JOURNAL OF ANIMAL SCIENCE
The Premier Journal and Leading Source of New Knowledge and Perspective in Animal Science

Population viability analysis on domestic horse breeds (Equus caballus)

J. P. Thirstrup, L. A. Bach, V. Loeschcke and C. Pertoldi

J Anim Sci 2009.87:3525-3535.
doi: 10.2527/jas.2008-1760 originally published online Aug 14, 2009;

Population viability analysis on domestic horse breeds (*Equus caballus*)[1]

J. P. Thirstrup,* L. A. Bach,†[2] V. Loeschcke,* and C. Pertoldi*‡

*Department of Biological Sciences, Ecology and Genetics, University of Aarhus, Bldg. 1540, DK-8000 C, Denmark; †Department of Theoretical Ecology, Ecology Building, Lund University, SE-22362 Lund, Sweden; and ‡Mammal Research Institute, Polish Academy of Sciences, 17-230 Białowieża, Poland

ABSTRACT: In this study, we performed a population viability analysis on 3 domestic horse breeds (*Equus caballus*) of Danish origin, namely, the Frederiksborg, the Knabstrupper, and the Jutland breeds. Because of their small population sizes, these breeds are considered endangered. The Vortex software simulation package was used for the population viability analysis. First, we investigated the future viability of these breeds based on present demographic and environmental parameters. Second, a sensitivity analysis revealed the most important variables for the viability of these breeds. Third, we examined management scenarios in which one of the studbooks was closed. According to the Vortex analysis, 2 of the breeds (Knabstrupper and Jutland) will persist for the next 200 yr, whereas the smaller breed (Frederiksborg) could become extinct within 40 yr. The sensitivity analyses indicated that the variables concerning reproduction of the mares had the greatest impact, with the number of mares actively breeding being the most influential on the population forecasts. The results suggest that closing the Knabstrupper studbooks can be done only if increasing the number of mares actively breeding counteracts the loss of genetic variation attributable to such a management strategy. It is recommended, based on these results, that the number of Frederiksborg and Knabstrupper mares actively breeding must be increased to approximately 30% in the 2 breeds that are presently using only 13%, while leaving the third (Frederiksborg) at its present 30% level. Monitoring of the breeds in the future, however, may be exploited to adjust the breeding strategies. We suggest that the large amount of data required by Vortex makes it very useful for analyzing domestic animals because of the comprehensive data material often available. The results of this analysis accord with other studies on the Prezwalski horse, indicating robustness in the parameter sensitivity for horses.

Key words: breeding simulation, management, population viability analysis, sensitivity analysis

J. Anim. Sci. 2009. 87:3525–3535
doi:10.2527/jas.2008-1760

INTRODUCTION

Small populations tend to be inbred, demographically unstable, and vulnerable to environmental fluctuations, all of which further reduce their size. Such negative feedback is referred to an "extinction vortex" (Gilpin and Soulé, 1986; Miller and Lacy, 2005). Population viability analysis (**PVA**) estimates the vulnerability to extinction and explores management to ensure persistence (Lacy, 1993; Brook et al., 2000). The advantages of PVA are its ability to assess risk and uncertainty in data information (Reed et al., 2002). Vortex (Lacy, 1993) is a stochastic, individual-based PVA software developed for long-lived animals (Armbruster et al., 1999; Bustamante, 1996).

Three horse breeds are indigenous to Denmark and are endangered: the Frederiksborg (**FR**), the Jutland (**JU**), and the Knabstrupper (**KN**) breeds. The FR breed began in the 16th century at the Danish royal stables (Trock, 1986). A studbook was founded in 1861 and in the late 20th century, only horses with greater than 15/16 great-grandparents in the FR studbook were accepted; subsequently, the studbook was considered closed. The KN breed was originally part of FR and was bred for a special spotted pattern (Lunn, 1855; Lunn, 1966). In 1970, the KN founded its own open studbook, in which mares with no previous studbook records and

[1]We thank the breed associations for providing the studbooks and M. Davis, T. N. Kristensen (University of Aarhus, Denmark), and 2 anonymous reviewers for comments. This work was supported by the Danish Natural Science Research Council (Copenhagen, Denmark) for financial support (C. Pertoldi grant number: 21-01-0526, 21-03-0125, and 272-08-0567 and L. A. Bach grant number: 21-03-0382 and 21-05-0019).

[2]Corresponding author: lars.bach@teorekol.lu.se

Received December 23, 2008.
Accepted July 21, 2009.

stallions graded for other breeds were accepted when carrying the distinct spotted color. Soon only horses with greater than 12/16 great-grandparents in the KN studbook will be accepted. The JU (founded in 1861) was based on draft horses and accepted 5% Shire and Suffolk Punch breeds (Hedegaard, 2003). Here we aim to 1) predict the viability of the present breeding strategies, 2) identify the important variables for viability, and 3) explore the effect of closed studbooks on viability. Vortex has heavy data requirements (Lindenmayer et al., 1995), but because of a comprehensive database, extensive information is available. Similar data may be available from other domestic populations, but few PVA studies have been done and only once on horses (Slotta-Bachmayr et al., 2004).

MATERIALS AND METHODS

Animal Care and Use Committee approval was not obtained for this study because the data were obtained from an existing database.

Studbooks from 1970 to 2005 were available on request from the breed associations. A Web page and a database created by the Danish Department of Horse Breeding (available from http://www.hestedata.dk/AbonnementHesteData.htm) provided data encompassing individual information on pedigrees, inbreeding coefficients, number of progeny, birthdays of progeny, and grading results. On the same Web page, yearly reports from 1998 to 2006 were available, encompassing the number of services of individual stallions; the number of services the previous year that resulted in live foals, abortions, and stillborn foals; and unsuccessful services.

Simulation Software

Vortex 9.7 (Miller and Lacy, 2005) was used in the analysis. Vortex is a generic software package that simulates demographic events and models the population processes as discrete, sequential events. It follows each individual from birth to death and the transmission of genes through generations by generating pseudo-random numbers by a Monte Carlo simulation after a binomial distribution. It simulates deterministic and stochastic factors affecting the dynamics of populations. Each simulation was run for 1,000 iterations, running 200 yr (approximately 25 generations) with an extinction definition of a population size of less than 50 individuals (quasi-extinction threshold). We assumed that such small population sizes probably would induce serious changes in management of the breeds and that estimated parameters would not be valid at that point.

Parameters

Demographic Parameters. For most of the data required to run the analysis, the 3 breeds were similar. Horses are mature at the age of 3 yr (Linklater et al., 2004), but because grading for the studbook is performed in the autumn, they enter the breeding pool the following spring, when the breeding season starts. Mares produce 1 progeny per year because the period of gestation is 11 mo (Hammond, 1960; Rossdale and Short, 1967). Mares seldom produce twins, and if they do, at least one of the offspring will likely die (Giles et al., 1993). The generation time is 8 yr and the sex ratio is 50:50. The age of horses spans from 1 to more than 30 yr (Paradis, 2002; Brosnahan and Paradis, 2003), but there is large variation in the age of horses because some are killed at a young age owing to illness, breeding problems, or injury (Baker and Ellis, 1981; Leblond et al., 2000), whereas some survive until senescence. The age class suffering most from premature mortality is 0 to 1 yr of age (Baker and Ellis, 1981) for both sexes, but because of breeding policies in domestic horses, few stallions are graded for the breeding pool and most of the stallions born are castrated before the age of 3. Active breeding stallions typically stay in the breeding pool for much longer than the mares. From studbook counting (number of foals born in a given year minus individuals graded 3 or more years later), it was revealed that 65 to 70% of female foals and only 6 to 20% of male foals reach maturity and are graded. Death rate in each age class was estimated from the literature (Baker and Ellis, 1981; Cohen, 1994; Leblond et al., 2000). Mortality of 3-yr-old males was simulated as "harvest," which means that they were removed from the breeding pool because of undesirable morphology or temperament. The young stallions are slaughtered for meat or castrated and used as riding horses.

The percentage of mares in the breeding pool was estimated as the number of foals born divided by the number of mares registered in the studbook in the period from 1985 to 2005. The percentage of males in the breeding pool could be calculated from the database created by the Danish Department of Horse Breeding.

Maximum age of breeding females was estimated by examining 100 mares from each breed considered past the age of breeding (more than 25 yr). In JU, only 4% of the mares were bred before the age of 5 yr and 5% were bred after the age of 16 yr. In KN, 7% were bred before the age of 5 yr and 5% were bred after the age of 19 yr. In FR, 6% were bred before the age of 6 yr and 8% were bred after 18 yr of age.

There are several differences among the 3 breeds. First, there are more mares in the JU breed than in the other 2 breeds (Kruskal-Wallis test: $P = 0.0012$; Mann-Whitney pairwise comparisons: $P < 0.01$; Bonferroni corrected). This finding might be due to the purpose of the breeds because FR and KN are mainly used for riding and recreation purposes, whereas JU is a draft horse. The FR and KN mares might be used for sport riding or competition instead of breeding. There is not as much interest in driving and pulling labor as there is in riding, and JU mares might be used for breeding instead of pleasure. Second, the mean age of stallions and the maximum age of horses breeding are less in JU

Table 1. Initial conditions and basic parameters[1]

Variable	Knabstrupper, mean ± SE	Jutland, mean ± SE	Frederiksborg, mean ± SE
Simulated for	200 yr	200 yr	200 yr
Iterations	1,000	1,000	1,000
Quasi-extinction threshold	50 individuals	50 individuals	50 individuals
Lethal equivalents	3.14	3.14	3.14
Percentage attributable to recessive lethals	50	50	50
Polygynous	Yes	Yes	Yes
Minimum age of breeding, yr	5	5	6
Maximum age of breeding, yr	19	16	18
Sex ratio, % of males	50	50	50
Percentage of litter size 0	86.24 ± 1.85	69.46 ± 2.39	86.92 ± 1.14
Percentage of litter size 1	13.76 ± 1.85	30.54 ± 2.39	13.08 ± 1.14
Mortality rate at 0 to 1 yr	20.00 ± 1.6	17.00 ± 1.6	16.00 ± 1.6
Mortality rate at 1 to 2 yr	10.00 ± 0.86	12.50 ± 0.86	11.00 ± 0.86
Mortality rate at 2 to 3 yr	9.00 ± 1.1	6.00 ± 1.1	7.00 ± 1.1
Mortality rate at 3 to 4 yr	1.00 ± 0.5	1.00 ± 0.5	1.00 ± 0.5
Mortality rate at adult	1.00 ± 0.5	1.00 ± 0.5	1.00 ± 0.5
Percentage of males in the breeding pool	72.87	67.15	66.75
Specified age distribution	Yes	Yes	Yes
Initial population size	762	794	795
Density-dependent reproduction	No	No	No
Carrying capacity	840 ± 84	875 ± 87.5	875 ± 87.5
Harvest (males at 3 yr)	27	33	27
Supplemented females	9	No	No
Supplemented males	1	No	No

[1]SE attributable to environmental variation.

compared with KN and FR. Third, fewer stallions are castrated in JU and significantly more stallions have been graded in JU than in the other breeds (Mann-Whitney pairwise comparisons, Bonferroni corrected, $P < 0.0001$). In FR and KN, some stallions stay in the breeding pool for a very long time and some of these may service the majority of the mares, whereas other stallions have only a few services in their lifetime. The JU stallions stay in the breeding pool only for a few years, and most stallions of this breed have services. The JU stallions have on average more services during their lifetime than stallions in the other breeds. The difference between JU and the other 2 breeds is that the turnover rate is faster in stallions in the JU breed compared with the other breeds. Finally, the KN breed has an open studbook, but the intention is to close it. The number of horses supplemented was calculated from studbooks as number of F_1 each year. (We use the term "supplement" to describe the introduction of animals into the breed.) At present, 9 mares with no previous studbook records and 1 stallion of a foreign breed are graded for the KN studbook each year. See Table 1 for the values used for basic simulations of the horse breeds.

Environmental Variation. Vortex provides the option of modeling density-dependent reproduction. However, because some criticisms have been raised against using a density-dependent model (Boyce, 1992; Mills et al., 1996; Brook et al., 1997) and because it was not possible to detect density-dependent breeding, this option was not used. The option of "correlation between reproduction and survival" was not used, both because there was no support for assuming this correlation and because the sensitivity analysis did not reveal this variable as being important (results not shown). Nor was the option "catastrophes" used. The 3 breeds are scattered nationwide and a catastrophe embracing such a large part of the breeds or country was assumed to be unlikely.

Carrying capacity could not be estimated because it depends on the demand of potential buyers, and therefore varies with fashion among horse owners and other socioeconomic factors. It was assumed that the breeds have not reached the ceiling. Carrying capacity was set to the present population size plus 10% to ensure that chaotic population dynamics, caused by increased competition in populations at carrying capacity, will not occur. Variation in carrying capacity caused by environmental variation was likewise impossible to estimate, but based on the literature (Song, 1996; Penn et al., 2000), it was set to 10% of the carrying capacity (probably a rather conservative estimate).

Inbreeding and Genetic Management. Severe negative effects of inbreeding, that is, inbreeding depression, on traits that are closely related to fitness, fecundity, and survival are well documented in wild (Crnokrak and Roff, 1999; Hedrick and Kalinowski, 2000) and captive populations (Kristensen and Sørensen, 2005; Boakes et al., 2007), but no overall correlation between inbreeding, microsatellite heterozygosity, and mean squared allelic distance (d^2) in Lipizzan horses was found (Curik et al., 2003). However, wild populations with low heterozygosity but good apparent fitness have been observed (e.g., Paetkau et al., 1998).

In this analysis, we detected no sign of inbreeding depression, measured as correlations between inbreeding coefficients and percentage of unsuccessful matings, number of stillborn or malformed foals, and number of abortions. These variables relate only to fetus mortality. It is possible that other life history traits might be affected, but from the data available, it was not possible to examine other traits and estimate lethal equivalents. It was decided to use the estimate of 1.57 lethal equivalents per haploid genome given by Ralls et al. (1988). This choice is also a default option in Vortex and is recommended by Miller and Lacy (2005). Vortex takes only juvenile survival into account, and the median value for juvenile survival of 1.57 lethal equivalents per haploid genome in 40 mammalian species given by Ralls et al. (1988) seemed to be reasonable. Vortex assumes that the founder population is unrelated (Lacy, 1993), and each individual from the founder population is assigned 2 unique alleles. This assumption results in underestimation of the level of inbreeding because individual inbreeding coefficients calculated from studbooks unveiled inbreeding in the 3 breeds. Vortex also provides an option of simulating genetic management whereby it is possible to avoid breeding between related individuals. This option seemed relevant because most breeders have access to studbooks when choosing appropriate mates.

Conducting the Analysis

Simulations and Sensitivity Analysis. A basic simulation was conducted for each of the 3 breeds to examine how the estimated parameters would affect the results. To investigate the parameters most sensitive to the survival of the breeds, a sensitivity analysis was performed. We conducted individual analyses for each parameter, in which the chosen parameter was given variable values and all other parameters were kept constant (Jørgensen, 1988). The sensitivity index of a parameter (S_x) was defined as

$$S_x = (\Delta X/X)/(\Delta \text{parameter}/\text{parameter}),$$

where ΔX is the change in the observed response variable (e.g., population size) and parameter is the examined parameter (e.g., percentage of mares breeding). Because the sensitivity test showed that the percentage of mares breeding was one of the most sensitive parameters, a threshold for how small the percentage could be was examined.

Management of KN. Because the KN association intends to close the studbook in the near future, we investigated whether this was a reasonable management option. A threshold number of supplemented mares, whereby the breed would persist with the present population size without genetic deterioration, was investigated. This was done by gradually reducing the number of supplemented mares, assuming that other parameters were kept constant.

RESULTS

Simulations

From basic simulations using the estimated parameters, it was evident that the KN and JU breeds are likely to survive for the next 200 yr but that the FR breed is likely to become extinct within this period. According to the Vortex simulation, it will become extinct within 30 to 40 yr. However, KN will have a population size two-thirds the size of the present population. For results from simulations using basic parameters for the horse breeds, see Table 2 and Figure 1. Deterministic growth rate, stochastic growth rate, probability of extinction, population size of extant populations, population size across all populations, final expected heterozygosity, final number of alleles, median and mean time to extinction, and their SE are shown.

Final observed heterozygosities ($\mathbf{H_o}$) for the 3 breeds are as follows (mean ± SE): KN: 0.9989 ± 0.0016; JU: 0.957 ± 0.012; and FR: 0.983 ± 0.00 (FR calculated from the first 38 yr of the simulation). Inbreeding coefficients can be calculated from $1 - H_o$ (Lacy, 1993; Miller and Lacy, 2005); therefore, the mean final inbreeding coefficients for the 3 breeds are as follows: KN: 0.0011; JU: 0.043; and FR: 0.017.

The KN will have more fixed alleles and more lethal recessive alleles per diploid genome than the JU and FR. The FR will lose alleles and genetic diversity and decrease in population size at a greater rate than the 2 other breeds (Figure 1).

Sensitivity Analysis

From the sensitivity analysis, it is clear that the most vulnerable parameters of the 3 breeds are associated with the number of reproducing mares. The 2 most important parameters for all 3 breeds are the increase in maximum age of breeding and the percentage of mares breeding (Table 3). A decrease in female mortality rate and the number of females supplemented seems to increase the viability of KN, measured as the mean final population size and mean stochastic growth rate. In addition, a decrease in JU female mortality rate will increase the viability of JU. Environmental variation seems to have only a minor effect on the 3 breeds. The JU is affected by carrying capacity, even though the mean final population size is 17% below carrying capacity. For KN and JU, variation in the sex ratio will have an effect on viability.

At least 20% of the mares in KN and 30% of the mares in JU and FR have to breed to provide a positive stochastic growth rate and a final population size equal to or greater than the current 750 individuals (Figure 2). The options of including or excluding inbreeding depression (which includes the presence of lethal alleles subject to purging) and genetic management (which prevents breeding individuals with kinship of more than 0.125) had no effect on viability for any of the breeds (i.e., *t*-tests for stochastic growth rate and final population size could not reject the H_o hypothesis of no differences in any of the breeds for the 2 options; results not shown).

Management of KN

With the present breeding strategies, the KN population has to be supplemented with at least 1 stallion and 10 mares per year to provide a population size of more than 500 individuals and a positive growth rate (Figure 3). If a management strategy is going to be implemented when the supplementation ceases, it must be counteracted by increasing the number of breeding mares (Figure 4). At least 25% of the mares in the KN population have to breed to sustain the present population size. On the other hand, more than 30% of the mares breeding will not increase the population size because it is confined by carrying capacity. Genetic diversity (final expected heterozygosity) will decrease and inbreeding will increase if supplementation is excluded (Figure 5). If supplementation is sustained, more than 2 stallions and 2 mares supplemented per year will not improve the genetic diversity.

DISCUSSION

The results of simulations using basic parameters for the 3 horse breeds showed that with the present breeding management, JU most likely will persist, with a population size comparable with the present and a positive growth rate. The KN will survive for the next 200 yr with the present breeding strategy, but with a somewhat reduced population size and a negative growth rate. According to the simulation, FR will become extinct in approximately 40 yr if the present breeding strategy is continued. This may seem somewhat surprising because KN stems from FR, which has not been declining in size for the last 2 decades, and the number of horses selected for the studbook has been rather constant over the years. However, in contrast to KN, the FR breed may still suffer from the closed studbook. Because the FR breed did not show signs of a decline in census size, the predictions based on Vortex may fail to forecast the future of this breed. One must keep in mind that simulations are not mirrors of the real world, and quantitative results must be interpreted with some caution (Beissinger and Westphal, 1998). Instead of taking absolute results literally, it is wise to examine different rates of demographic parameters, incorporate uncertainty, examine different management scenarios, and examine how different model structures affect the outcome (Beissinger and Westphal, 1998), and in this way place more attention on qualitative interpretations and the relative values.

Table 2. Results from simulations using basic parameters for the breeds[1]

Scenario[2]	det-r	stoc-r (SE)	PE	N-extant (SE)	N-all (SE)	H_e (SE)	AlleIN (SE)	MedianTE	MeanTE
Basis–KN	−0.039	−0.002 (0.023)	0.000	447.04 (34.39)	447.04 (34.39)	0.9949 (0.0004)	452.76 (13.39)		
Basis–JU	0.014	0.012 (0.021)	0.000	750.47 (65.22)	750.47 (65.22)	0.9534 (0.0094)	43.65 (5.33)		
Basis–FR	−0.050	−0.089 (0.058)	1.000	0.00 (00.00)	0.00 (00.00)	0.0000 (0.0000)	0.00 (0.00)	30	30.8

[1]det-r = deterministic growth rate; stoc-r = mean stochastic growth rate; PE = probability of extinction; N-extant = mean population size of extant populations; N-all = mean population size across all populations; H_e = mean final expected heterozygosity; AlleIN = mean final number of alleles; MedianTE = median time to extinction; MeanTE = mean time to extinction. SE are shown in parentheses.

[2]KN = Knabstrupper; JU = Jutland; FR = Frederiksborg.

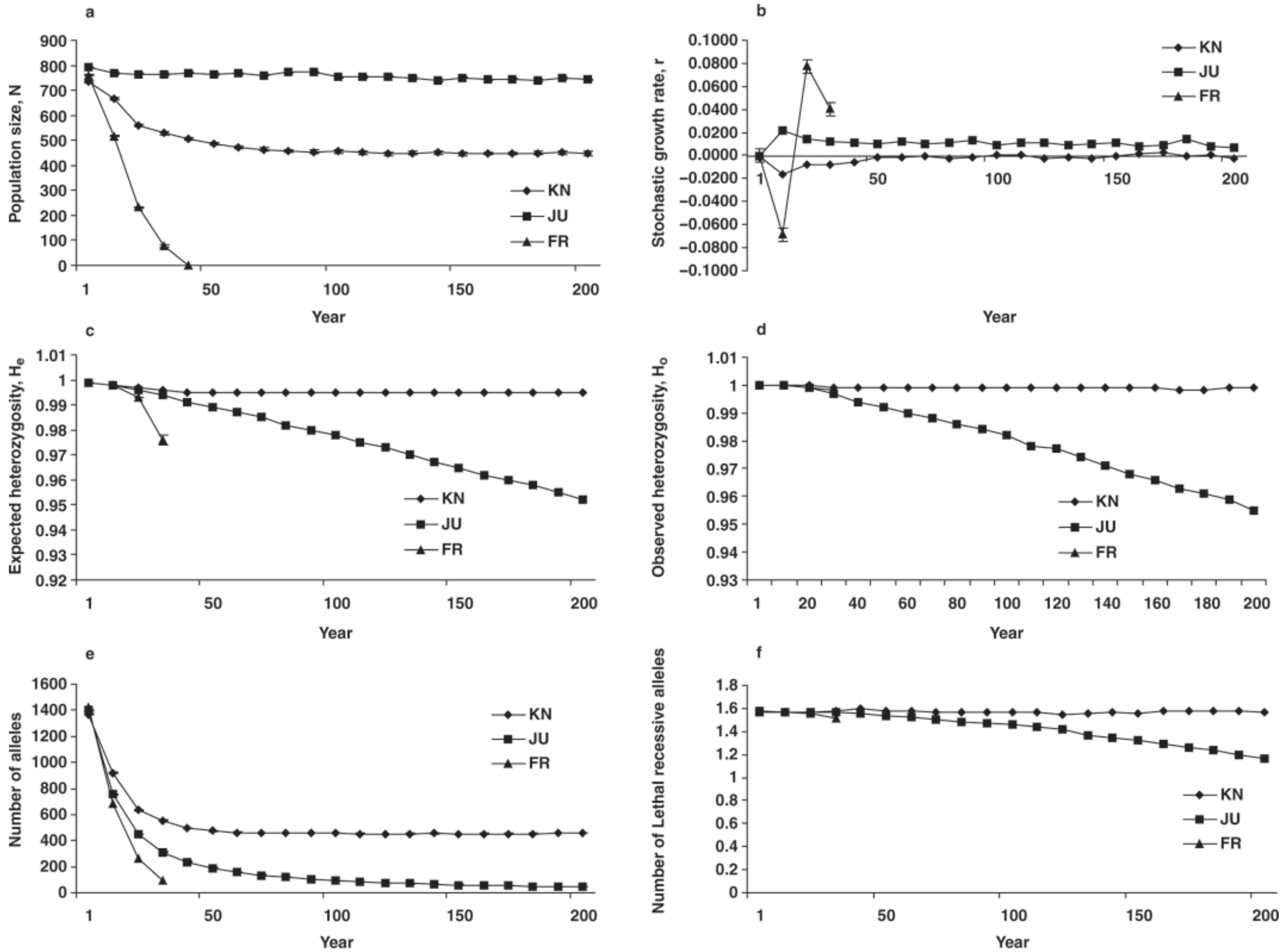

Figure 1. Mean population size (±SE; a), stochastic growth rate (±SE; b), expected heterozygosity (H_e; c), observed heterozygosity (H_o; d), number of alleles (e), and number of lethal recessive alleles (f) for the 3 breeds across a simulation run for 200 yr and 1,000 iterations, using basic parameters. KN = Knabstrupper; JU = Jutland; FR = Frederiksborg.

The sensitivity test revealed that the most important parameters for the viability of the horse breeds were parameters concerning reproduction of the mares. Only 13 to 14% of the mares breed in KN and FR. This corresponds to 80 to 90 foals born per year, one-half of which are females. Given a subadult mortality rate of 30 to 35% for the mares, the horses can hardly reproduce themselves. For the maintenance of the horses, it is important to double the share of mares breeding in the KN and FR breeds. In the JU breed, the percentage of mares breeding is at an acceptable level, but it should not be reduced. Another sensitive parameter is an enlargement of the reproductive age of the mares. This can be very difficult to accomplish, because the maximum age of breeding already is at the limit of what is biologically possible. Likewise, a decrease in female mortality rate is probably not possible for the same reason. Environmental variation had only a minor effect on the 3 breeds, except for variation in the sex ratio. If, by chance, more males are born, fewer mares will grow to the reproductive age and thereby diminish the viability of the horses. In the PVA study on Przewalski horses performed by Slotta-Bachmayr et al. (2004), a sensitivity test also unveiled the maximum age of reproduction and fecundity rates as being some of the most important parameters for their persistence. The congruence between our results and the results of Slotta-Bachmayr et al. (2004) indicates a generalization in the sensitivity of parameters for horses. The low percentage of stallions in the breeding pool compared with the number of mares seemingly had no effect on viability. Apparently, the percentage of stallions in the breeding pool is enough to sustain the viability of the populations.

Basic simulation of the FR breed showed very rapid extinction of the breed, which is not in accordance with the actual situation. The sensitivity test showed that the parameters most important to the viability of FR are those concerning the reproductive age of the mares. When estimating these parameters, we may have been too conservative. Six percent of the breeding mares are less than 6 yr old and 8% of the mares are more than 18 yr old. Increasing the reproductive period in the simulation from 6 to 18 yr to 5 to 19 yr could not pre-

Table 3. Results of sensitivity analysis for the 3 breeds[1]

	Variable changed,[2] index value				
	KN		JU		FR
Parameter changed	r	N	r	N	r
Demographic parameter					
Increase in females in first year of breeding	2.50	0.58	7.95	3.73	0.26
Decrease in females in first year of breeding	NC[3]	0.56	0.05	0.17	0.29
Increase in maximum year of breeding	10.00	3.13	10.80	0.54	2.07
Decrease in maximum year of breeding	10.00	2.74	14.99	2.93	2.40
Increase in males in first year of breeding	2.5	0.44	4.55	0.05	NC
Decrease in males in first year of breeding	2.0	0.43	0.36	0.01	1.07
Increase in percentage of females breeding	5.00	1.79	7.27	0.39	0.37
Decrease in percentage of females breeding	10.00	1.92	17.27	3.94	1.1
Increase in percentage of males breeding	NC	0.04	1.82	0.35	NC
Decrease in percentage of males breeding	NC	0.02	1.82	0.13	NC
Increase in female mortality rate	5.00	0.83	6.36	0.96	0.37
Decrease in female mortality rate	NC	1.02	8.18	0.35	0.12
Increase in male mortality rate	5.00	0.02	1.82	0.48	0.24
Decrease in male mortality rate	NC	0.09	0.91	0.16	NC
Increase in percentage harvested[4]	NC	0.04	2.73	0.28	0.61
Decrease in percentage harvested	NC	0.13	0.91	0.23	0.49
Increase in females supplemented	NC	0.92			
Decrease in females supplemented	4.5	0.90			
Increase in males supplemented	NC	0.05			
Decrease in males supplemented	3.00	0.68			
Environmental variation					
Increase in carrying capacity (K)	NC	0.04	0.91	0.35	NC
Decrease in K	NC	0.13	6.36	2.07	0.24
Increase in variation in K	NC	0.02	1.82	0.60	0.12
Decrease in variation in K	NC	0.02	1.82	0.07	0.12
Increase in variation in females breeding	NC	0.09	1.82	0.19	NC
Decrease in variation in females breeding	NC	0.11	1.82	0.13	0.12
Increase in variation in female mortality	NC	0.04	1.82	0.37	NC
Decrease in variation in female mortality	NC	NC	1.82	0.19	NC
Increase in variation in male mortality	NC	0.02	1.82	0.35	NC
Decrease in variation in male mortality	NC	0.04	1.82	0.29	NC
Increase in sex ratio (proportion of males)	5.00	1.52	10.91	3.12	NC
Decrease in sex ratio (proportion of males)	5.00	1.94	7.27	0.48	0.12

[1]See explanation for calculation of index values in the Materials and Methods section. Greater index values indicate that the parameter is more sensitive to the viability of the breeds.

[2]KN = Knabstrupper; JU = Jutland; FR = Frederiksborg. r = index based on mean stochastic growth rate; N = index based on mean population size (N for FR could not be calculated because the population became extinct in all cases).

[3]NC = no change was observed in the variable.

[4]Harvest indicates that the males were removed from the breeding pool because of undesirable morphology or temperament.

vent extinction alone; it would only postpone it for approximately 10 yr. The FR breed association has only recently closed the studbook and some of the horses supplemented before the closure might still have an effect on the viability of the population (not captured by the simulation). The KN breed association has kept the studbook open, and simulation of a closed studbook also resulted in extinction of this breed (data not shown).

The sensitivity test did not reveal that a decrease in supplemented horses in KN would have a huge effect on the viability of the breed, but the management analysis showed that closure of the studbook would have a detrimental effect unless the number of mares breeding was increased to counteract this. Although the sensitivity test did not uncover the parameter as being important, that might have been because it does not matter if 10, 9, or 5 horses are supplemented as long as they do not enter the breeding pool. As well as for the main population, only 13 to 14% of the supplemented mares are expected to breed.

The period of 25 generations might not be enough to capture a time lag effect in stochasticity effects (Lande 2002) or genetic impairment caused by deleterious alleles (Gilligan et al., 1997). On the other hand, a period of more than 200 yr would violate the assumption of unchanged environmental and demographic parameters, and there has to be a trade-off between the 2 options.

The simulated genetic diversity and inbreeding level might be underestimated. Vortex assumes that the founder population is not related (Lacy, 1993). Therefore, it cannot be modeled that there is inbreeding in the 3 breeds, as is evident from pedigree examination. The simulation showed that JU and FR lost genetic variation and increased inbreeding through the years, whereas KN did not. In addition, the number of alleles was reduced at a slower rate in KN relative to the other 2 breeds. Because of the open studbook, and therefore supplementation of horses, new alleles are brought to the breed to restore genetic diversity. If KN chooses to close the studbook, it will, according to the results from our simulation, lose some of this genetic diversity.

Some of the parameters hardest to estimate in our analysis were mortality rates for the different age classes. In Denmark, there is no tradition of reporting the death of horses, and some of the horses registered in the studbook may have been dead for several years. According to the sensitivity test, these parameters were not the most important to the viability of the breeds. It is therefore unlikely that error in estimating mortality rates would influence the results. Simulation processes can be used to unravel uncertainty about data information (Reed et al., 2002) and to direct attention toward areas where more information needs to be gathered. Concerning these 3 horse breeds, relevant data seem to be available for proper simulation, and no further data collection is necessary.

Because it was uncertain why Vortex was unable to predict the future of FR, it might be interesting to examine whether there is a time lag effect in exclud-

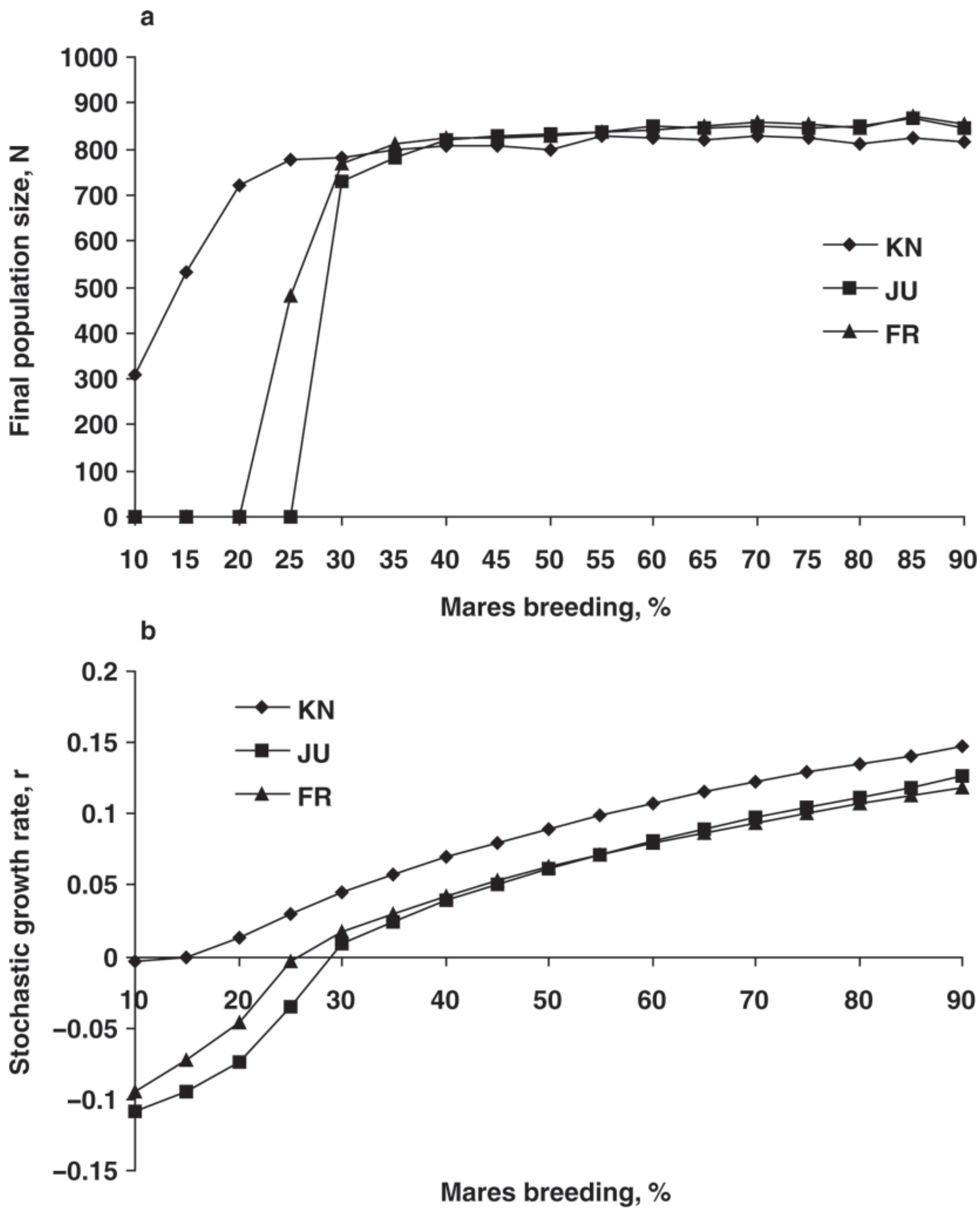

Figure 2. Mean final population size (a) and stochastic growth rate (b) of the 3 breeds as a function of percentage of mares breeding. The simulation was run for 200 yr using basic parameters. KN = Knabstrupper; JU = Jutland; FR = Frederiksborg.

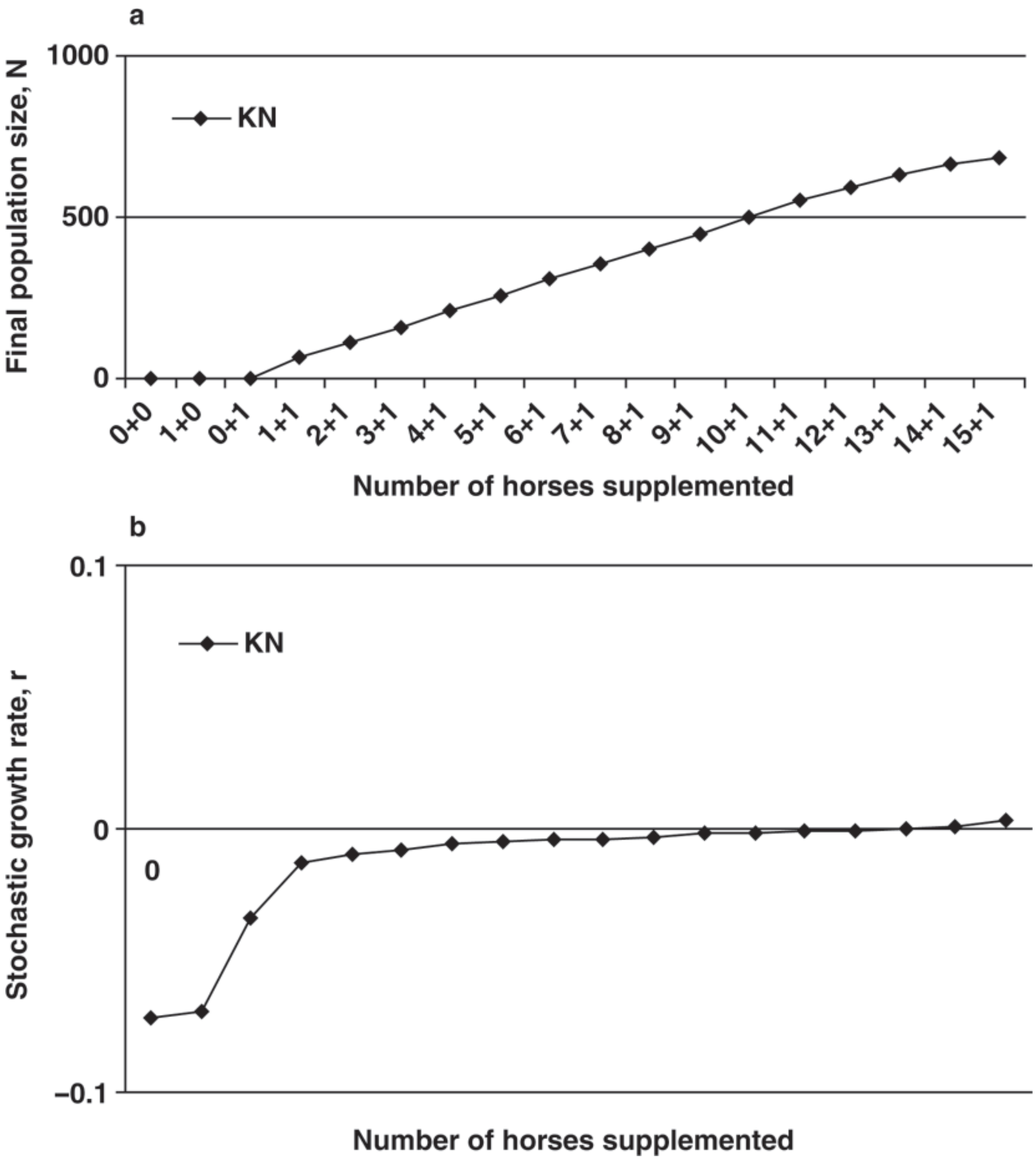

Figure 3. Mean final population size (a) and stochastic growth rate (b) of Knabstrupper (KN) as a function of horses supplemented each year. The first number is mares and the second number is stallions (e.g., 3 + 1 = 3 mares and 1 stallion supplemented). The simulation was run for 200 yr using basic parameters.

ing supplementation and to investigate whether mares supplemented 20 yr ago still have an effect on the present population. In addition, because of the comprehensive data on domestic animals, often dating far back in time, these may be useful in testing the predictability of PVA in general.

In conclusion, the most important parameters for the viability of all 3 breeds are parameters concerning reproductivity of the mares. The small percentages of mares in the breeding pools of KN and FR are detrimental and must be doubled to sustain the present population size. The number of mares breeding in JU should not be reduced. The KN breed association intends to close the studbook. If increasing the number of mares in the breeding pool does not counteract this, the breed will probably become extinct. It is recommended that the breeds be monitored in the future and be examined to find whether an increase in the percentage of mares breeding would have the expected positive effect. Population viability analysis has been criticized for its huge data requirements (Boyce, 1992; Beissinger and Westphal, 1998; Ludwig, 1999), which are not available for many species. This analysis has shown that PVA can be extremely useful in managing domestic breeds, both because of the comprehensive data available for most domestic breeds and because it is possible to monitor the results of management strategies very closely. Using an adaptive management approach by monitoring the horse breeds and continuing to study the viability of the horses might answer questions about the effectiveness of recovery plans (Beissinger and Westphal, 1998; Ludwig and Walters, 2002). Finally, the sensitivity analyses seem to be the only way to disclose cryptic interactions among parameters. Therefore, we encourage the use of

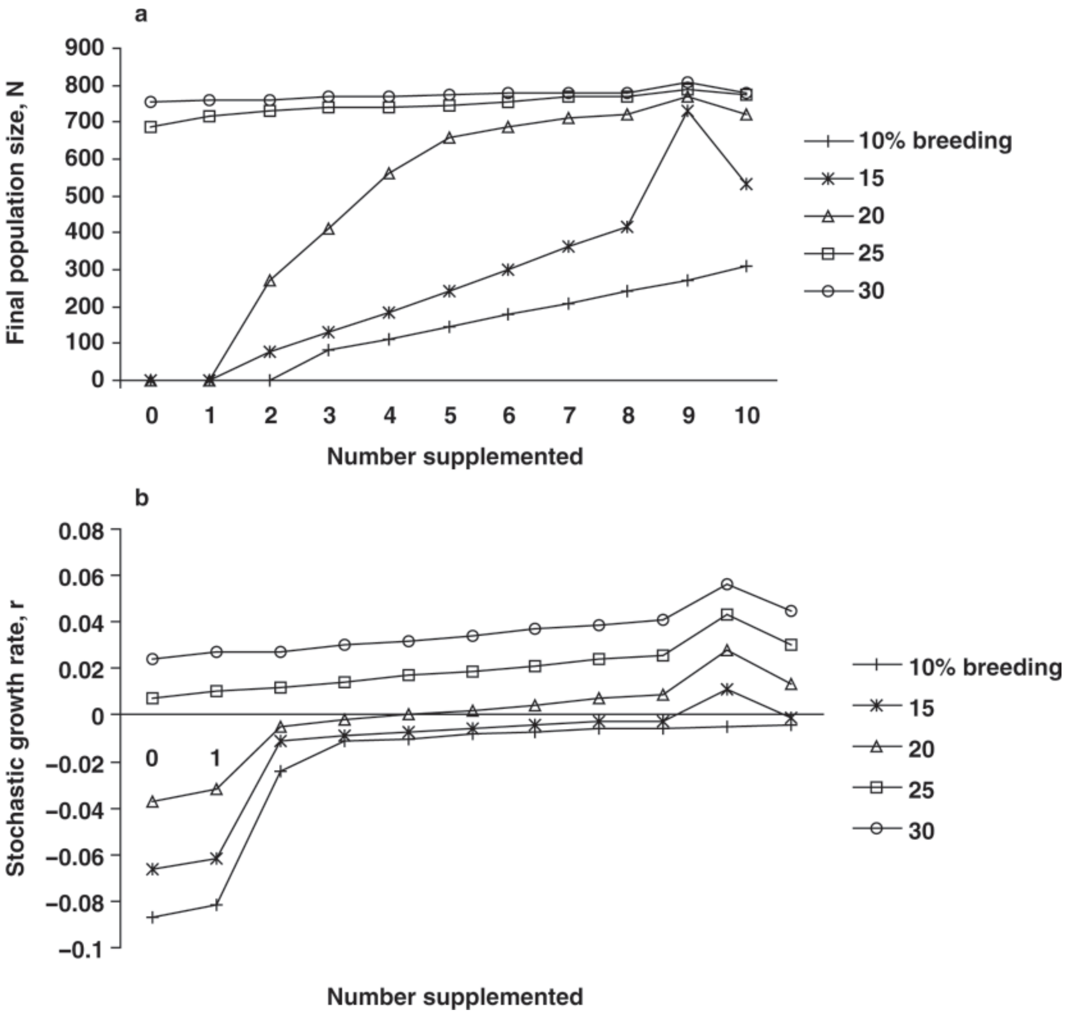

Figure 4. Mean final population size (a) and stochastic growth rate (b) of Knabstrupper (KN) as a function of number of mares supplemented each year and percentage of mares breeding. The simulations were run for 200 yr using basic parameters.

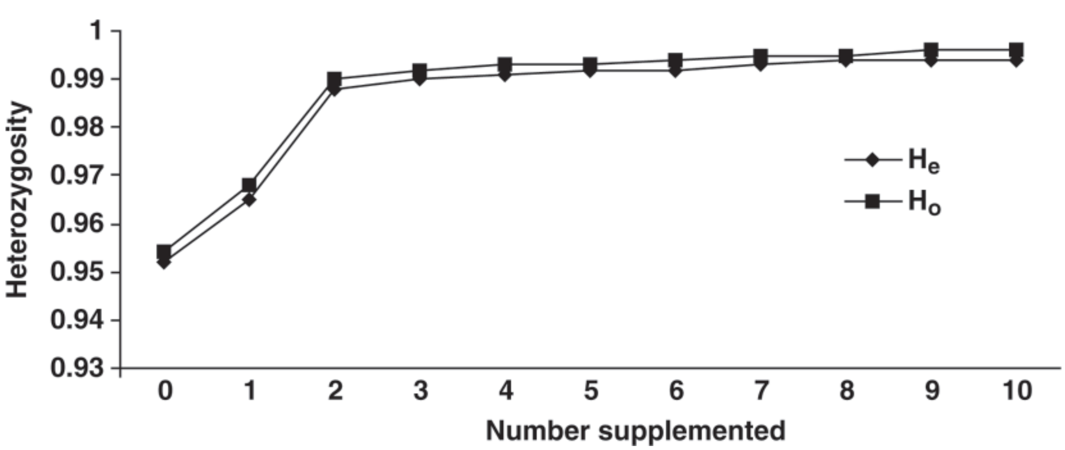

Figure 5. Expected (H_e) and observed (H_o) heterozygosity for Knabstrupper (KN) as a function of number of mares supplemented each year. Percentage of mares breeding was set to 25%; otherwise, basic parameters were used. The simulation was run for 200 yr.

this type of stochastic methodology, for other domestic breeds and wildlife species, when appropriate data are available.

LITERATURE CITED

Armbruster, P., F. Prithiviraj, and R. Lande. 1999. Time frames for population viability analysis of species with long generations: An example with Asian elephants. Anim. Conserv. 2:69–73.

Baker, J. R., and C. E. Ellis. 1981. A survey of post mortem findings in 480 horses from 1958 to 1980: (1) Causes of death. Equine Vet. J. 13:43–46.

Beissinger, S. R., and M. I. Westphal. 1998. On the use of demographic models of population viability in endangered species management. J. Wildl. Manage. 62:821–841.

Boakes, E. H., J. Wang, and W. Amos. 2007. An investigation of inbreeding depression and purging in captive pedigreed populations. J. Hered. 98:172–182.

Boyce, M. S. 1992. Population viability analysis. Annu. Rev. Ecol. Syst. 23:481–506.

Brook, B. W., L. Lim, R. Harden, and R. Frankham. 1997. Does population viability analysis software predict the behaviour of real populations? A retrospective study on the Lord Howe Island wood hen *Tricholimnas sylvestris.* Conserv. Biol. 82:119–128.

Brook, B. W., J. J. O'Grady, A. P. Champman, M. A. Burgman, R. H. Akcakaya, and R. Frankham. 2000. Predictive accuracy of population viability analysis in conservation biology. Nature 404:385–387.

Brosnahan, M. M., and M. R. Paradis. 2003. Demographic and clinical characteristics of geriatric horses: 467 cases (1989–1999). J. Am. Vet. Med. Assoc. 223:93–98.

Bustamante, J. 1996. Population viability analysis of captive and released bearded vulture populations. Conserv. Biol. 10:822–831.

Cohen, N. D. 1994. Causes of and farm management factors associated with disease and death in foals. J. Am. Vet. Med. Assoc. 204:1644–1651.

Crnokrak, P., and D. A. Roff. 1999. Inbreeding depression in the wild. J. Hered. 83:260–270.

Curik, I., P. Zechner, J. Sölkner, R. Achmann, I. Bodo, P. Dovc, T. Kavar, E. Marti, and G. Brem. 2003. Inbreeding, microsatellite heterozygosity, and morphological traits in Lipizzan horses. J. Hered. 94:125–132.

Giles, R. C., J. M. Donahue, C. B. Hong, P. A. Tuttle, M. B. Petritesmurphy, K. B. Poonacha, A. W. Roberts, R. R. Tramontin, B. Smith, and T. W. Swerczek. 1993. Causes of abortion, stillbirth, and prenatal death in horses—3,526 cases (1986–1991). J. Am. Vet. Med. Assoc. 203:1170–1175.

Gilligan, D. M., L. M. Woodworth, M. E. Montgomery, D. A. Briscoe, and R. Frankham. 1997. Is mutation accumulation a threat to survival of endangered populations. Conserv. Biol. 11:1235–1241.

Gilpin, M. E., and M. E. Soulé. 1986. Minimum viable populations: Processes of species extinction. Pages 19–34 in Conservation Biology: The Science of Scarcity and Diversity. Sinauer Associates, Sunderland, MA.

Hammond, J. 1960. Farm Animals: Their Breeding, Growth and Inheritance. Edward Arnold, London, UK.

Hedegaard, E. 2003. Jyder—Heste og Folk. Den Jydske Hests Historie, Arkona, Denmark.

Hedrick, P., and S. T. Kalinowski. 2000. Inbreeding depression in conservation biology. Annu. Rev. Ecol. Syst. 31:139–162.

Jørgensen, S. E. 1988. Fundamentals of Ecological Modelling. Elsevier Science Publishers BV, Amsterdam, the Netherlands.

Kristensen, T. N., and A. C. Sørensen. 2005. Inbreeding—Lessons from animal breeding, evolutionary biology and conservation genetics. Anim. Sci. 80:121–133.

Lacy, R. C. 1993. Vortex: A computer simulation model for population viability analysis. Wildl. Res. 20:45–65.

Lande, R. 2002. Incorporating stochasticity in population viability analysis. Pages 18–40 in Population Viability Analysis. S. R. Beissinger and D. R. McCullough, ed. The University of Chicago Press, Chicago, IL.

Leblond, A., I. Villard, E. Leblond, P. Sabatier, and A. J. Sasco. 2000. A retrospective evaluation of the cause of death of 448 insured French horses in 1995. Vet. Res. Commun. 24:85–102.

Lindenmayer, D. B., M. A. Burgman, H. R. Akçakaya, R. C. Lacy, and H. P. Possingham. 1995. A review of the generic computer programs ALEX, RAMAS/space and VORTEX for modelling the viability of wildlife metapopulations. Ecol. Modell. 82:161–174.

Linklater, W. L., E. Z. Cameron, E. O. Minot, and K. J. Stafford. 2004. Feral horse demography and population growth in the Kaimanawa Ranges, New Zealand. Wildl. Res. 31:119–128.

Ludwig, D. 1999. Is it meaningful to estimate a probability of extinction? Ecology 80:298–310.

Ludwig, D., and C. J. Walters. 2002. Fitting adaptive management into viability analysis into adaptive management. Pages 511–520 in Population Viability Analysis. S. R. Beissinger, and D. R. McCullough, ed. The University of Chicago Press, Chicago, IL.

Lunn, N. 1966. Mere om Knabstrupperne. Hipol. Tidsskr. 8:4–7.

Lunn, W. 1855. Nogle oplysninger om Knabstrupperstutteriet og dens afstamning. Tidsskr. Vet. :97–117.

Miller, P. S., and R. C. Lacy. 2005. VORTEX: A Stochastic Simulation of the Extinction Process. Version 9.50 User's Manual. Conservation Breeding Specialist Group, Sapple Valley, MN.

Mills, L. S., S. T. Hayes, C. Baldwin, M. J. Wisdom, J. Citta, D. J. Mattson, and K. Murphy. 1996. Factors leading to different viability predictions for a grizzly bear data set. Conserv. Biol. 10:863–873.

Paetkau, D., L. P. Waits, P. L. Clarkson, L. Craighead, E. Vyse, R. Ward, and C. Strobeck. 1998. Variation in genetic diversity across the range of North American brown bears. Conserv. Biol. 12:418–429.

Paradis, M. R. 2002. Demographics of health and disease in the geriatric horses. Vet. Clin. North Am. Equine Pract. 18:391–398.

Penn, A. M., W. B. Sherwin, G. Gordon, D. Lunney, A. Melzner, and R. C. Lacy. 2000. Demographic forecasting in koala conservation. Conserv. Biol. 14:629–638.

Ralls, K., J. D. Ballou, and A. Tempelton. 1988. Estimates of the lethal equivalents and the cost of inbreeding in mammals. Conserv. Biol. 2:185–193.

Reed, J. M., L. S. Mills, J. R. Dunning, E. S. Menges, R. McKelvey, S. R. Frye, M. C. Beissinger, Anstett, and P. Miller. 2002. Emerging issues in population viability analysis. Conserv. Biol. 16:7–19.

Rossdale, P. D., and R. V. Short. 1967. The time of foaling of thoroughbred mares. J. Reprod. Fertil. 13:341–343.

Slotta-Bachmayr, L., R. Beogel, P. Kaczensky, C. Stauffer, and C. Walzer. 2004. Use of population viability analysis to identify management priorities and success in reintroducing Prezwalski's horses to Southwest Mongolia. J. Wildl. Manage. 68:790–798.

Song, Y. L. 1996. Population viability analysis for two isolated populations of Haianan Eld's deer. Conserv. Biol. 10:1467–1472.

Trock, C. 1986. Heste og ponyavl. Skarv naturforlag, Copenhagen, Denmark.