Inbreeding and outbreeding in African rhinoceros species

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Abstract

Effective breeding strategies in ex situ conservation require an optimal balance between inbreeding and outbreeding, as both can lead to a decrease in population fitness. Thus optimizing breeding strategies to maintain genetic diversity entails a profound knowledge of the actual situation (including conservation units). This study examines the consequences of inbreeding and outbreeding in captive populations of two threatened species, the white and the black rhinoceros (*Ceratotherium simum* and *Diceros bicornis*), based on data from recent studbooks (2004). We also assessed the conservation units of the black rhinoceros, whose classification into subspecies remains a matter of discussion. Theory predicts that juvenile mortality increases with increasing degree of inbreeding. We calculated inbreeding coefficients and examined possible correlations with juvenile mortality rates. To assess the conservation units of the black rhinoceros, we compared juvenile mortality rates of outbred animals with those of non-outbred animals and additionally performed a geographical distance analysis. With both approaches we aimed to draw breeding borderlines between putative conservation units to preserve genetic diversity. Our assessment of the current inbreeding situation based on records in international studbooks was severely limited by small sample sizes in both the white and the black rhinoceros. For the same reason we could not evaluate the conservation units in the black rhinoceros. Nonetheless, we conclude that inbreeding and outbreeding must be followed closely in both species, as their consequences can be severe.

Additional key words: *Ceratotherium simum*, *Diceros bicornis*, distance analysis, evolutionary significant units, juvenile mortality, conservation units, studbook

Résumé

Les stratégies efficaces de reproduction ex situ exigent un équilibre optimal entre les croisements consanguins (inbreeding) ou non (outbreeding), étant donné que chacun peut entraîner une dégradation de la santé de la population. L'optimisation des stratégies de croisement, pour maintenir la diversité génétique, suppose une connaissance approfondie de la situation exacte des croisements (y compris les unités de conservation). Cette étude recherche les conséquences de l'inbreeding et de l'outbreeding dans les populations captives de deux espèces menacées, les rhinocéros blancs et les noirs (*Ceratotherium simum* et *Diceros bicornis*), basées sur les données reprises dans les livres d'origine (2004). Nous avons aussi évalué les unités de conservation des rhinocéros noirs dont la classification en sous-espèces reste matière à discussion. La théorie prédit que la mortalité juvénile augmente avec le taux d'inbreeding. Nous avons donc calculé les coefficients d'inbreeding et examiné les corrélations possibles avec le taux de mortalité juvénile. Pour évaluer les unités de conservation des rhinos noirs, nous avons comparé le taux de mortalité juvénile des animaux résultant de croisements non consanguins avec celui d'animaux consanguins et nous avons aussi réalisé une analyse de la distance géographique. Par ces deux approches, nous avons voulu tracer les limites des croisements entre des unités de conservation putatives, pour préserver la diversité génétique. Notre évaluation de la situation de l'inbreeding actuel, basée sur des rapports des livres d'origine internationaux, a été gravement limitée étant donné la très petite taille des échantillons, aussi bien chez les rhinos blancs que chez les noirs. C'est pour cette raison aussi que nous n'avons pas pu évaluer les unités de conservation des rhinocéros noirs. Néanmoins, nous concluons qu'il faut suivre de près l'inbreeding et l'outbreeding chez les deux espèces car leurs conséquences peuvent être très sérieuses.

Introduction

The conservation of threatened and endangered species is an important task as many of these species will not survive without appropriate protection and management strategies. Both African rhinoceros species are threatened: the black rhinoceros (*Diceros bicornis*) is classified as *Critically Endangered* in the IUCN 2004 *Red List of Threatened Species*, the southern white rhinoceros (*Ceratotherium simum simum)* is classified as *Near-Threatened,* and the northern white rhinoceros (*Ceratotherium simum cottoni*) as *Critically Endangered* (Baillie et al. 2004).

Species conservation can take place either in their natural habitats (in situ conservation) or in captivity (ex situ conservation) (Convention on Biological Diversity 1992). Since in situ and ex situ conservation do not exclude one another, both approaches are used today to attempt to assure the future existence of many threatened or endangered species. Both African rhinoceros species are bred in captivity in zoos worldwide and their global breeding is coordinated by Dr med. vet. Andreas Ochs, with the help of international studbooks kept for both species (Ochs 2005a, 2005b).

In captive breeding, it is essential to closely monitor and coordinate mating to maintain a viable captive population for the long term (World Zoo and Aquarium Association 2005). Uncoordinated breeding may lead to inbreeding (among relatives) (Hartl 2000) or outbreeding (between genetically distant individuals) (Lynch 1997). Any can have negative effects, termed inbreeding and outbreeding depression (Lynch 1997), on the survival and reproduction of animals in the wild. Outbreeding might happen in the wild due to human-made corridors, as well as in captivity (Wright 1977; Lasley 1978). In inbreeding, the negative effects appear because deleterious recessive alleles become homozygous (Falconer 1989; Lynch 1997). Causes for the negative effects of outbreeding are more complex. One reason is the breakdown of biochemical or physiological compatibility between the genes in gene complexes of a population due to incompatible genes from another population being incorporated. Another cause is the displacement of the genes adapted to the environment of a population

through an overwhelming immigration of genes from another population not adapted to this environment, leading to a hybrid genotype with reduced fitness in any environment (Lynch 1997).

The aim of any breeding guideline is to avoid inbreeding and outbreeding, and thus to evade their possible effects. One way to avoid outbreeding effects is to have well-founded knowledge of the existing subgroups or subspecies within a species, since outbreeding can occur by breeding between individuals belonging to distant subgroups or subpopulations because they usually are genetically distant animals.

It is not difficult to avoid outbreeding in the white rhinoceros since its two subspecies—the southern white rhinoceros, *C.s. simum,* and the northern white rhinoceros, *C.s. cottoni*—are known and accepted. Separated breeding of these subspecies should continue to maintain the genetic variability for each subspecies separately. The situation in the black rhinoceros is more complicated because there is considerable disagreement concerning the number and status of subspecies. Depending on the author, there are between 4 and 16 black rhinoceros subspecies (fig. 1) (Zukowsky 1964; Groves 1967, 1983, 1993; Du Toit 1987; Du Toit et al. 1987; Fouraker and Wagener 1996; Rookmaker 1998; Emslie et al. 1999). In captive breeding, only the two subspecies *Diceros bicornis minor* and *Diceros bicornis michaeli* (based on the subgroups of Du Toit et al. 1987) are currently considered. To avoid the negative effects of outbreeding and to maintain the genetic diversity in the black rhinoceros, it is essential to assess the subgroups or subspecies that should be preserved. These subgroups or subspecies are also called conservation units or evolutionary significant units, since taxonomic subspecies are not always the smallest entities that should be preserved (Ryder 1986).

The aims of this study are to present current information on international captive breeding in both African rhinoceros species, and to give pragmatic information on the conservation units of the black rhinoceros, which could then be used to conserve the species. To achieve this, we analysed inbreeding coefficients and juvenile mortality (mortality in the first two months) based on studbook data on the two African rhinoceros species. To assess the conservation
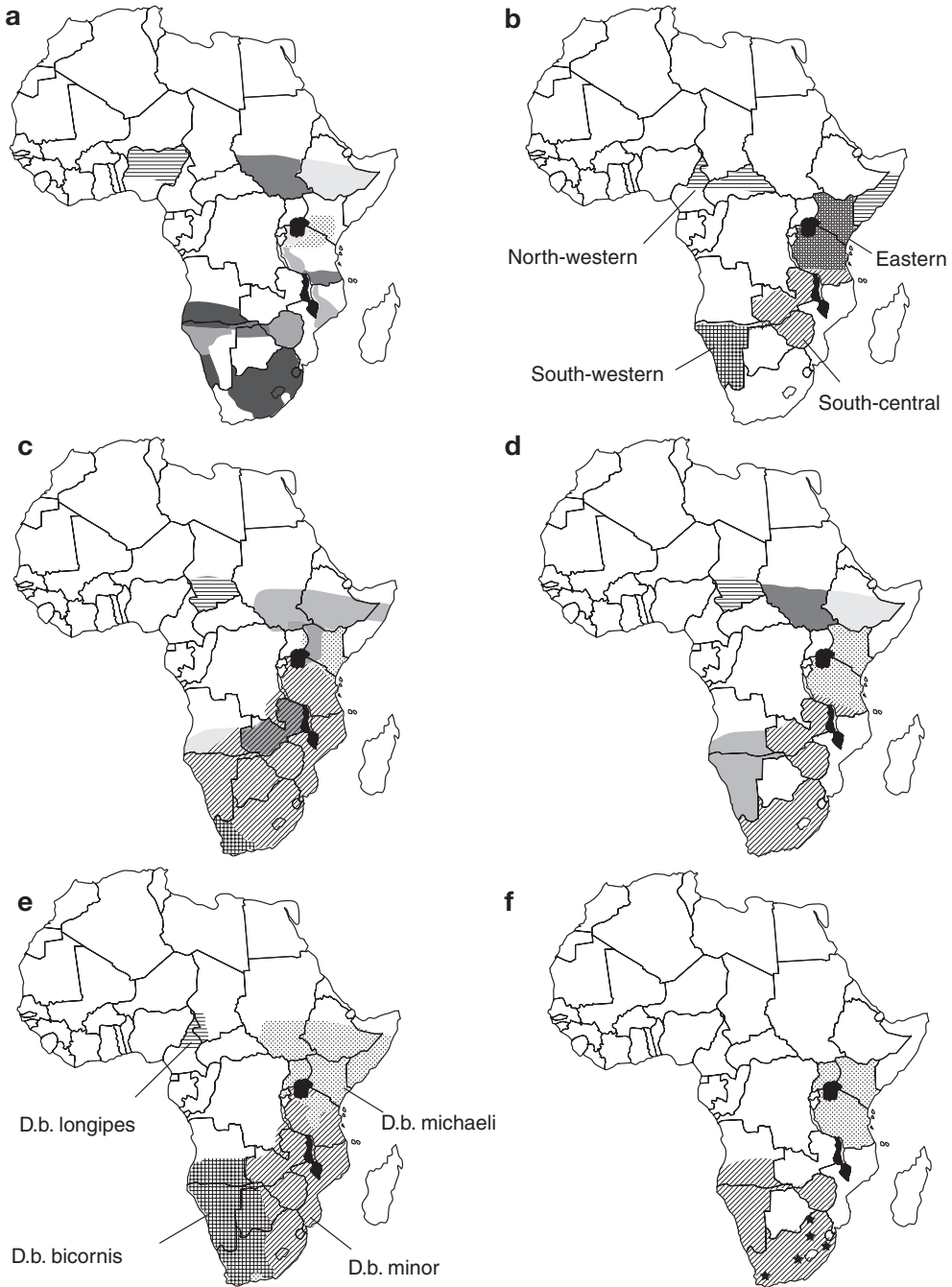
Figure 1. Subspecies of the black rhinoceros (number of different subspecies in parenthesis) according to *a*) Zukowsky 1964 (16), *b*) Du Toit et al. 1987 (4), *c*) Groves 1993 (9), *d*) Rookmaker 1998 (6), *e*) Emslie et al. 1999 (4), and f) International studbook (Ochs 2005b) (2). Each grey tone and each pattern represents a different subspecies; the four most consistent are *D.b. michaeli* = dotted pattern, *D.b. minor* = diagonally striped, *D.b. longipes* = horizontally striped, *D.b. bicornis* = gridlike pattern. In *b* the authors defined sub-groups, which seem to coincide with the subspecies. Therefore the patterns in this figure are similar, but not identical. The stars in southern Africa in *f* represent artificially introduced populations of *D.b. michaeli.* Distributions shown are based on written descriptions and are not precise.

units of the black rhinoceros we reviewed the existing literature, analysed outbreeding between putative subspecies and performed a geographical distance analysis. Since both species have been bred in captivity for over 150 years, we expected inbreeding in both species and consequently also an increase in juvenile mortality with increasing inbreeding coefficient (Wright 1977; Lasley 1978). In the black rhinoceros subspecies we expected to find outbred animals, or hybrids between the putative subspecies, with a higher juvenile mortality than non-outbred animals.

Material and methods

Our study was based on the 10th editions of the *International studbook for the African white rhinoceros* and the *International studbook for the African black rhinoceros* (Ochs 2005a, 2005b). For both studbooks, only entries before the official deadline, 31 December 2004, were considered. These datasets gave a total sample size of 1494 individuals for the white rhinoceros and 919 individuals for the black rhinoceros. Both studbooks are divided into two subspecies. The studbook of the white rhinoceros consists of 1466 *C.s. simum* and 28 *C.s. cottoni* individuals. The studbook for the black rhinoceros contains 162 *D.b. minor* and 757 *D.b. michaeli* individuals.

As a first step, an electronic dataset was created for each studbook, which was then controlled and corrected for errors; this was often accomplished with the support of curators in the different zoos. The datasets were then analysed with the computer program Studbook v3.9 (Zschokke 2005). This program calculates inbreeding coefficients using the Additive Relationship Method (Ballou 2003).

The inbreeding coefficient in a studbook pedigree is the probability that the two alleles at homologous loci are identical as descendants from a known common ancestor of the parents (Wright 1922, 1969; Jacquard 1975). Founder animals are defined as wild-born animals not known to be related to any other individuals of the population, except their own offspring (Lacy 1989).

For the definition of conservation units in the black rhinoceros, the relevant literature on the subject was compiled (Zukowsky 1964; Groves 1967, 1983, 1993; Du Toit et al. 1987; Du Toit 1987; Emslie et al. 1999; Fouraker and Wagener 1996; Rookmaker 1998). Out of these hypotheses we selected five that to us seemed the most useful and testworthy because

they showed the most coincident distribution of the putative subspecies or subgroups (Groves 1967, 1993; Du Toit et al. 1987; Emslie et al. 1999; Rookmaker 1998). For each of the tested subspeciation theories, we assigned all founder animals to a possible subspecies or subgroup according to its capture location.

Based on this information, each zoo-born individual was then assigned to one or more subspecies according to the amount of corresponding founder genes it carried. Inbreeding coefficients and juvenile mortality (mortality in the first two months) of zoo-born animals were computed for each population. We analysed the relationship between inbreeding coefficients and juvenile mortality (as binary variable: survived or died) with a logistic regression for each species. Further, we controlled for effects other than inbreeding coefficients that are known to influence juvenile mortality in other species with a multifactorial logistic regression model. These factors were 1) parity (first offspring of a dam against all other offspring of same dam), 2) mean zoo generation (average of the number of zoo generations of both its parents plus one) and 3) age of dam.

To define possible breeding borderlines between the putative subspecies of the black rhinoceros we used a correlation analysis (χ^2-test) to test whether outbred animals (descending from parental individuals belonging to different putative subspecies) had a significantly higher juvenile mortality than non-outbred animals (descending from parents belonging to one putative subspecies), that is, whether they were affected by outbreeding depression.

Geographic distance can lead to genetic distance when populations are isolated from each other and, for example, when genetic drift or local adaptation occurs. Therefore, geographical distance should be considered when assessing conservation units. We consequently compiled the coordinates of the capture locations of the founder animals obtained from the studbooks. Using vector geometry, we assigned a distance vector to each zoo-born animal, equivalent to the geographical distance between the origins of the parental animals. The relationship between juvenile mortality (binary variable) and distance vectors was analysed with a logistic regression model. We expected juvenile mortality to increase with the geographical distance between the origins of the parental individuals.

Results

White rhinoceros (Ceratotherium simum)

Of the 1494 animals listed in the studbook, 752 (50.3%) were zoo-born. Out of these 752 only 16 (2.1%) animals were inbred, with inbreeding coefficients ranging from 0.125 to 0.25. All 16 inbred individuals belonged to the subspecies *C.s. simum*. Similarly, the vast majority (746) of the zoo-born animals belonged to *C.s. simum*, whereas only 6 (0.8%) were listed as *C.s. cottoni*, and one of these 6 was actually a hybrid between the two subspecies.

The average juvenile mortality rate of non-inbred white rhinoceros individuals was 14.7%, whereas the average juvenile mortality rate of inbred individuals was 18.7%. We found no significant effect of inbreeding on juvenile mortality (logistic regression: χ^2 = 0.29, $P = 0.58$). Keeping the same juvenile mortality rate of the inbred animals, it would need at least 640 inbred zoo-born animals to find a significant effect of inbreeding on juvenile mortality. If the total number of inbred zoo-born animals is kept constant, the juvenile mortality rate would need to be as high as 37.5% to detect a significant effect of inbreeding on juvenile mortality. Furthermore, we did not find any effect of the other variables examined (parity, mean zoo generation, age of dam) on juvenile mortality in the white rhinoceros.

Black rhinoceros (Diceros bicornis)

Of the 919 listed animals in the studbook, 512 (55.7%) individuals were born in captivity. Out of these only 30 (5.9%) were inbred animals, with inbreeding coefficients ranging from 0.0156 to 0.25.

The average juvenile mortality rate of non-inbred black rhinoceros individuals was 20.3%, whereas the average mortality rate of inbred individuals was 26.7%. We found no significant effect of inbreeding on juvenile mortality (logistic regression: $\chi^2 = 0.56$, $P = 0.45$). At constant juvenile mortality rate of inbred animals, the total number of inbred zoo-born individuals would have to be at least 300 to find a significant effect of inbreeding on juvenile mortality. Keeping the total number of inbred individuals equal, it would require a juvenile mortality rate as high as 36.7%.

Moreover, we could not find any significant influence of the other tested factors (parity, mean zoo generation, age of dam) on juvenile mortality.

Conservation units of the black rhinoceros

In all theories examined concerning subspecies or subgroups in the black rhinoceros, we found no significant increase in juvenile mortality in any of the possible hybrids compared with their parental subspecies. In consequence, no assessment of conservation units based on juvenile mortality of the hybrid offspring was possible.

As an illustrative example we present the results for the IUCN subspeciation theory (Emslie et al. 1999).

Most founders of the zoo population could be assigned to one of the three possible subspecies, as the fourth one proposed by Emslie et al. (1999) is not present in the studbook population. The three subspecies to which founders could be assigned to were *D.b. minor* (48 animals from south-eastern Africa—eastern South Africa to southern Tanzania), *D.b. michaeli* (132 animals from eastern Africa—Kenya, northern Tanzania, Uganda) and *D.b. bicornis* (3 animals from south-western Africa—western South Africa to Angola). A further 9 founders were assigned to a fourth group, called *D.b. michaeli/minor* because it was uncertain whether they belong to *D.b. minor* or *D.b. michaeli*. Table 1 shows the assignment of the zoo-born animals to the different groups and the juvenile mortality rate for each subgroup.

Comparing juvenile mortality, we did not find any significant differences between these groups (all $\chi^2 < 0.02$, df = 1, all $P > 0.9$). Thus no correlation between juvenile mortality and subspeciation could be proved for this subspeciation theory, or for the other theories tested.

Distance analysis

The logistic regression for the distance analysis of the black rhinoceros showed no correlation between geographical distance and juvenile mortality ($\chi^2 = 0.2$, df = 1, $P = 0.7$). Hence, we could not show outbreeding depression based on geographical distance.

Discussion

Due to the small number of inbred individuals in both African rhinoceros species, it was not possible to find a statistically significant relationship between inbreeding and juvenile mortality. Furthermore, we did not find a significant correlation between

Table 1. Offspring assignment according to the IUCN subspeciation theory

Subspecies, group	Number of individuals	Juvenile mortality rate (%)
D.b. michaeli	330	21.2
D.b. minor	71	19.7
D.b. bicornis	4	(0.0)
D.b. michaeli/minor	3	(0.0)
Hybrid *D.b. michaeli* x *D.b. minor*	71	23.6
Hybrid *D.b. michaeli* x *D.b. michaeli/minor*	24	20.8
Hybrid *D.b. minor* x *D.b. bicornis*	1	(0.0)
Hybrid *D.b. minor* x *D.b. michaeli* x *D.b. michaeli/minor*	8	(0.0)

The juvenile mortality rate (mortality in the first two months) in percentages is listed for each putative subspecies and for the observed hybrids the number of zoo-born individuals. Numbers in parenthesis are unreliable due to low sample size. Source: Emslie et al. 1999

are being introduced into zoo populations and used for breeding today (over the last five years more than 40 white rhinoceros and 4 black rhinoceros were introduced to the captive population from the wild).

This introduction of new genetic material prevents captive populations from inbreeding and therefore reduces the risk of inbreeding depression. However, coordinated breeding, and not primarily the introduction of wild-born animals, should

outbreeding and juvenile mortality in the black rhinoceros. Therefore, it was not feasible to assess the conservation units of this species. As the example of the IUCN subspeciation (Emslie et al. 1999) shows, the number of outbred animals in certain cases was as low as one (or even none, when considering other subspecies theories), which does not allow any statistical comparisons. We faced a similar sample size problem when analysing the influence of geographical distance between the parental origins on the juvenile mortality of the offspring.

Even though we could not statistically support the existence of inbreeding or outbreeding depression in the two African rhinoceros species, it cannot be concluded that they do not exist. Such a proof would require a larger number of inbred (at least 640 for the white rhinoceros and 300 for the black rhinoceros) and outbred animals. Of course, obtaining a large number of inbred or outbred individuals is not, and should never be, a goal of any breeding programme, since both inbreeding and outbreeding depression are known from many species to lead to a decrease in fitness (Wright 1977; Lasley 1978; Zschokke and Krummenacher, in preparation), which in populations with finite size can be fatal (Keller and Waller 2002).

The small number of inbred and outbred animals in the captive populations of white and black rhinoceros seems to reflect good breeding coordination with regard to avoiding inbreeding and outbreeding, and thus their respective effects. However, in the African rhinoceros species, especially in the white rhinoceros, this is probably not the only reason for low numbers of inbred animals; wild-born animals

be the principal strategy to avoid inbreeding and outbreeding and their effects (Frankham et al. 2002; World Zoo and Aquarium Association 2005). Captive breeding for conservation should be propagated as such and should not rely on the constant import of new wild-born animals. We are certainly aware of the difficulties complicating the breeding of African rhinoceros in captivity (Roth 2006), which makes implementing this policy difficult. However, recent research and developments in the field will hopefully improve this situation (Roth 2006), leading to higher breeding success and fewer introductions from the wild to the zoo population.

Moreover, it is important that inbreeding and outbreeding situations, and in particular the subspeciation of the black rhinoceros, are followed closely in the future. Inbreeding can act swiftly (Keller and Waller 2002), and the degree to which a species reacts to inbreeding varies among species (Zschokke and Krummenacher, in preparation). In this study we also found this reaction to inbreeding to be relatively weak for the African rhinoceros in comparison with that of other mammals and about as strong as could be expected considering their body mass. Furthermore, the genetic diversity present in the different subspecies or subgroups of the black rhinoceros must be preserved as the conservation of genetic resources is a main goal in conservation biology (Convention on Biological Diversity 1992). However, at the moment when outbreeding depression becomes detectable, the gene pools of the subspecies or subgroups of the black rhinoceros may already be blended and thus the valuable genetic diversity of the subspecies intermixed.

Conclusion

Therefore, we conclude with an appeal to the breeding coordinators and studbook participants to continue closely monitoring the development of inbreeding and outbreeding in African rhinoceros species, and if necessary to react on it with adequate changes in the breeding strategy. Moreover, we strongly agree with the demand for developing an international breeding strategy specific for each species (Foose and Wiese 2006), which should be followed by all institutions keeping African rhinos. Additionally, we endorse further molecular research as carried out recently by Harley et al. (2005), so that more precise genetic information on subspeciation will be revealed, as this is critically important to avoid outbreeding between subspecies.

Acknowledgements

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