

Genetic management of small animal populations

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Abstract: European zoos, associated in the European Association of Zoos and Aquaria (EAZA), established co-operative breeding programmes for zoo populations in 1985. European Endangered species Programmes (EEPs) and European Studbooks (ESBs) for some 250 species have been established as at March 2002. The goals of these programmes are to maintain viable zoo populations without (or with limited) import from the wild. These populations can serve, whenever feasible, as sources for reintroduction of endangered species. Retention of genetic variation in populations of endangered species is a prerequisite for their future survival. This means that conservation efforts should also include genetic management of zoo populations, especially when reintroduction is part of a conservation programme. Therefore, maintenance of sufficient levels of genetic variation and minimising inbreeding are important objectives of zoo breeding programmes. Population biologists who work for zoological gardens have developed various strategies, models and computer tools to assist zoo biologists in the co-operative management of zoo populations.

Keywords: population management, breeding programmes, genetic variation, studbooks.

Introduction

Zoological gardens started breeding programmes for the European bison or wisent (*Bison bonasus*) and Przewalski's horses (*Equus przewalskii*) at the beginning of the 19th century. These propagation programmes resulted in reintroduction of the European bison in Bialowieza Primeval Forest as early as 1929 (Pucek 1991); and reintroduction of the Przewalski's horse in Mongolia in 1992 (van Dierendonck & Wallis de Vries 1996).

Management strategies of the early breeding programmes were not developed in accordance with modern views of population genetics (Princée 1990). The most important goal was successful reproduction i.e. breeding numbers. Avoidance of inbreeding and/or maintenance of genetic variation were not taken into consideration, until the end of the 1970s (see for example Flesness 1977).

Regional zoo associations established captive (or ex situ) breeding programmes in the early

1980s for zoo populations. The major goal of these programmes is to maintain viable populations without (or with limited) import from the wild. These managed zoo populations could also serve as potential resources for reintroduction and re-stocking programmes whenever feasible.

European zoos, associated in the European Association of Zoos and Aquaria (EAZA), have established European Endangered species Programmes (EEPs) and European Studbooks (ESBs) for some 250 species as at March 2002. The following sections will describe the various issues, from theoretical considerations to practical implementations, which play important roles in the daily practice of modern zoo breeding programmes.

Importance of genetic variation

Populations with low genetic variation are expected, according to evolutionary theory, to have lower adaptive potentials to cope with environ-

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mental changes than populations with high levels of genetic variation. The environment not only changes over time due to, for example, climatic changes but also fluctuates annually, seasonally and even daily. Therefore, genetic variation in a population is important to adapt (or to be adapted) to both short-term fluctuations and long-term changes in the environment. A classical example which illustrates this importance is the survival of dark forms of the peppered moth (*Biston betularia*) in industrialised (polluted) areas (Kettlewell 1973).

Zoo animals live in a relatively stable environment which prevents exposure to the harsh and extreme conditions, such as depletion of food resources, that may occur in their natural habitat. However, this does not imply that maintenance of genetic variation is not important for zoo populations. First, zoo populations could serve as resources for reintroduction. It is clear that a reintroduced population requires adaptive potentials to cope with the natural environment. Thus the source (=zoo) population must also have this adaptive potential. Second, zoo populations are also exposed to changes in environmental conditions, such as exposure to new viral strains that are transmitted by live-stock. Therefore, an important objective of zoo breeding programmes is to preserve at least 90 percent of the original 'wild' genetic variation for a period of 100 to 200 years (Soulé et al. 1986).

Genetic loss

Small populations lose genetic variation due to genetic drift. The smaller the population the larger genetic drift is (see Wright 1931). This can be illustrated with historical trends in population size and genetic variation in the zoo population of Przewalski's horses since 1900. Figure 1 shows population size, as computed from stud-book data, and expected genetic variation as estimated with the genetic simulation ChromoFlow (Princée 1998). Two major historic trends can be observed. The first trend refers to a period of slow growth from 24 horses in 1901 to 58 in

1959. The second trend refers to the period 1960-1994 during which the population increased to 1293 horses. Gene diversity and observed heterozygosity declined until the mid 1960s. Note that gene diversity decreases gradually, while the decline pattern of observed heterozygosity shows fluctuations. Although gene diversity and observed heterozygosity have increased since 1965, both values as of 31 December 1994 were 84.5 and 79.6 percent of the original (wild) genetic variation, respectively.

Inbreeding depression

Inbreeding, i.e. mating between relatives, results in an increase in homozygosity in populations. This may result in reduced 'fitness', the relative ability of individuals to pass on gametes to the next generation. Individuals with a high proportion of homozygous loci often have lower fitness than heterozygotes, and deleterious recessive alleles can be expressed due to consanguineous matings of homozygotes. The effects of inbreeding on fitness are referred to as 'inbreeding depression' (Roughgarden 1979). Inbreeding depression resulting from the expression of lethal alleles or obviously detrimental alleles is more likely to be detected than that due to alleles that only slightly reduce fitness. For example, blindness in wolves (*Canis lupus*) has a genetic basis and only occurs in inbred packs descended from specific founder lineages in the Scandinavian zoo population (Laikre & Ryman 1991).

Figure 2 illustrates the probability (risk) that deleterious alleles are expressed in offspring of a full-sib (brother x sister) mating. Individual 5 has a probability of 0.25 (25%) that it is homozygous at a locus for one of the ancestral alleles of individuals 1 and 2. If these ancestors are carriers of deleterious alleles at multiple loci (genes) then the probability increases. Ralls et al. (1988) observed a range of lethal equivalents for survivorship of offspring in first-degree matings between -1.4 and 30.3 (a median value of 3.1) in 40 captive mammalian populations. Lethal

equivalents can refer to single alleles at different loci or to combined lethal effects of several deleterious alleles at different loci.

Detecting inbreeding depression

Sensitivity to inbreeding depression may vary with species or even with populations (Shields 1987). Comparative studies between groups of inbred and non-inbred individuals, using quantitative measures that reflect fitness, are required to detect slightly deleterious alleles. Ralls & Ballou (1983) compared infant mortality between groups of inbred and non-inbred mammals living in zoos. This study showed that infant mortality

in inbred groups was generally higher than in non-inbred groups.

Differences in sensitivity to inbreeding depression between species or populations, as observed in the study of Ralls et al. (1988), may be the result of past natural inbreeding in these species and populations. For example, natural populations that frequently undergo (and survive) severe bottlenecks are expected to be less sensitive to inbreeding depression than large outbred populations. Frequencies of recessive deleterious alleles in such populations are thought to be reduced in subsequent generations by both the bottleneck and inbreeding, which expose recessive alleles to selective forces.

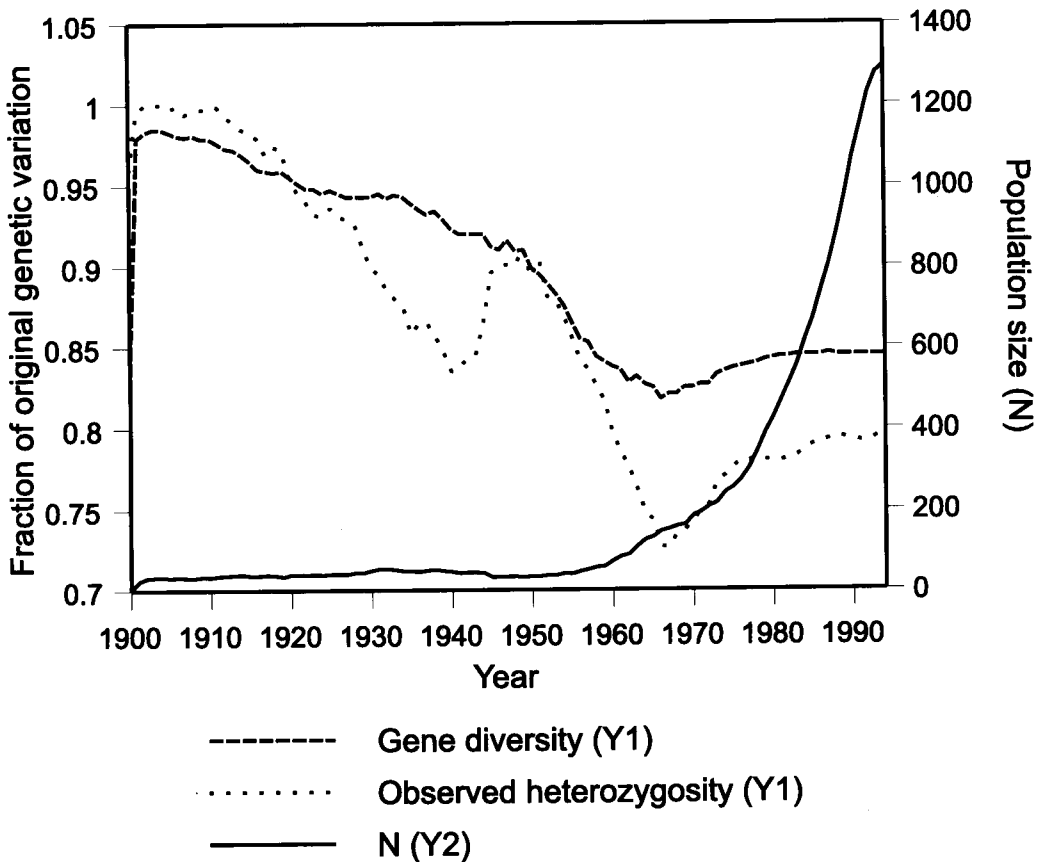
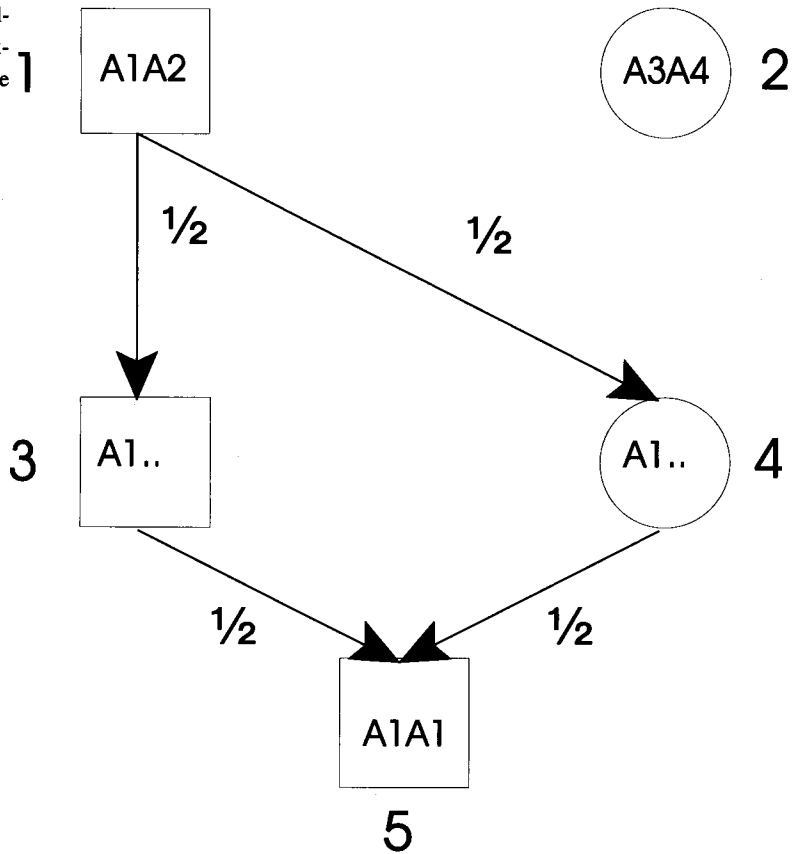


Figure 1. Numbers of living individuals (N; Y2-axis) and fractions of original (wild) gene diversity (Y1-axis) and observed heterozygosity (Y1-axis) as expected in the studbook population of Przewalski's horses (*Equus przewalskii*) at census dates (31 December) between 1900 and 1994. From: Princée 1998.

Figure 2. Pedigree of full-sib mating. See text for explanation. From: Princée 1998.



Inbreeding in natural populations

Inbreeding depression is not an artefact of zoo conditions, as suggested by some authors (e.g. Merola 1994), but has also been documented in various natural populations (e.g. Frankham 1995). A high incidence of malocclusion, an anomaly which results in shortened mandibles, has been observed in an isolated population of the red fox (*Vulpes vulpes*) in the North Holland Dune Reserve, The Netherlands. This population descends from a few founders and genealogical studies suggest that this anomaly has a genetic basis (Bouwmeester et al. 1989).

Sex-biased dispersal patterns of sub-adult or young individuals have been observed in various mammalian species like primates (Pusey & Packer 1987). Such dispersal patterns can be effective in avoiding full-sib matings, but do not

fully exclude inbreeding. In this, the spatial distribution of social groups and the dispersal distances determine to what extent the level of inbreeding increases over generations in the population(s).

Studbook management

It is clear that maintenance of genetic variation and avoidance of inbreeding are important in order to establish self-sustaining zoo populations and to maintain the potential for future reintroduction. This genetic management requires that pedigree data of each individual are available to species managers. Data on individual animals in EEPs are maintained in studbooks. The International Species Information System (ISIS) has developed software - the Single Population Animal

Record Keeping System (SPARKS) - to computerise studbooks (Scobie & Flesness 1989). This software produces various reports such as historical listings, listings on birth and deaths, and reports per individual.

Furthermore, various additional computer tools have been developed to assist species managers in decision-making. For example, the programme GENES (Lacy 1994) estimates the expected level of genetic variation that has been retained in (zoo) populations, provides ranked lists of individuals that are considered genetically important, and also produces tables with inbreeding coefficients of possible matings.

Species managers can base breeding recommendations on the results of these genetic analyses. In this, logistics and (social) compatibility between potential breeding partners need also to be taken into account. For example, exchanges of animals between zoos in different countries (or continents), which require long periods of quarantine, may be less favoured.

Incomplete pedigree data

Genetic management of zoo populations is generally based on 'animal-by-animal recommendations' (Ballou & Lacy 1995), using tools as described above. However, this type of management is not applicable when pedigree data are incomplete. Information on parentages is often missing in populations of species with complex mating structures and/or species that are housed in colonies. However, genetic management of such species is not impossible. Princée (1995, 1998) developed 'low-intensity management' for social breeding groups. This type of management takes into account species-specific social (mating) structure and reproductive parameters such as gestation length, interbirth interval and reproductive life-span. These data can be used to reconstruct incomplete pedigrees.

Table 1 presents possible parents, based on biological data, of Przewalski's horses with unknown parents, which were born in herds in Askania Nova. This information can be used to reconstruct the gap in the pedigree of this zoo

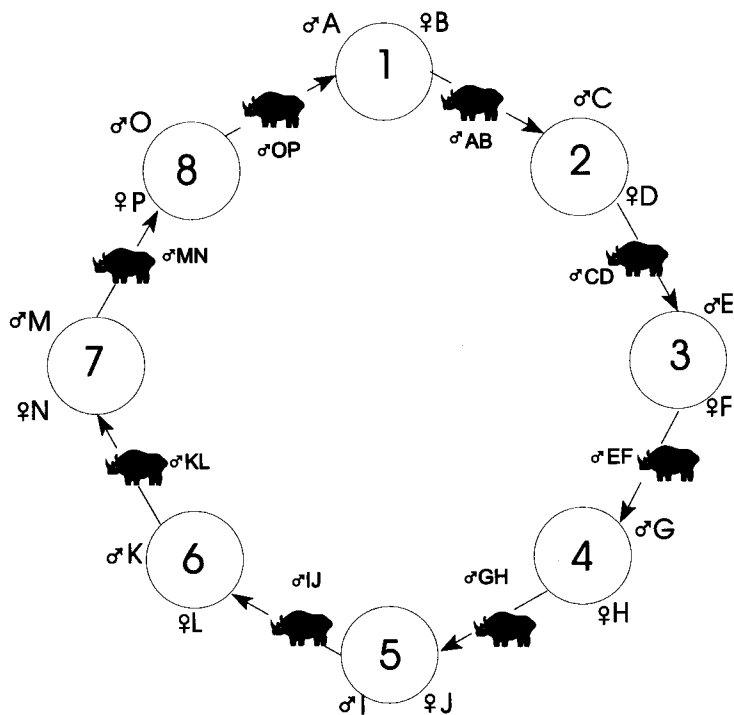
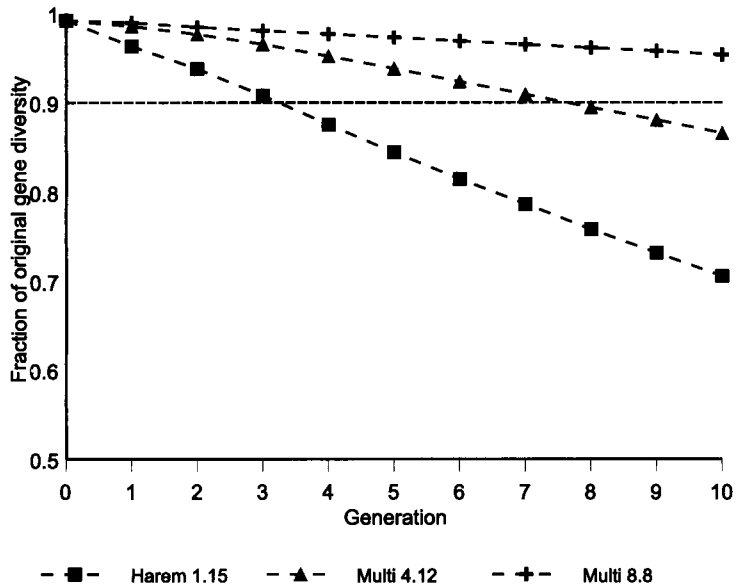


Figure 3. Maximal Avoidance of Inbreeding (MAI) scheme for eight breeding groups in the first generation. Bloodlines of paternal and maternal lines in each breeding group and bloodlines of male offspring are presented for each breeding group. Arrows indicate the dispersal of male offspring from natal to host group. From: Princée 1998.

Figure 4. Effect of number of breeding males in breeding groups on genetic loss. The number of males and females in groups are notated as M.F. (e.g. Harem 1.15). Indicated is the minimum fraction (0.9) of original gene diversity that should be conserved in small populations. From: Princée 1998.



population. However, reconstruction of pedigrees largely depends on the proportion of incomplete data. It may be obvious that this method cannot be used if too many assumptions have to be made.

Social groups

Low-intensity management can also be used to manage colonies as 'black-boxes'. Inbreeding in colonies can be avoided by exchanging animals according the Maximal Avoidance of Inbreeding (MAI) schemes (Wright 1921, Princée 1986, Princée 1995, Princée 1998). In this, information on natural dispersal patterns is used to select animals that will be exchanged between social groups. The MAI scheme uses single maternal and paternal lineages (or bloodlines) for each group. It assumes that all offspring are full-sibs, regardless of the actual composition of the breeding group. The MAI schemes are developed to avoid/minimise inbreeding in populations composed of social groups or colonies. Figure 3 shows a MAI scheme for eight breeding groups in the first generation. Princée (1998) developed algorithms to compute the exchange pattern for each group and for each future gener-

ation.

Since MAI schemes do not require information on pedigree patterns within groups or colonies, and exchanges are based on (sex-biased) dispersal patterns, they could potentially be applied in management of fragmented wild populations.

Genetic costs

Genetic variation is optimally preserved if all animals in a population produce equal numbers of offspring. However, the reality - both in captivity and in the wild - is different as most animals, especially those living in social groups with rank hierarchies, do not have the same chance to reproduce. This results in higher rates of genetic loss than under genetically optimal conditions. Princée (1995) used the simulation model GeneFlow to study the effects of social (mating) structure on genetic loss. Figure 4 shows genetic loss in populations of equal size ($N=64$) in which the number of breeding males per group is varied. Note that genetic loss in harem groups is substantially higher than in a population with groups that are composed of equal number of breeding males and breeding females.

Management measures

Management measures to reduce genetic loss in zoo populations focus on improving chances of reproductive success of individuals. In this, it would be tempting to house animals in breeding pairs (as often happened in the past) since this increases the chance of equal reproductive success. However, such a measure can dramatically violate the species-specific social structure, actually resulting in low reproductive success. An alternative measure is to maintain animals in the minimal group size that has been observed in natural populations.

Figure 5 shows results of simulations with the model GeneFlow (Princée 1998) on the effect of sizes of harem groups. Populations that are divided into small harem groups lose less genetic variation than populations with large harem groups. This means that genetic loss in social species can be reduced while the species-specific social structure can be maintained.

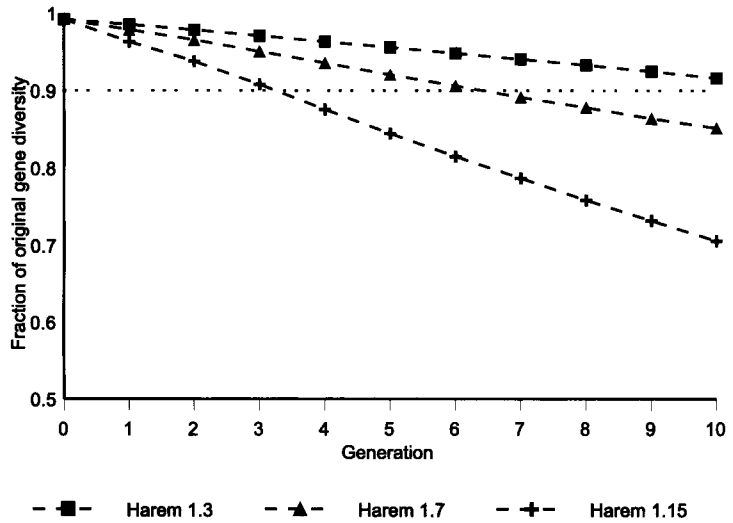
Wildlife management

Zoological gardens have almost 25 years of experience in population management that is



Long-term strategies: Przewalski's horses have been reintroduced in the original habitat in Mongolia almost a century after a breeding programme was initiated in zoological gardens. *Photograph: Edgar van der Grift.*

Figure 5. Effect of sizes of harem groups on genetic loss. The number of males and females in harem groups are notated as M.F. (e.g. Harem 1.3). Indicated is the minimum fraction (0.9) of original gene diversity that should be conserved in small populations. From: Princée 1998.



aimed at maintenance of genetic variation and avoidance (minimising) of inbreeding. In this, the introduction of the personal computer in the early 1980s has resulted in a rapid development of computer tools – often designed and programmed by zoo staff – to register data on zoo animals and to analyse genetic and demographic processes in zoo populations. In particular, the simulation models which are used to analyse pedigrees have generated more knowledge on the process of genetic loss in small populations (and the effects of social mating systems).

The experiences and knowledge of zoos are becoming increasingly important in management of wild populations. Habitat destruction and expansion of human activities result in further fragmentation and/or isolation of natural populations of endangered species. It means that animals may need to be translocated in order to avoid/minimise inbreeding in small sub-populations. In this, the MAI schemes could be applied in wildlife management to manage sub-populations in different nature reserves.

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Table 1. Possible parents of Przewalski's horses (*Equus przewalskii*) with unknown parents at Askania Nova. Numbers of individuals, dams and sires refer to international studbook numbers. Sire and dams that are presented in *italicised* text are assumed to be the parents. n/a = not applicable: sire or dam are known. From: Princée (1998).

| # | Date of birth | Possible sire(s) | Possible dam(s) |
|------|-----------------------|--|--|
| 826 | 22-05-79 | n/a | 283, 490, 528, 637, 675, 706, 711 |
| 966 | 12-05-81 | 259, 605, 764, 821 | 283, 525, 602, 620 |
| 1203 | 19-04-84 | 259, 533, 821, 893, 896, 900, 963, 970, 980, 1008 | n/a |
| 1214 | 04-05-84 | 259, 533, 821, 893, 896, 900, 963, 970, 980, 1008, 1044, 1048 | n/a |
| 1336 | 16-05-85 | 259, 533, 821, 893, 896, 963, 980, 1008, 1044, 1048 | 244 ¹ , 490, 1077, 1114 |
| 1339 | 19-05-85 | n/a | 244 ¹ , 490, 1077, 1114 |
| 1478 | 13-06-86 | n/a | 490, 528, 620, 959, 987, 1114, 1215, 1221 |
| 1550 | 02-05-87 | n/a | 987, 1043, 1215, 1221 |
| 1553 | 04-05-87 | n/a | 987, 1043, 1215, 1221 |
| 1598 | 05-06-87 | 533, 821, 893, 896, 963, 980, 1008, 1044, 1048, 1145, 1178, 1214, 1231, 1331, 1338, 1348 | 987, 1043, 1215, 1221 |
| 1637 | 08-08-87 | 533, 821, 893, 896, 963, 980, 1008, 1044, 1145, 1178, 1214, 1231, 1331, 1338, 1348 | n/a |
| 1724 | 30-05-88 | 533, 821, 893, 896, 963, 980, 1008, 1044, 1145, 1178, 1214, 1231, 1331, 1338, 1348 | 525, 528, 812, 846 1077, 1215, 1456, 1464, 1467, 1468 |
| 1754 | 26-06-88 | 533, 821, 893, 896, 963, 980, 1008, 1044, 1145, 1178, 1214, 1231, 1331, 1338, 1348 | 525, 528, 812, 846, 1077, 1215, 1456, 1464, 1467, 1468, 1478 |
| 4035 | 18-04-89 ² | n/a | 812, 987, 1077 ³ , 1456, 1468, 1478, 1511 |
| 4733 | 29-11-89 ² | 533, 821, 893, 896, 963, 980, 1008, 1044, 1145, 1178, 1214, 1231, 1331, 1338, 1348, 1500, 1568, 1598, 1607 | 812, 1456, 1467 ⁴ , 1468, 1478, 1595, 1600 |
| 4502 | 05-05-90 | n/a | 525, 528, 812, 846, 1456, 1595, 1703 |
| 4657 | 18-05-90 | 1619 | 1639 |
| 4056 | 03-11-90 ² | n/a | 1305 |
| 4077 | 15-02-91 ² | n/a | 1265, 1276 |
| 4064 | 16-09-91 ² | n/a | 859 |
| 4072 | 22-08-92 ² | n/a | 859 |
| 5070 | 02-09-92 | 1720 | n/a |
| 5097 | 11-05-94 | 1178, 1331, 1348, 1697, 1920, 1976 | n/a |

¹ Dam 490 was beyond reproductive age (and died in June 1986)

² Abortion or stillbirth

³ Died at same date as date of birth of 4035

⁴ Produced 4038 (stillbirth) at same date as date of birth of 4733

Source: International studbook of Przewalski's horses

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Samenvatting

Genetisch beheer van kleine dierpopulaties

Europese dierentuinen die lid zijn van de European Association of Zoos and Aquaria (EAZA) startten in 1985 met gecoördineerde fokprogramma's voor dierentuin populaties. Ruim 250 European Endangered species Programmes (EEPs) en Europese studbooks (ESBs) zijn sinds die tijd opgezet. Het doel van fokprogramma's is het behouden van levensvatbare dierentuinpopulaties zonder (of met sporadische) import van wildvang-dieren. Deze populaties dienen, wanneer mogelijk, als bronnen voor herintroductie programma's van bedreigde diersoorten.

Behoud van genetische variatie in populaties van bedreigde diersoorten wordt als een belangrijke voorwaarde voor het overleven beschouwd. Dit betekent dat genetisch beheer van dierentuinpopulaties, zeker als herintroductie een rol speelt, in behoudsprogramma's moeten zijn opgenomen. Populatiebiologen die werkzaam zijn voor dierentuinen hebben verschillende strategiemodellen en computerprogramma's ontwikkeld ten behoeve van het gezamenlijk beheer van dierentuinpopulaties.

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