

Short communication

Parity as a major factor affecting infant mortality of highly endangered Indian rhinoceros: Evidence from zoos and Dudhwa National Park, India

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ABSTRACT

The Indian rhinoceros (Rhinoceros unicornis) is a highly endangered species that inhabits only three political states. Recently, Zschokke and Baur [Zschokke, S., Baur, B., 2002. Inbreeding, outbreeding, infant growth, and size dimorphism in captive Indian rhinoceros (Rhinoceros unicornis). Canadian Journal of Zoology 80, 2014-2023] found that the offspring of matings between captive Indian rhinoceros individuals from the Kaziranga and Chitwan populations had high mortality rates. These authors suggested that these two populations are partially genetically incompatible and, thus, they proposed that these would be separated into two subspecies. In this study we compiled data from a captive population with data from Dudhwa National Park (India), where rhinoceroses were successfully reintroduced in 1984. In Dudhwa, the breeding male came from the Kaziranga population and four out of the five breeding females came from the Chitwan population. In spite of these different origins, the Dudhwa population has bred very well. We analyzed, the factors influencing infant mortality of 22 Dudhwa and 181 captive calves. Outbreeding (matings between animals from Kaziranga and Chitwan) did not play any role in infant mortality. From our data, we can conclude that parity, not outbreeding, is responsible for infant mortality in the Indian rhinoceros. Thus, we are unable to agree with Zschokke and Baur's suggestion that the Chitwan and Kaziranga populations belong to separate subspecies. Rather, we propose that the hybridization of captive animals from Chitwan and Kaziranga, as well as those in the wild, should help save the genetic diversity of this highly endangered species.

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1. Introduction

The Indian rhinoceros (Rhinoceros unicornis L., 1758) is an endangered species according to the World Conservation Union (IUCN) red data list of threatened species (Baillie et al., 2004). No more than 2400 rhinoceroses live in India, Nepal and Bhutan (Dinerstein, 2003; Hlavacek et al., 2005). There are around 146 captive animals, which came from only two wildlife reserves (Hlavacek et al., 2005). The first reserve is the Kaziranga National Park, Assam (India) and the second one is The Royal Park of Chitwan Valley (Nepal; Zschokke et al., 1998; Hlavacek et al., 2005).

Recently, Zschokke and Baur (2002) analyzed the infant mortality rates of a captive rhinoceros population. They found higher infant mortality rates in the outbred individuals (i.e., the offspring of matings between individuals from the Kaziranga and the Chitwan populations) than in the non-outbred ones (i.e., the offspring of matings between individuals from the Kaziranga population), suggesting that the two populations are partially genetically incompatible. They suggested that "the two populations of the Indian rhinoceros may be genetically differentiated. Until more is known about the genetic relationship between the two populations, it would therefore be advisable to discontinue matings between individuals from the two populations and to encourage matings among individuals from the Chitwan population." If this suggestion is accepted it will considerably alter the captive breeding strategy of Indian rhinoceros and the general conservation of the species as documented in case of European bison (Bison bonasus; Olech and Perzanowski, 2002). Nevertheless, the discussion has not considered relatively recent population in Dudhwa. The reintroduction of Dudhwa population began in 1984 when two males and three females were imported from Pabitora Wildlife Sanctuary in Assam (Kaziranga origin). Two of the females died during the translocation or shortly after it. Four more females were imported in 1985 from Chitwan National Park in Nepal (Sale and Singh, 1987). One bull died in 1988 (Sinha and Sawarkar, 1991). The first calf was born in 1989. Since that time the population has grown to 21 individuals in 2004 (Sinha et al., 2004). Thus, the Dudhwa population represents a unique, free-living population composed of outbred animals (as defined by Zschokke and Baur (2002), i.e., the offspring of matings between individuals from the Kaziranga and the Chitwan populations). Moreover, the reintroduction in Dudhwa is a good example for other conservation effort with rhinoceroses (Santiapillai and Suprahman, 1986) and the study of this population is highly recommended (Linklater, 2003).

The captive Indian rhinoceros population is small, with limited reproductive potential (Hlavacek, 2003; Hlavacek et al., 2005). Dividing this population into two subspecies, as suggested by Zschokke and Baur (2002), would make it nearly impossible to avoid inbreeding problems within the next generations. Since this is very important for the long-term viability of the rhinoceros, the aim of the present study was to complete the data examined by Zschokke and Baur (2002) with recent progeny, data from Dudhwa and to reanalyze their conclusions.

2. Materials and methods

2.1. Animals

One author (S.P.S.) collected data on births/abortions in rhinoceroses from Dudhwa National Park. The data from the captive population were summarized in the international studbook (Hlavacek, 2003). For comparative analyzes, infant mortality was only considered over the first six months of life. Any stillbirths and individuals that died before they were six months old were considered to be infant deaths. All abortions (gestation < 400 days) were excluded from the analysis.

We only analyzed infant mortality, since the difference between the outbred and non-outbred animals was based on variation of infant mortality within and between rhinoceros population (Zschokke and Baur, 2002). We used the same classification of inbreeding and outbreeding as that of Zschokke and Baur (2002). Thus, the founders and offspring of the founders of the captive and Dudhwa population were labelled as "non-inbred". All of the other animals were regarded as "inbred". The origin (i.e. from Assam or Nepal) of the male labelled n. 157, according to the studbook in the Patna Zoo, was not specified. Thus, we excluded the data from his three offspring from our analysis. We differentiated the captive mothers according their origin (i.e. if they were born in the wild or the zoo). There were 30 zoos for 181 of the calves, therefore, the factor zoo could not be tested since would make the convergence of the model (see below) questionable.

2.2. Statistics

We analyzed the data using the SAS System V 9.1 (SAS Institute Inc., Cary, North Carolina). To assess the impact of outbreeding on infant mortality, we applied an analysis of categorical repeated measurements, based on the generalized estimating equation approach (Liang and Zeger, 1986) using the GENMOD procedure (SAS Institute Inc.). The GENMOD procedure was designed to model the probability of death of an infant. To account for the repeated measures on the same individuals across the observation period, the analysis was performed with the individual's mother and father as a "Subject" in the REPEATED statement. The explanatory variables were: outbreeding (yes or no), inbreeding (yes or no), captivity (Dudhwa or Zoo), sex (male, female, or unknown), mother's origin (wild or captive; referred as "Zoo generation" in Zschokke and Baur, 2002), mother's parity (primiparous or multiparous), mother's age, and father's age. All of the explanatory variables and interaction terms were tested, but were not reported unless they were statistically significant (P < 0.05).

3. Results

The numbers of rhinoceros born during the period of time from the beginning of 1989 to June 2004 in Dudhwa and from the beginning of 1956 to December 2002 in captivity included in analysis are given in Table 1. In Dudhwa, we recorded the first successful reproduction of the second generation of outbred animals (of both Kaziranga and Chitwan origin) in the world.

Table 1 – Summary of the data on the sample size								
Location	Number of outbred ^a calves	Number of died outbred calves	Number of mothers of outbred calves	Number of non-outbred ^b calves	Number of died non-outbred calves	Number of mothers of non-outbred calves		
Dudhwa	19	5	8	3	1	1		
Zoos	13	6	6	168	36	47		

Note that no calf of both parents originated from Chitwan has been born in Dudhwa or in captivity.

a Outbred calves = one parent originated from Chitwan and the other one from Kaziranga.

b Non-outbred calves = both parents originated from Kaziranga.

Predictor	Initial analysis containing all predictors (interactions terms were also tested, but are not shown here)			Final model containing only significant predictors		
	d.f.	χ^2	Р	d.f.	χ^2	Р
Mother's age	1	5.31	0.0212	1	4.49	0.0342
Mother's age (parity)	-	-	-	1	8.47	0.0036
Inbreeding	1	0.42	0.5188	-	-	-
Outbreeding	1	3.42	0.0645	-	-	-
Sex ^a	2	4.70	0.0954	-	-	-
Parity	1	8.27	0.0040	-	-	-
Father's age	1	2.32	0.1277	-	-	-
Mother's origin	1	2.31	0.1286	-	-	-
Captivity	1	1.51	0.2194	-	-	-

a Two degrees of freedom for sex class: male, female and sex unknown.

Table 3 – Summary of the effect of parity on Indian rhinoceros infant mortality								
Mother's parity	Dudhwa po	opulation	Zoos population					
	Number of calves born	Number of calves died	Number of calves born	Number of calves died				
Primiparous	9	4	53	17				
Multiparous	13	2	128	25				

The results of the initial model (with all of the factors) and the final logistic regression model are showed in Table 2. We found that the only factors that significantly explained infant mortality were the mother's age and parity (Table 3). Infant mortality increased with increasing age of the mother and this increase was much higher and steeper in primiparous mothers than in multiparous ones.

We also compared the infant mortality rates of the outbred calves in Dudhwa with that of the non-outbred calves in captivity. A Fisher exact test did not reveal any difference in these rates (P = 0.326).

4. Discussion

The results of this study do not support the conclusions of the previous report by Zschokke and Baur (2002). Our completed data set did not reveal any significant role of outbreeding in the rate of infant mortality in Indian rhinoceroses. The reason for the difference between the present and previous research results may lie in the statistics used by Zschokke and Baur. When examining the data analyzed by Zschokke and Baur,

(i.e., the records up to the end of 2001 without those from Dudhwa), we found that the outbred class contained only 10 animals. Of these, five were primiparous and five were multiparous. Only one of the five primiparous animals survived, while four of the five multiparous animals survived. In our analysis, while captive outbred primiparous mothers reared only one out of six calves, the same mothers, when multiparous, reared six out of seven calves. Fourteen (22%) out of 63 calves born to primiparous mothers were outbred, whereas 17 (12%) out of 140 calves born to multiparous mothers were outbred. Therefore parity, not outbreeding, was apparently responsible for the infant mortality seen in these Indian rhinoceroses. Thus, it would be necessary to test the interaction between outbreeding and parity in the Zschokke and Baur's model. Another possible flaw in the statistics used by Zschokke and Baur (2002) should be mentioned. In their data analysis, some of the parents occurred repeatedly. For example, up to December 2001 there were 38 mothers that had previously reproduced at least two times. All of these females that had produced at least three progeny were in the nonoutbred class. These repeated measurements on these

individuals were not considered in Zschokke and Baur's model. Thus, the use of these dependent repeated measurements as individual observations in their statistical model is an example of pseudoreplication (Hurlbert, 1984).

Similar to that previously reported (Baur and Studer, 1995; Zschokke et al., 1998; Zschokke and Baur, 2002), we found that the rate of infant mortality in Indian rhinoceroses is higher in primiparous mothers than in multiparous ones. Higher rates of infant mortality in primiparous mothers compared to that in multiparous ones has been reported for many ungulate species, including the feral horse (*Equus caballus*; Duncan, 1992; but see Monard et al., 1997), domestic cattle (*Bos taurus*; Nix et al., 1998; Johanson and Berger, 2003), and red deer (*Cervus elaphus*; Wass et al., 2003). In most cases this was due to lack of adequate maternal experience of primiparous females.

For conservation purposes we also identified another important factor. When comparing the infant mortality rates of the outbred free-living Dudhwa rhinoceroses with the nonoutbred captive rhinoceroses, we did not find any difference (Table 1). Mortality of wild Indian rhinoceros calves would mainly come as a result of poaching, predation by tigers (Panthera tigris), inter-male fighting, and male infanticide (Laurie, 1982; Laurie et al., 1983; Dinerstein et al., 1988; Dinerstein, 1991; Talukdar and Bora, 1998). According to records, most of these factors have been implicated in the mortality of Dudhwa rhinoceros calves (e.g., the strongest factor causing mortality of Dudhwa calves is tiger predation; Sinha et al., 2004). Alternatively, none of these factors could be responsible for infant mortality of the captive rhinoceroses. Captive rhinoceros calves are under human care, including veterinary care and hand-rearing. These factors could not be considered in the present as well as previous statistical analyzes. This further supports the vitality of the free-living population in Dudhwa. Zschokke and Baur (2002) stated that "in captivity, the Indian rhinoceros breeds fairly well". However, the total captive population of Indian rhinoceroses has not increased well: from 127 rhinoceros in 1991 to only 137 in 2001, including three imported animals from the wild during that period (Wirz-Hlavacek, 1997; Zschokke and Baur, 2002). Contrary to this, the wild populations of Indian rhinoceroses in Kaziranga, Chitwan, Bardia, as well as in Dudhwa, grow rather quickly (Dinerstein and McCracken, 1990; Dinerstein and Jnawali, 1991; Zschokke et al., 1998; Dinerstein, 2003; Sinha et al., 2004). Reproduction of wild rhinoceroses is apparently much better than that in captivity, despite the existence of additional factors causing mortality in the wild and absence of veterinary care (Conway and Goodman, 1989; Swaisgood et al., 2006).

Next, Zschokke and Baur (2002) stated that "of the seven outbred individuals that were alive in captivity on 31 December 2001, four were mature, but none of them had reproduced". On the other hand, in Dudhwa, the outbred rhinoceroses have reached the second generation (Sinha et al., 2004).

The captive population originated from 38 founders, who are genetically very unequally represented in the present captive population (Hlavacek, 2003). The four best represented founders, who have contributed half of all of the genes, have come from Kaziranga. Based on our analysis of the data from both the captive and Dudhwa populations, we are unable to support the proposal of Zschokke and Baur (2002) that Chitwan (Nepal) and the Kaziranga (Assam) populations form separate subspecies. Thus, in captivity, breeding of genetically underrepresented animals, without any regard to their origin, should be encouraged.

5. Conclusion

In conclusion, the purpose of our paper has not been to decry the work of Zschokke and Baur (2002), who have presented excellent results on gravidity, birth mass and infant growth of the endangered Indian rhinoceroses. Rather, our purpose was to address problems of methodology which have resulted in scientific findings which could cause errors in the management of an endangered species. Based on our reanalysis, we can make very important recommendations for managers of the highly endangered Indian rhinoceros. In addition to demonstrating that outbreeding is not problematic, our results suggest that females should be allowed to reproduce as early as possible, since infant mortality rates are higher in older mothers than in younger ones.

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