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Selection against Fox-Colour in Przewalski's Horses (*Equus przewalskii*) – Implications for Genetic Management

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With 5 Figures

Introduction

The Przewalski's horse belongs to the group of oldest self-sustaining populations in captivity. Otherwise, we would not be here in Leipzig, discussing management and future of this unique wild horse. After almost a century in captivity this species is even at the dawn of its re-introduction into wild habitat. Taking into account the number of almost 900 animals in the current population, we may state that we have saved this species from total extinction.

But, every glorious story contains also some less glorious events. The history of Przewalski's horses in captivity started at the beginning of this century. Words as "population genetics", "inbreeding" and "founder representation" did not exist in those times. Other views and opinions (e.g. with respect to selection and inbreeding) of those who founded the captive population had their effects on the current and future population.

However, we should not judge whether decisions in the past were good or wrong. Instead we should decide how to implement new views and knowledge in management of Przewalski's horses.

One of the "history" effects we have to deal with is the expression of the "fox" allele. There are different opinions among owners of Przewalski's horses with respect to management of this phenotypic feature. These opinions can be divided in the "genetic" and the "phenotypic" management approach. Both approaches have been described and discussed by PRINCÉE et al. (1990). This paper presents the results of a study on the "behaviour" of the "fox" allele in the studbook population as on 31 December 1989 and the effects of management measures with respect to "fox" colour.

Inheritance of fox colour

Most important is to study the inheritance pattern of the "fox" allele. Without a clear understanding of its genetics, no management will be possible.

So far, no results of breeding experiments with "fox" coloured horses are available. Nevertheless, the assumption that "fox" colour is inherited as a recessive allele on a single locus seems reasonable. Arguments for this type of inheritance pattern are based on (1) information on inheritage of fox (i.e. chestnut, red) in domestic horses (*Equus caballus*) (TROMMERSHAUSEN-SMITH, 1979) and (2) information from matings in Przewalski's horses that produced fox-coloured offspring (see Table 1). These matings resulted in 25% "fox" and 75% "non-fox" coloured offspring. This is in accordance with the expected frequencies of dominant/recessive heterozygote matings.

Origin of "fox" allele

It has been suggested that the "fox allele" originates from the domestic horse #229 or from founders that would be hybrids of Przewalski's horses and Mongolian domestic horses (e.g. #18). But, from an evolutionary point of view there is no reason to assume that the "fox" allele is a specific for domestic horses: it could be just a "rare" wild allele.

However, the question whether "fox" originates from domestic or Przewalski's horses is, in my opinion, an academic question. We probably will never be able to trace its real origin.

Therefore, we should concentrate on the facts: (1) "Fox" coloured animals have been observed in the population. (2) There is a controversy with respect to acceptance of this phenotype. The following sections will describe some "behavioural" aspects of the "fox" allele in the captive population.

Table 1. Numbers of "fox" coloured and "non-fox" coloured offspring in breeding combinations of Przewalski's horses (that produced "fox" coloured offspring). Sire # and Dam # refer to international studbook numbers. The expected number of "fox" coloured offspring is based on the assumption that "fox" colour is inherited as a recessive allele on a single locus

Sire	Dam	Number of offspring		
#	#	Fox	Non-fox	Total
81	82	1	2	3
118	119	1	3	4
120	72	1	0	1
185	247	1	8	9
187	189	1	5	6
281	372	2	2	4
281	864	1	1	2
281	1264	1	1	2
293	529	2	6	8
314	386	1	1	2
466	1020	1	3	4
499	386	1	10	11
499	506	1	10	11
499	629	1	5	6
517	530	1	8	9
517	582	1	7	8
519	540	2	2	4
523	344	2	6	8
523	576	3	4	7
571	554	1	3	4
584	578	1	3	4
584	847	1	3	4
689	344	1	0	1
739	838	1	2	3
1153	576	1	0	1
Total		31	95	126
Expected		31.5	94.5	126

Frequency of "foxes" in the population

Numbers and percentages of "fox-coloured" offspring per generation group are presented in Figures 1 and 2, respectively. The generation of an individual is calculated by the Zooresearch Studbook Management software. Wild-caught horses are regarded as generation zero (0) and their offspring as generation one (F1). Offspring that are produced by matings between generation groups belong to highest generation group among the parents plus one.

The number of "fox-coloured" animals seems to increase per generation (Fig. 1). However, the size of the captive population has increased enormously, resulting in smaller percentages of "fox-coloured" horses for later generations. The frequencies of "foxes" for generations 6 to 11 range between 1–3% (Fig. 2).

The "Przewalski's horse population does not behave like a random breeding population. The relatively large percentages in the third and fourth generation (see Fig. 2) might be due to inbreeding and selective breeding in the early history of the population. No fox coloured offspring are found in the fifth generation. This might be the effect of mixing different breeding lineages. Non-random breeding and the small number of offspring in young generation groups (10 and 11) also affect the percentages of "fox-colour". Percentages in these groups do not necessarily represent values for "final" percentages.

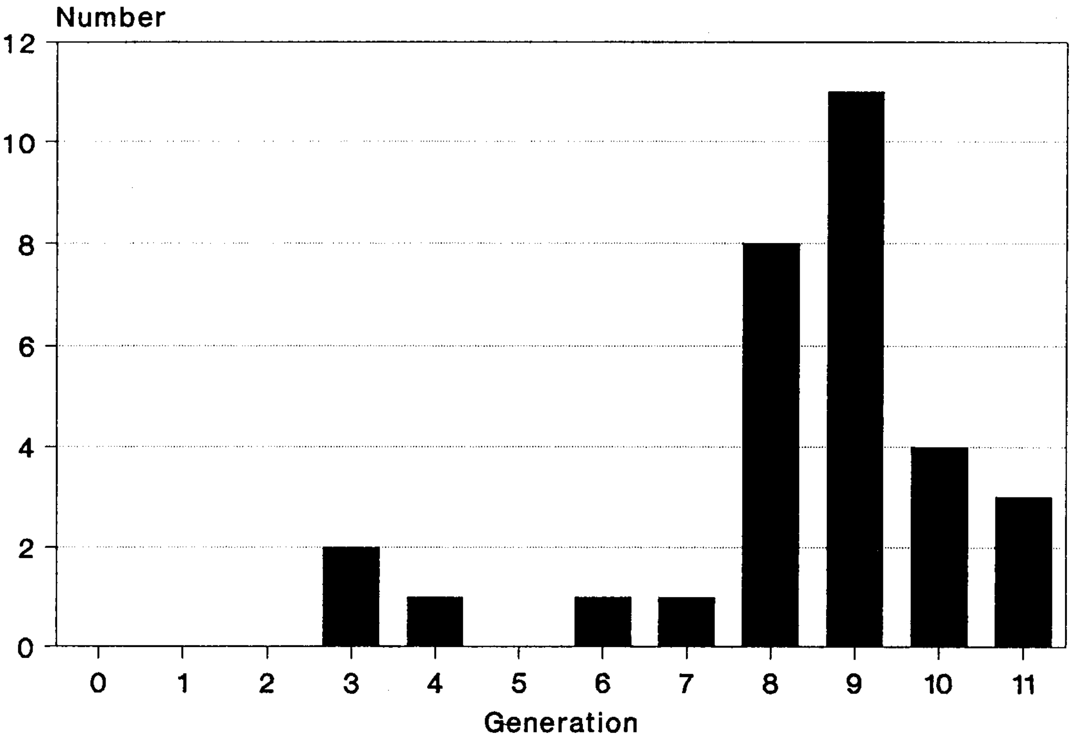

Fig. 1. Number of "fox-coloured" offspring in generation groups of Przewalski's horses

Carriers of the "fox" allele

Probabilities (risks) that individuals are fox-carrier, under the assumption that "fox-colour" is inherited as a recessive allele on a single locus, have been estimated for all individuals in the pedigree. Two categories of "fox" carriers can be distinguished: true carriers and possible carriers. Within the latter group different classes of probabilities are used i.e. exact risks and estimated risks. The following section describes the classification of carrier groups, the type of risk and the method of calculation:

(1) True carriers. These are horses that produced "fox" coloured offspring. These individuals have an exact risk (probability) of 1.0 that they are carrier.

(2) Possible carriers. Three categories can be distinguished within this group:

(a) Offspring of real carriers. These horses have an exact risk of 0.5 of being carrier.

(b) Ancestors of true carriers. These horses have an minimal estimated risk of 0.5 of being fox carrier.

(c) Offspring of parents that have a risk of being fox carrier. The risk for these horses can be calculated by using the following formulae:

$$\text{Risk} = (\text{Risk}_{\text{Sire}} + \text{Risk}_{\text{Dam}})/2 - (\text{Risk}_{\text{Sire}} \times \text{Risk}_{\text{Dam}})/4$$

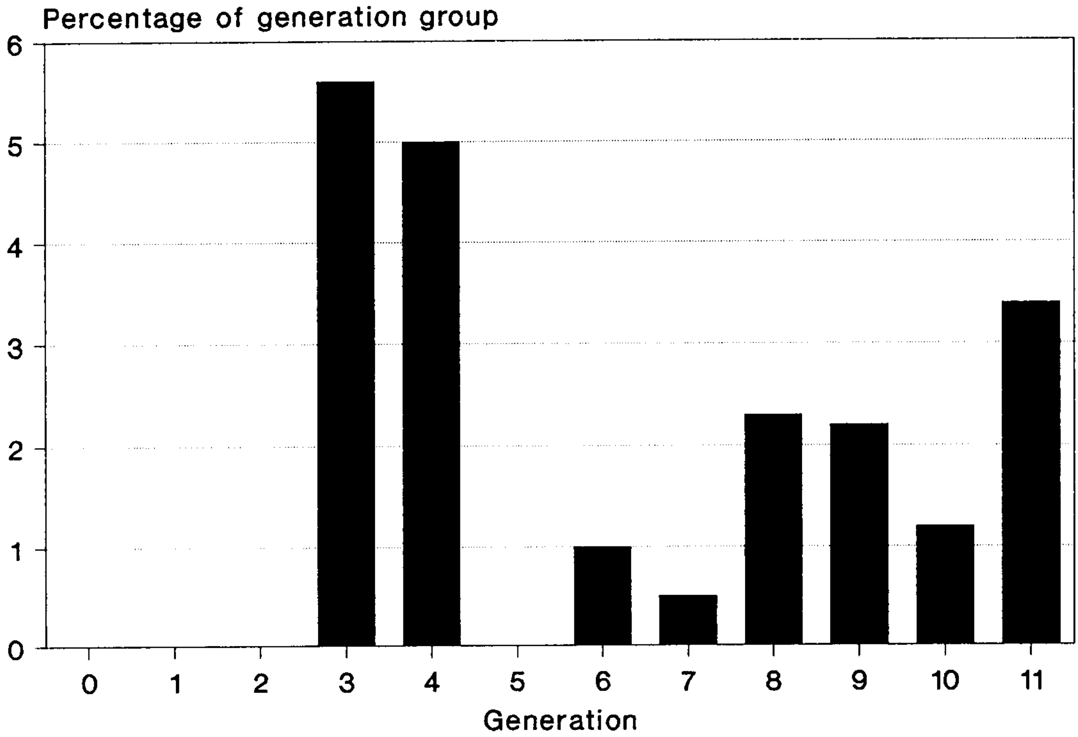

Fig. 2. Percentage of "fox-coloured" offspring in generation groups of Przewalski's horses

No differences between exact and estimated risks in the parental group has been made. This means that the probabilities that have been calculated for this category of possible carriers have to be considered as estimates.

Figure 3 shows minimal risks that a founder is a "fox" carrier. Several founders have an equal (minimal) risk to have been carrier of the "fox" allele. Note that the domestic horse (DOM) has a lower risk of being carrier than several other founders.

Figure 4 shows the number of horses in the current population that are (1) true carriers, (2) offspring or parents from true carriers (These animals have an (estimated) risk of 0.5), (3) estimated risks smaller than 0.5 and (4) estimated risk between 0.5 and 1.0.

Selection against the "fox" allele

Five models of selection management are compared with respect to effect on genetic variation:

Model I. No selection. Population size is 887.

Model II. True male carriers are removed from the (breeding) population. Six stallions will be removed. Size of breeding population will be 881.

Model III. True male and true female carriers are removed from the (breeding) population. Population size will be 868.

Model IV. Removal of true carriers, their parents (minimal risk of 0.5) and offspring of these carriers (risk of 0.5). Population size will be 813.

Model V. Removal of all possible carriers with estimated risks larger than 0.25. Population size will be 292.

Models II and III could be considered as mild selection. Model V is an extreme selection model that reduces the breeding population to 292 individuals. The criterium of 0.25 in this model is arbitrary. Removing all horses in the population that have a risk of "being" fox carrier would result in loss of the entire population.

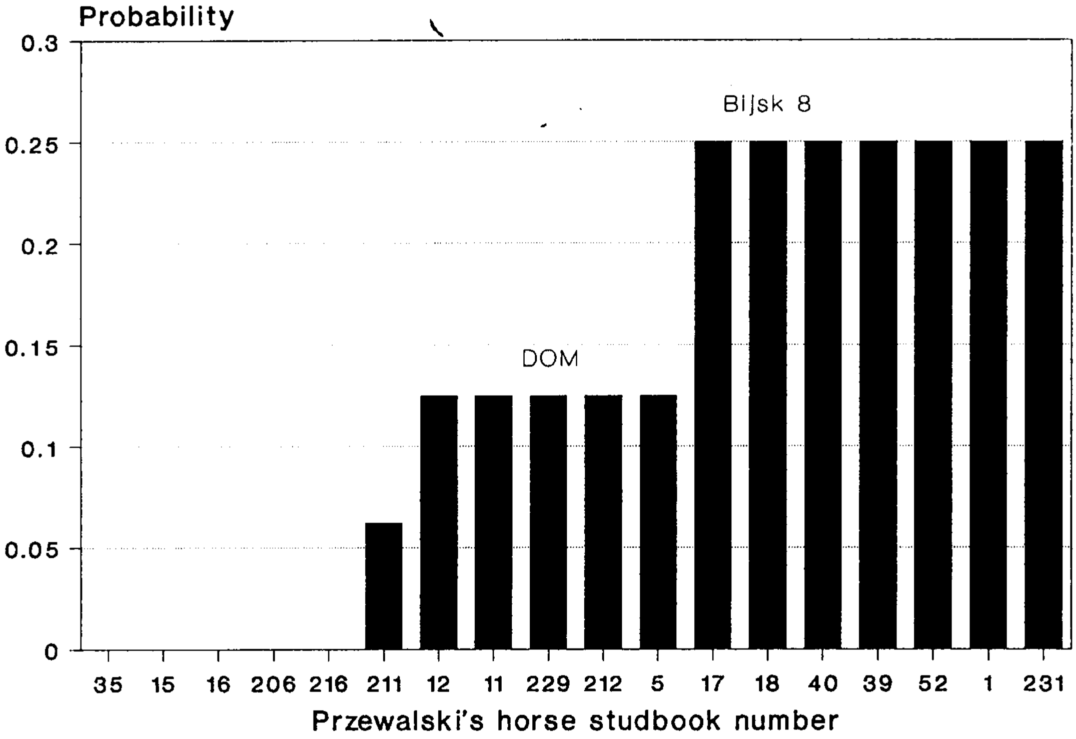

Fig. 3. Probabilities that founders of Przewalski's horse population are carrier of the "fox" allele. See text for further details

The computer simulation model GeneFlow (Princée, 1988) has been used to estimate genetic variation in the living population according the described selection models. The simulations were carried out with 50 runs over 25 loci. Five allelic variants (with frequency 0.20 in the source population) were assumed per locus.

Three measures of genetic variation have been used. The first measure is gene diversity (Nei, 1975). The second measure is the proportion of heterozygous loci in the population. The third measure is the number of unique alleles in the population. All measures are expressed as percentages of the levels in the source population. In this, the domestic horse has been considered as originated from the wild Przewalski's horse population.

Results of geneflow simulation experiments are presented in Figure 5. These results suggest that mild selection (Model II and III) has hardly any influence on genetic variation in the population.

Discussion

Mild selection that includes removal of male and/or female carriers of the "fox" allele has hardly any effect on the genetic variation in the living population. A small founder population and selection and inbreeding in the past, have resulted in a relatively low genetic variation in the living population.

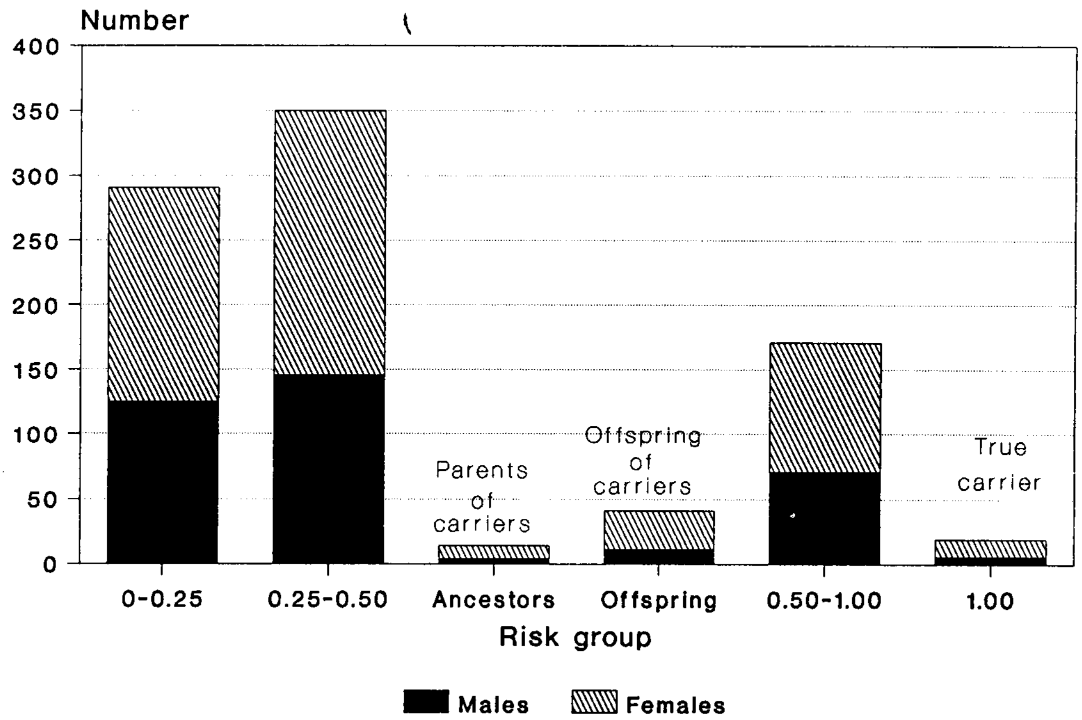

Fig. 4. Number of Przewalski's horses per risk class of being "fox" carrier. Dark bars represent number of males, shaded bars represent number of females. See text for further details

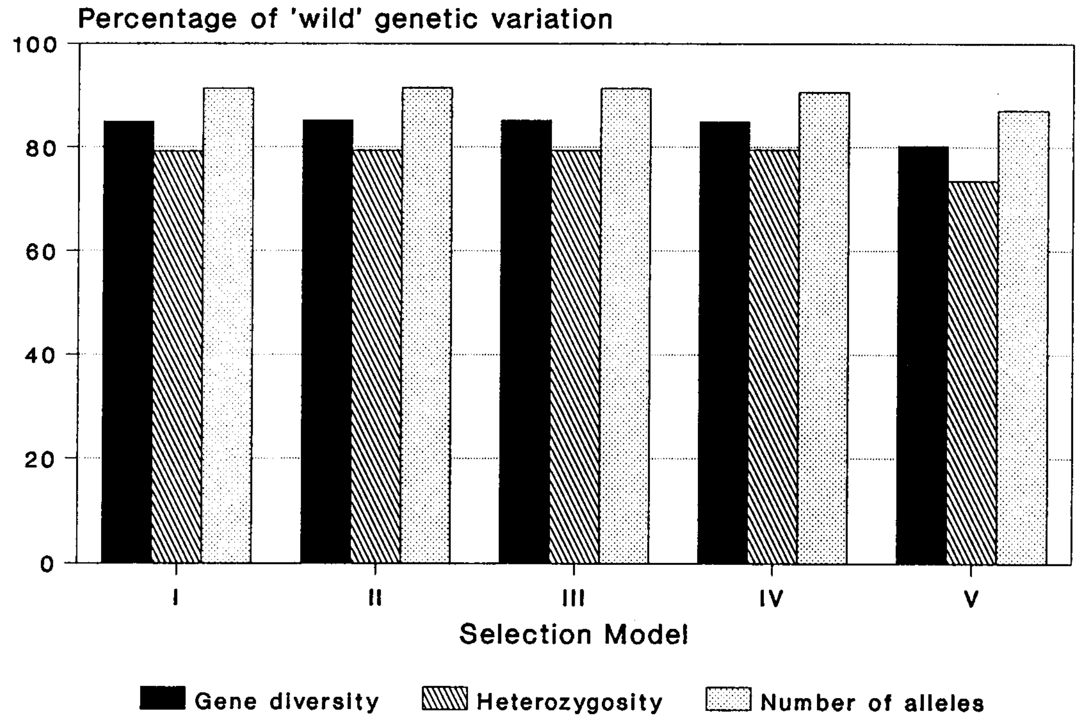

Fig. 5. Results of GeneFlow simulation experiments on the effects of selection models I to V (see text) on genetic variation in the living studbook population of Przewalski's horses as on 31 December 1989. Three measures of genetic variation are presented: gene diversity (dark bar), heterozygosity (shaded bar) and number of alleles (gray bar). Measures are presented as percentages of genetic variation in the source population (i.e. wild population). See text for further details

This means that animals in the population tend to share a number of the same allelic variants. Removal of a small number of these animals does not directly result in removal of allelic variants from the current population.

Theoretically, very rare alleles might get lost. However, given the genetic processes that occurred in the captive population of Przewalski's horses, rare alleles might already be lost or, as in the case of the "fox-allele", have increased to higher frequencies.

In my opinion it is important to realize that we are discussing the implementation of mild selection to minimize undesired effects that have been caused by selection and inbreeding in the past.

In this special case of Przewalski's horses, – because of the large population size and because of the relatively high number of generations, the population has lived since its foundation –, mild selection could be tolerable. But, we should be aware that, – generally speaking –, selection is a dangerous tool that always can result in unpredictable negative effects.

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