0.245	0.269	0.270	0.272	0.184	0.270	0.264	0.191	0.098	0.270	0.267	0.269
9125	0.180	0.162	0.225	0.269	0.237	0.241	0.285	0.163	0.241	0.224	0.170	0.097	0.241	0.234	0.245
9109	0.207	0.215	0.263	0.207	0.288	0.288	0.242	0.210	0.288	0.297	0.207	0.115	0.288	0.269	0.265

	MALES				MALES			
FEMALE	9140	9123	9112		FEMALE	9140	9123	9112
168	0.204	0.237	0.300		1064	0.265	0.246	0.386
228	0.199	0.190	0.320		1071	0.268	0.240	0.396
267	0.221	0.237	0.281		1125	0.256	0.274	0.288
268	0.419	0.285	0.241		1155	0.256	0.273	0.288
277	0.266	0.243	0.298		1167	0.195	0.183	0.119
278	0.221	0.264	0.281		1179	0.270	0.246	0.435
339	0.281	0.234	0.362		1232	0.265	0.246	0.386
380	0.286	0.264	0.259		1240	0.256	0.274	0.288
406	0.282	0.246	0.357		1287	0.199	0.269	0.187
408	0.286	0.264	0.259		1291	0.191	0.187	0.189
458	0.313	0.273	0.305		1310	0.249	0.221	0.248
480	0.286	0.264	0.259		1312	0.283	0.239	0.173
498	0.257	0.258	0.326		1315	0.274	0.249	0.367
535	0.308	0.267	0.268		1332	0.249	0.220	0.248
545	0.257	0.258	0.326		1363	0.190	0.185	0.211
569	0.282	0.246	0.357		1370	0.265	0.246	0.386
608	0.239	0.248	0.316		1388	0.093	0.116	0.130
618	0.272	0.261	0.305		1393	0.163	0.176	0.208
635	0.272	0.321	0.293		1398	0.176	0.184	0.223
639	0.268	0.240	0.488		9114	0.254	0.244	0.344
667	0.127	0.124	0.086		9132	0.182	0.175	0.258
668	0.126	0.120	0.082		9133	0.190	0.182	0.233
694	0.244	0.206	0.135		9127	0.273	0.252	0.361
697	0.244	0.207	0.135		9115	0.270	0.251	0.339
700	0.373	0.442	0.199		9113	0.265	0.263	0.324
712	0.284	0.254	0.346		9119	0.199	0.269	0.187
713	0.268	0.240	0.396		9120	0.199	0.271	0.189
722	0.257	0.284	0.326		9122	0.260	0.319	0.270
736	0.239	0.261	0.316		9124	0.260	0.319	0.270
737	0.459	0.266	0.299		9125	0.225	0.209	0.241
822	0.284	0.254	0.346		9109	0.263	0.269	0.288

	MALES														
FEMALE	1160	1170	1190	1190	1200	1210	1210	1250	1280	1310	1310	1350	1360	1360	1400
168	0.208	0.300	0.104	0.141	0.163	0.250	0.141	0.314	0.224	0.323	0.345	0.300	0.141	0.314	0.204
228	0.271	0.320	0.104	0.141	0.147	0.213	0.141	0.282	0.234	0.302	0.319	0.320	0.141	0.282	0.157
267	0.228	0.281	0.107	0.160	0.181	0.236	0.141	0.281	0.239	0.327	0.381	0.281	0.141	0.281	0.189
268	0.265	0.241	0.161	0.240	0.078	0.142	0.088	0.253	0.330	0.238	0.212	0.241	0.088	0.253	0.179
277	0.228	0.298	0.141	0.198	0.122	0.175	0.132	0.323	0.262	0.241	0.231	0.298	0.132	0.323	0.176
278	0.228	0.281	0.107	0.160	0.181	0.262	0.141	0.281	0.239	0.301	0.328	0.281	0.141	0.281	0.216
339	0.289	0.362	0.113	0.162	0.133	0.216	0.119	0.310	0.279	0.360	0.372	0.362	0.119	0.310	0.182
380	0.240	0.259	0.134	0.200	0.130	0.186	0.114	0.267	0.282	0.280	0.287	0.259	0.114	0.267	0.187
406	0.273	0.357	0.113	0.162	0.137	0.225	0.119	0.331	0.290	0.414	0.427	0.357	0.119	0.331	0.194
408	0.240	0.259	0.134	0.200	0.130	0.186	0.114	0.267	0.282	0.334	0.287	0.259	0.114	0.267	0.187
458	0.262	0.305	0.134	0.200	0.120	0.201	0.114	0.373	0.375	0.314	0.312	0.305	0.114	0.373	0.197
480	0.240	0.259	0.134	0.200	0.130	0.186	0.114	0.267	0.282	0.280	0.287	0.259	0.114	0.267	0.187
498	0.258	0.326	0.113	0.162	0.141	0.234	0.119	0.326	0.274	0.345	0.360	0.326	0.119	0.326	0.206
535	0.240	0.268	0.151	0.219	0.100	0.155	0.110	0.288	0.293	0.236	0.212	0.268	0.110	0.288	0.181
545	0.258	0.326	0.113	0.162	0.141	0.286	0.119	0.326	0.274	0.345	0.360	0.326	0.119	0.326	0.206
569	0.273	0.357	0.113	0.162	0.137	0.225	0.119	0.331	0.290	0.365	0.379	0.357	0.119	0.331	0.194
608	0.243	0.316	0.110	0.161	0.161	0.235	0.130	0.329	0.257	0.362	0.490	0.316	0.130	0.329	0.197
618	0.249	0.305	0.124	0.181	0.136	0.210	0.116	0.322	0.278	0.463	0.349	0.305	0.116	0.322	0.197
635	0.249	0.293	0.124	0.181	0.136	0.217	0.116	0.297	0.278	0.306	0.310	0.293	0.116	0.297	0.256
639	0.281	0.448	0.113	0.162	0.135	0.220	0.119	0.346	0.310	0.376	0.388	0.396	0.119	0.346	0.188
667	0.123	0.086	0.377	0.107	0.174	0.066	0.058	0.088	0.124	0.083	0.080	0.086	0.058	0.088	0.191
668	0.118	0.082	0.227	0.104	0.196	0.061	0.052	0.084	0.122	0.079	0.075	0.082	0.052	0.084	0.337
694	0.198	0.135	0.214	0.191	0.155	0.088	0.064	0.140	0.233	0.132	0.121	0.135	0.064	0.140	0.185
697	0.199	0.135	0.238	0.191	0.145	0.088	0.064	0.140	0.233	0.132	0.121	0.135	0.064	0.140	0.198
700	0.427	0.199	0.247	0.297	0.097	0.135	0.104	0.208	0.355	0.196	0.178	0.199	0.104	0.208	0.185
712	0.275	0.346	0.124	0.181	0.126	0.208	0.116	0.367	0.353	0.350	0.355	0.346	0.116	0.367	0.189
713	0.281	0.396	0.113	0.162	0.135	0.220	0.119	0.346	0.310	0.376	0.388	0.488	0.119	0.346	0.188
722	0.258	0.326	0.113	0.162	0.141	0.234	0.119	0.326	0.274	0.345	0.360	0.326	0.119	0.326	0.232
736	0.243	0.316	0.110	0.161	0.161	0.248	0.130	0.329	0.257	0.349	0.370	0.316	0.130	0.329	0.211
737	0.269	0.299	0.137	0.201	0.108	0.184	0.103	0.292	0.310	0.302	0.295	0.299	0.103	0.292	0.187
822	0.275	0.346	0.124	0.181	0.126	0.208	0.116	0.465	0.353	0.350	0.355	0.346	0.116	0.465	0.189
826	0.101	0.106	0.083	0.383	0.084	0.237	0.367	0.107	0.091	0.104	0.110	0.106	0.367	0.107	0.075
830	0.086	0.093	0.157	0.054	0.432	0.086	0.066	0.092	0.069	0.096	0.105	0.093	0.066	0.092	0.170
831	0.111	0.119	0.089	0.228	0.093	0.271	0.523	0.121	0.102	0.118	0.124	0.119	0.523	0.121	0.084
841	0.281	0.396	0.113	0.162	0.135	0.220	0.119	0.346	0.310	0.376	0.388	0.396	0.119	0.346	0.188
917	0.265	0.298	0.124	0.181	0.132	0.207	0.116	0.289	0.280	0.300	0.304	0.298	0.116	0.289	0.191
921	0.224	0.273	0.102	0.151	0.168	0.244	0.132	0.269	0.231	0.297	0.328	0.273	0.132	0.269	0.192
933	0.239	0.296	0.105	0.152	0.148	0.380	0.121	0.292	0.249	0.313	0.331	0.296	0.121	0.292	0.193
945	0.278	0.359	0.118	0.171	0.131	0.214	0.118	0.357	0.332	0.421	0.429	0.359	0.118	0.357	0.189
948	0.224	0.214	0.181	0.186	0.140	0.152	0.090	0.218	0.256	0.219	0.216	0.214	0.090	0.218	0.276
952	0.223	0.214	0.169	0.186	0.145	0.152	0.090	0.218	0.256	0.219	0.216	0.214	0.090	0.218	0.269
961	0.275	0.346	0.124	0.181	0.126	0.208	0.116	0.367	0.450	0.350	0.355	0.346	0.116	0.367	0.189
964	0.281	0.384	0.113	0.162	0.135	0.220	0.119	0.346	0.310	0.433	0.446	0.430	0.119	0.346	0.188
988	0.258	0.303	0.129	0.191	0.128	0.197	0.115	0.317	0.317	0.315	0.321	0.303	0.115	0.317	0.188
1021	0.281	0.372	0.113	0.162	0.135	0.220	0.119	0.346	0.310	0.400	0.412	0.372	0.119	0.346	0.188
1028	0.223	0.214	0.169	0.186	0.145	0.152	0.090	0.218	0.256	0.219	0.216	0.214	0.090	0.218	0.269
1035	0.224	0.214	0.181	0.186	0.140	0.152	0.090	0.218	0.256	0.219	0.216	0.214	0.090	0.218	0.276
1063	0.239	0.296	0.105	0.152	0.148	0.263	0.121	0.292	0.249	0.313	0.331	0.296	0.121	0.292	0.193

	MALES														
FEMALES	1160	1170	1190	1190	1200	1210	1210	1250	1280	1310	1310	1350	1360	1360	1400
1064	0.262	0.386	0.120	0.171	0.133	0.212	0.122	0.398	0.298	0.347	0.355	0.386	0.122	0.398	0.189
1071	0.281	0.396	0.113	0.162	0.135	0.220	0.119	0.346	0.310	0.376	0.388	0.396	0.119	0.346	0.188
1125	0.308	0.288	0.147	0.174	0.137	0.184	0.104	0.264	0.267	0.277	0.281	0.288	0.104	0.264	0.229
1155	0.308	0.288	0.141	0.174	0.139	0.184	0.104	0.264	0.267	0.277	0.281	0.288	0.104	0.264	0.226
1167	0.178	0.119	0.285	0.167	0.156	0.094	0.086	0.123	0.188	0.116	0.109	0.119	0.086	0.123	0.248
1179	0.280	0.435	0.121	0.173	0.130	0.208	0.119	0.361	0.294	0.339	0.344	0.480	0.119	0.361	0.187
1232	0.262	0.386	0.120	0.171	0.133	0.212	0.122	0.398	0.289	0.347	0.355	0.386	0.122	0.398	0.189
1240	0.308	0.288	0.147	0.174	0.137	0.184	0.104	0.264	0.267	0.277	0.281	0.288	0.104	0.264	0.229
1287	0.184	0.187	0.175	0.143	0.166	0.139	0.084	0.190	0.200	0.192	0.193	0.187	0.084	0.190	0.345
1291	0.176	0.189	0.111	0.214	0.111	0.279	0.319	0.194	0.192	0.199	0.206	0.189	0.319	0.194	0.136
1310	0.296	0.248	0.175	0.177	0.139	0.152	0.091	0.225	0.256	0.233	0.233	0.248	0.091	0.225	0.190
1312	0.229	0.173	0.168	0.374	0.081	0.190	0.228	0.180	0.273	0.171	0.161	0.173	0.228	0.180	0.143
1315	0.279	0.367	0.124	0.178	0.127	0.205	0.119	0.366	0.304	0.361	0.365	0.367	0.119	0.366	0.187
1332	0.295	0.248	0.164	0.177	0.144	0.152	0.091	0.225	0.256	0.233	0.233	0.248	0.091	0.225	0.183
1363	0.185	0.211	0.109	0.209	0.111	0.285	0.319	0.219	0.210	0.216	0.223	0.211	0.319	0.219	0.136
1370	0.262	0.386	0.120	0.171	0.133	0.212	0.122	0.398	0.289	0.347	0.355	0.386	0.122	0.398	0.189
1388	0.115	0.130	0.145	0.081	0.439	0.121	0.093	0.129	0.102	0.135	0.148	0.130	0.093	0.129	0.166
1393	0.175	0.208	0.097	0.190	0.121	0.318	0.322	0.206	0.175	0.215	0.228	0.208	0.322	0.206	0.139
1398	0.184	0.223	0.101	0.195	0.117	0.303	0.321	0.223	0.188	0.231	0.242	0.223	0.321	0.223	0.145
9114	0.262	0.344	0.112	0.161	0.148	0.228	0.124	0.338	0.283	0.427	0.497	0.344	0.124	0.338	0.193
9132	0.196	0.258	0.101	0.195	0.114	0.297	0.321	0.234	0.206	0.247	0.256	0.258	0.321	0.234	0.136
9133	0.193	0.233	0.106	0.204	0.110	0.291	0.320	0.244	0.276	0.234	0.239	0.233	0.320	0.244	0.137
9127	0.259	0.361	0.125	0.180	0.129	0.206	0.121	0.457	0.310	0.334	0.338	0.361	0.121	0.457	0.190
9115	0.265	0.339	0.118	0.171	0.135	0.215	0.118	0.334	0.294	0.477	0.427	0.339	0.118	0.334	0.192
9113	0.284	0.324	0.136	0.177	0.133	0.195	0.113	0.361	0.289	0.305	0.309	0.324	0.113	0.361	0.210
9119	0.184	0.187	0.175	0.143	0.166	0.139	0.084	0.190	0.200	0.192	0.193	0.187	0.084	0.190	0.345
9120	0.186	0.189	0.250	0.144	0.155	0.142	0.087	0.192	0.201	0.194	0.195	0.189	0.087	0.192	0.272
9122	0.272	0.270	0.149	0.179	0.137	0.184	0.104	0.261	0.267	0.269	0.272	0.270	0.104	0.261	0.272
9124	0.272	0.270	0.144	0.179	0.140	0.184	0.104	0.261	0.267	0.269	0.272	0.270	0.104	0.261	0.268
9125	0.285	0.241	0.199	0.164	0.144	0.155	0.102	0.217	0.234	0.225	0.228	0.241	0.102	0.217	0.215
9109	0.242	0.288	0.122	0.181	0.146	0.224	0.122	0.298	0.269	0.308	0.315	0.288	0.122	0.298	0.206



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Recommended breeder code for individual identification of Przewalski-Horses. The code is to use together with the breeder number, e.g.

DE 8 is: 1495 M Denver 8 Gino.

Adelaide	AD	Gdansk-Oliva	GO	München	H
Alma-Ata	AA	Genk	GE	Münster	MU
Anvers	AN	Gramat	GR	Neumünster	NM
Arnhem	AR	Habana	HB	Neuwied	NW
Askania Nova	A	Halle	HA	New York	YO
Barcelona	BA	Helsinki	HL	Nieborow	NB
Bekesbourne- Lympe	HO	Herberstein	HR	Nikolaev	NI
Berlin-Ost	BT	Hilvarenbeek	HI	Norderheide	NO
Berlin-West	BZ	Jersey	JE	Nürnberg	NU
Bern	BE	Karaganda	KA	Oberwil	OB
Bernburg	BG	Karl-Marx-Stadt	KM	de Ooij	OJ
Braniewo	BO	Karlsruhe	KR	Paignton	PG
Bratislava	BR	Keokuk	KE	Paris	PA
Brownsville	BV	Kiev	KV	Peking	PE
Budapest	BU	Kingussie	KI	Pforzheim	PF
Calgary	CG	Kisinev	KS	Poznan	PO
Canyon	CC	Köln	KO	Praha	P
Cardigan	CN	Krakow	KW	Riga	RI
Catskill	CA	Kurgan	KN	Roma-Bordi	RB
Cavriglia	CV	Langenberg	LG	Rostock	RK
Cevennes	CS	Leipzig	LE	Rostov	RO
Chester	CH	Lelystadt	LL	Rotterdam	BP
Chiba	CB	Leningrad	LN	Sababurg	SA
Chicago-Bell- Ranch	CR	Lodz	LZ	Salzburg	SG
Colombo	CO	London	LO	San Diego	SD
Colwyn Bay	CL	Los Angeles	LA	Schwerin	SN
Denver	DE	Lymington	LY	Seul	SE
Dubbo	DU	Marwell	MA	Springe	SP
Duisburg	DG	Memphis	ME	Stuttgart	ST
Edmonton	ED	Midway Manor	MM	Taipei	TI
Front Royal	WN	Minnesota	LK	Tallinn	TA
Frösön	FR	Montpellier	PA	Taskent	TS
		Moskva	MO	Termez	TE