Interbirth intervals are associated with age of the mother, but not with infant mortality in Indian rhinoceroses

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Abstract

Rhinoceroses are among the most endangered mammals in the world. Despite a recent increase in numbers in most wild populations, poaching or political instability may exterminate large populations very quickly. Therefore, captive or ex situ rhinoceros populations can play an important role in their conservation. Previous studies identified infant mortality and interbirth intervals among the main parameters affecting the viability and survival of rhinoceros populations. In our study, we tested the recently suggested prediction that in captive Indian rhinoceros Rhinoceros unicornis, longer interbirth intervals may result in higher infant mortality. We also examined the factors that are the main predictors of infant mortality and interbirth intervals using the studbook data on Indian rhinoceros born in zoos worldwide as well as data from Dudhwa National Park, India, where rhinoceroses were successfully reintroduced. We found no association between interbirth intervals and infant mortality. In both populations, the main predictor of infant mortality was mother’s parity, with higher mortality in calves born to primiparous mothers. In addition, we found that the interbirth intervals were shorter in zoos than in Dudhwa and that they increased with increase in age of the mother, which was the only factor affecting interbirth interval in both populations. Our results show that the same factors affect both parameters in both populations and thus illustrate that the reproduction and infant survival of Indian rhinoceroses in zoos reflect the natural pattern. Furthermore, we suggest that in captivity, the interbirth intervals could be slightly prolonged to approach the situation in the wild.

Key words: calf mortality, interbirth interval, parity, Rhinoceros unicornis, zoo.
Kaziranga, Manas, Orang, Pobitara, and Valmiki). Therefore, even though the captive or ex situ population is much smaller, it can be considered much safer and very valuable for the conservation of this species. If poaching in South Asia reached the same level as currently in Africa, the wild populations of Indian rhinoceros would disappear in few years, and the captive population, spread over 3 continents, would be of considerable value for the survival of the species. However, despite substantial progress during the last 15 years in rhinoceros husbandry, the reproductive rate of some captive rhinoceros populations remains lower than that reported from the wild (Swaissgood et al. 2006). Thus, studying reproductive parameters of captive rhinoceros is of high importance for their conservation in general. Among these parameters, infant mortality and interbirth intervals are considered to be the most important ones (Hermes et al. 2014). Since Hermes et al. (2014) reported that Indian rhinoceros in captivity have a more limited reproductive lifespan than expected given their actual lifespan due to tumours in their reproductive tract, interbirth intervals may prove especially important for ex situ as well as for in situ breeding and conservation.

In various ungulate species, infant mortality is affected by several factors, which are either parental characteristics, such as mother’s parity (Nix et al. 1998; Johanson and Berger 2003; Wass et al. 2003; Ibáñez et al. 2013), her age (Ibáñez et al. 2013), inbreeding (Ballou and Ralls 1982; Cassinello 2005), the sex of the previous offspring (Clutton-Brock 1985; Clutton-Brock and Jason 1986; Berteaux 1993), the social rank of the mother (Lloyd and Rasa 1995; Newby 1995; Zschokke et al. 1998), mother’s origin (wild/captive (Baur and Studer 2002), thus, it seems that interbirth intervals may affect infant mortality in Indian rhinoceros; nevertheless, the direct evidence for such a relationship is missing. On the other hand, it could be argued that after shorter interbirth intervals the mother might be more exhausted than after longer intervals resulting in higher mortality of the calf. Therefore, it is very important to test the possible association between interbirth interval and infant mortality.

A crucial way to detect whether captivity has certain negative effects on the reproduction of zoo populations is to compare the infant mortality and female fecundity between the captive population and the wild one (with regard to the importance of studying wild rhinoceros populations; see Linklater 2003). Among wild Indian rhinoceros populations, the best studied is the reintroduced one in Dudhwa, National Park and Tiger Reserve (Dudhwa NP), Uttar Pradesh, India (Sinha and Sawarkar 1991; Sinha et al. 2004; Sinha et al. 2010). This population has successfully grown from 5 founders (1 male and 4 females) reintroduced in 1984–1986 to 33 individuals in 2014. During this period, all rhinoceros in Dudhwa were individually recognized. The data for this population are very valuable in particular as this population is the only wild population of Indian rhinoceros that includes “outbred, non-outbred, inbred and non-inbred” calves as classified by Zschokke and Baur (2002), thus allowing comparison with the captive population.

In this study, we focused on what affects infant mortality and interbirth intervals in Indian rhinoceros in captivity using studbook data and compared this to data from Dudhwa NP. We tested the prediction that the length of interbirth intervals might be associated with higher infant mortality in the calf produced at the end of the respective interval and in the subsequent calf. In addition, we examined if the length of interbirth intervals affects potential fertility by comparing the last known interbirth intervals of each individual female. In this case, we predicted that the last interbirth interval of females who did not reproduce anymore even though they lived with a male and weaned the last offspring were longer than those of females that could not reproduce any longer due to objective reasons, that is, lived without an adult male, died shortly after producing their last offspring, or lived with a dependent calf at the beginning of 2014.

Materials and Methods

Data collection

One author (SPS) collected data on births in rhinoceroses from Dudhwa NP (Sinha et al. 2010). Data on individual Indian
rhinos were gathered from the latest edition of the International studbook for Indian rhinoceroses (von Houwald 2014). The data were generated from SPARKS software (manufactured by International Species Information System, USA). Two individuals were not included in our analyses; one (stb. n. 4) was born of a wild-captured mother on a boat in 1948 and the other (stb. n. 493) was born to an unknown mother in Patna Zoo, India. In total, we used data for 325 individuals born to 93 mothers in 41 various zoos worldwide and for 46 individuals born to 11 mothers in Dudhwa NP.

For comparison with previous studies, we considered cumulative infant mortality over 3 time scales: whether a stillbirth (we combine cases labeled as “stillbirth” and “premature” into one category called “stillbirths”) occurred or not (Hermes et al. 2014) or over the first month (including stillbirths; Hermes et al. 2014) or the first 6 months of life (including stillbirths; Zschokke and Baur 2002; Pluháček et al. 2007). Therefore, any stillbirths (analysis a) and individuals that died before they were 1 month old (analysis b) or 6 months old (analysis c) were considered to be infant deaths. We used the same classification of inbreeding (inbred: inbreeding coefficient $>0$; non-inbred: inbreeding coefficient $=0$), and outbreeding (outbred: ancestors of both Assam as well as Nepal origin; non-outbred: all ancestors of either Assam or Nepal origin) as that of Zschokke and Baur (2002) and the same classification of “breeder” (“early”: age of the first reproduction $<7$ years; “late”: age of the first reproduction $\geq7$ years) as that of Hermes et al. (2014). In line with the suggestion of Rookmaaker (2002) and Zschokke et al. (2011), we considered male stb. n. 157 as of Nepal origin and labeled all his descendants in Patna Zoo as “outbred.” We removed all interbirth intervals that were shorter than 450 days (shorter than the gestation period for the species; Lang et al. 1977) from the analyses. Since wild-caught females older than 6 years when captured can thus not be assumed as nulliparous (Dinerstein and Price 1991; 15 captive born individual females gave birth before reaching the age of 6 years; von Houwald 2014), we removed their first offspring from analyses dealing with parity ($n=5$ cases: stb. n. 23, 28, 29, 57, and 304).

**Statistics**

Data were analyzed using the SAS System, version 9.4. Because infant mortality and interbirth intervals are affected by different factors in the 2 populations (captive and Dudhwa, e.g., most cases of infant mortality in Dudhwa were caused by tiger predation or by male infanticide; Sinha et al. 2010) we first tested all data combined and if the effect of captivity was significant, then we performed separate analyses for each population.

**What affects infant mortality**

To test infant mortality, we used an analysis of categorical repeated measurements based on the generalized estimating equation approach (Liang and Zeger 1986), using logistical regression (GENMOD procedure). We tested the probability that offspring was a stillbirth (analysis a) or that it died within 1 month (analysis b) or 6 months (analysis c). The explanatory variables were: captivity (Dudhwa or zoo) outbreeding (outbred or non-outbred), inbreeding (inbred or non-inbred), sex (male, female, or unknown), mother’s origin (wild or captive), mother’s parity (primiparous or multiparous), continent (America, Asia, and Europe), breeder category (early, late), mother’s age, and father’s age. For each particular analysis, a full model containing all explanatory variables and first-order interaction terms was initially fitted. Then, the explanatory variables were removed with a stepwise procedure using QIC criteria in GENMOD. Thus, all of the explanatory variables and interaction terms were tested, but were not reported unless they were statistically significant ($P<0.05$). Comparisons of proportions were counted using $z$-statistics (Stokes et al. 2012).

All these analyses on infant mortality were performed in two steps. In the first step, we included all variables mentioned above and in the second step, we included also interbirth interval and excluded mother’s parity. All offspring of primiparous females were removed from the second step analysis. To approach normal distribution, the interbirth intervals were log transformed.

To detect if the interbirth interval length could have an effect on any subsequent birth, we performed a separate analysis (di), where we tested the possible effect of the interbirth interval between calves “a” and “b” on the mortality within the first month of life of the calf “c.” Calves “a,” “b,” and “c” were sequential offspring of the same female. In this model, all explanatory variables were the same as in the previous ones.

**What affects interbirth intervals**

Factors influencing interbirth intervals were tested using a multivariate general linear mixed model (GLMM, PROC MIXED, SAS). Fixed factors (independent variables) tested in this model were the same as those used in logistic regression models (GENMODs). Moreover, we added another independent variable (the type of interval) for each individual mother: whether the interbirth interval was her last (“last”) or not (“other”). In this analysis, the parity was considered as a numerical variable. Mother’s and father’s identity were used as the random factors.

To detect if the interbirth interval length can affect further fertility, we performed separate GLMM, introducing a new independent variable labelled “potential breeding” for the last intervals only. Potential breeding was defined as “yes” if the female was alive 3 years after her last parturition, a male was kept in the same zoo for at least several years after the birth of the last calf, she had not produced any offspring in the last 3 years and she was younger than 30 years since the oldest captive female gave birth when 32 years old.

We started with the full model including all of the fixed effects. The significance of each fixed effect in the GLMM was assessed using an $F$-test. Non-significant fixed effects were sequentially dropped unless they improved the quality of the model (using AIC criteria for comparing the models). The within-group means were appropriately adjusted for the other effects in the model (LSMEANS statement). The differences between the means were tested by $t$-test. With multiple comparisons, we used the Tukey–Kramer adjustment.

In all models (GENMODs or GLMMs), repeated measures on the same mother were handled with the individual mother entering the model as a subject in the repeated statement.

**Results**

**What affects infant mortality**

Out of 325 Indian rhinos born in captivity from 1956 to the end of 2013, 23.7% (77 individuals) died within the first 6 months of their lives, including 21.8% (71 specimens) that died within 1 month, which involves 11.4% (37 cases) stillbirths (in the studbook referred exactly as 34 stillbirths plus 3 premature births). In Dudhwa NP, 46 rhinos were born between 1989 and 2013 and 21.7% (10 calves)
died within the first 6 months, including 10.9% (5 cases) that died within one month, which involves 4.3% stillbirths (2 specimens).

For the combined population (Dudhwa and zoos), we found that the probability that a stillbirth occurred was affected only by the parity ($\chi^2 = 8.09, P = 0.0044$), with more stillbirths being produced by primiparous mothers (19.2%, $n = 99$) than by multiparous ones (7.5%, $n = 267$).

The probability that the infant died within the first month of life was higher in captivity than in Dudhwa NP ($\chi^2 = 3.75, P = 0.0429$). When considering only the captive population, infant mortality within 1 month of age was affected by parity ($\chi^2 = 9.34, P = 0.0022$), breeder ($\chi^2 = 4.26, P = 0.0390$), continent ($\chi^2 = 9.40, P = 0.0091$), and by the interaction between breeder and continent ($\chi^2 = 6.68, P = 0.0354$, Figure 1). Again, infant mortality was higher in primiparous mothers (35.2%, $n = 88$) than in multiparous ones (16.8%, $n = 232$). In American zoos, Indian rhinos suffer higher mortality (30.4%, $n = 135$) than in European (16.8%, $n = 119$), $z = 3.27, P = 0.0011$) or Asian ones (13.6%, $n = 66$, $z = 2.06, P = 0.0395$). Whereas in European zoos, late breeders experience higher infant mortality than early breeders, no significant difference for early and late breeders was found in American and Asian zoos (Figure 1).

In the Dudhwa population, infant mortality was higher in primiparous mothers (27.3%, $n = 11$) than in multiparous ones (5.7%, $n = 35$, $\chi^2 = 14.03, P = 0.0002$) and in inbred ones (12.5%, $n = 24$), than in non-inbred (9.1%, $n = 22$, $\chi^2 = 4.04, P = 0.0443$).

When considering infant mortality within the first 6 months of life, we found no effect of captivity. Again, parity was the only factor affecting infant mortality ($\chi^2 = 11.77, P = 0.0006$; primiparous: 38.4%, $n = 99$, multiparous: 18.0%, $n = 267$). No other factor including interbirth interval affected infant mortality.

When the mortality of the calf “c” was tested, we found no effect of any factor including the interbirth interval between the two previous offspring (“a” and “b”; $\chi^2 = 0.03, P = 0.8707$, ns).

What affects interbirth intervals

In the captive population, the shortest interbirth interval lasted for 457 days, the longest one 4,127 days and the average (±SD) was 1,038.50 ± 563.37 days ($n = 230$). In Dudhwa NP, the shortest interbirth interval was 615 days and the longest 3,634 days. The average interbirth interval was longer in Dudhwa (1,474.03 ± 690.69 days, $n = 35$) than in captivity ($F_{1,184} = 6.17, P = 0.0139$).

**Discussion**

In contrast to our first prediction, we found no association between interbirth intervals and infant mortality either in the zoos or in Dudhwa, irrespective of the criterion of mortality used (stillbirth, 1 month, and 6 months). In addition, the interbirth interval length was not related to subsequent calf mortality and potential reproduction was not affected by the length of the last interbirth interval of each individual female, as far as can be determined from the use of the studbook data. Similarly, in the Dudhwa population, prolonged interbirth intervals of older females did not prevent their successful reproduction. Therefore, according to our findings, prolonged interbirth intervals do not result in higher calf mortality in Indian rhinoceros as was suggested recently (Hermes et al. 2014). Moreover, we identified two aspects of the study of Hermes et al. (2014) which may be worthy of discussion. First, they interpreted calf mortality within the first month as stillbirths. However, in the studbook (von Houwald 2014) stillbirths are defined only as young born dead (comprising 37 cases: 34 born dead and 3 premature). The different definitions of the same word may be confounding. As the mortality of live-born calves may be caused by many factors, such as absence of lactation, maternal aggression, trauma, etc., it would be better to avoid them ($n = 34$ live-born calves that died within 30 days) in the...
study, which explains infant mortality mostly by problems in the female reproductive tract. Second, it is not clear how the study of Hermes et al. (2014) accounts for the repeated measurements over the same mother and avoids the problem of pseudoreplication (Hurlbert 1984). Despite these two aspects, we would like to stress the significance of the study of Hermes et al. (2014), which pointed out very important problems of reproduction and infant mortality in the Indian rhinoceros’ captive population.

Our results strongly confirmed previous studies reporting that the mother’s parity remains the main predictor of infant mortality in Indian rhinoceros (Baur and Studer 1995; Zschokke and Baur 2002; Pluháček et al. 2007; Hermes et al. 2014) as well as in other ungulates in captivity and in the wild (Nix et al. 1998; Johanson and Berger 2003; Wass et al. 2003; Ibáñez et al. 2013). We also found that continent and, within Europe, breeder category affected infant mortality but only when mortality within the first month of infant age was considered. Based on the studbook data, where in many cases the exact cause of mortality is unknown, it remains difficult to provide any explanation of the variability in infant mortality on different continents. Nevertheless, given the importance of infant mortality for the sustainability of the population, the higher infant mortality rate in North American zoos compared with European and Asian zoos represents an interesting topic for future research. As far as we are aware, husbandry practices with regard to pregnant females before and after birth now seem to be similar in Europe and North America. However, as opposed to Europe, “there are institutions in the US with very large great one-horned rhino enclosures that have been breeding the species by allowing the bull to run with the cows and minimizing any intervention by animal care staff” (Metrione and Eyres 2014). Supervision and management are or were thus less intensive than in Europe and may have led to a higher calf mortality in the first month, for example, in San Diego Zoo Safari Park, which produced more than half of the calves born at that continent: 51%, n = 135, and where some births happened on the outdoor exhibits (Jane Kennedy, pers. com.). As far as stillbirths are concerned, more research into the causes should be encouraged on all continents as very little is known about the causes responsible for the high stillbirth rate in this species (Metrione and Eyres 2014).

Nevertheless, no other of the tested factors including outbreeding (mating between individuals from Assam and Nepal; Zschokke and Baur 2002) affected infant mortality. The results of the study (Pluháček et al. 2007), which showed no effect of outbreeding on infant mortality, was later negatively assessed by Zschokke et al. (2011, p. 2708), stating that it “was based on a larger sample size, but comprised biased assumptions, like the assignment of one individual (‘Raju’, SB#157) to the Assam population, even though it was caught in the Champaran Forest (State of Bihar, India, across the border from Chitwan NP, Nepal).”

However, the offspring of this individual were not assigned to the Assam population, but instead omitted from the study. In the current study, we did not omit the offspring of this male (n = 4) from the analyses but considered them as outbred as suggested by Zschokke et al. (2011). Nevertheless, and although in fact a much larger sample size was used than in all previous studies, outbreeding did not affect infant mortality. Therefore, we encourage the interbreeding of individuals coming from these two populations to preserve higher genetic variability (Foose and Wiese 2006).

Infant mortality in the captive population and in the Dudhwa population was almost the same; only when the 1-month mortality criterion was used, the higher mortality in captivity was shown. However, since various factors contributing to infant mortality in Dudhwa are absent in captivity (tiger predation, male infanticide, and limited veterinary care), the infant mortality in the captive population is in fact higher. Although we cannot omit the possibility that any stillbirth was not detected in Dudhwa, yet we think that this possibility remains low because the population, which lives in a confined area of 27 km² is monitored daily by forest guards and rangers. Nevertheless, if the rate of stillbirth and infant mortality in Dudhwa were slightly higher than recorded it would approach the rate of infant mortality in captivity, which remains rather high. Therefore, the research leading to the improvement of captive Indian rhinoceros calf survival and female’s fertility (e.g., finding ways to reduce the formation of tumors in the reproductive tract or to lower the number of infant deaths caused by trauma and infections (Hermes et al. 2014) is very important and needed.

We documented that the length of the interbirth intervals increased with increase in age of the mother in the captive as well as in the Dudhwa population. Longer interbirth intervals in older mothers were also reported for other wild populations of Indian rhinoceros (Chitwan; Dinerstein and Jnawali 1991; Dinerstein and Price 1991; Dinerstein 2003). In line with the study of Hermes et al. (2014), we found that this increase was steeper in captive late breeders than in captive early breeders. Thus, our evidence supports the conclusion of Hermes et al. (2014) that earlier pregnancy results in higher fecundity in captive Indian rhinoceros. It should be also noted that the length of interbirth interval varied among individual zoos, thus illustrating the effect of husbandry on interbirth intervals. Therefore, the effect of individual zoo should be considered in further studies analyzing interbirth intervals. Since the same factor (age of the mother) affected interbirth intervals in the captive and in the wild (Dudhwa) population in the same way, we suggest that the captive population reflects the natural pattern of reproduction in this regard.

We also found evidence that the interbirth intervals in Dudhwa lasted longer than those in the zoos. It might be argued that longer interbirth intervals in Dudhwa were caused by the fact that only 1 breeding male was present in Dudhwa for a long period, thus mating could be delayed. However, the population is limited to a small fenced area of 27 km², which makes the hiding of an estrus female very unlikely. In addition, the average interbirth interval of the Dudhwa population is within the range of those reported for other wild populations in Bardia and Chitwan (Table 1). Hermes et al. (2014) suggested that “although not documented for the Indian rhinoceros, such calculation assumes that animals could get pregnant during post-partum oestrus, thus creating an intercalving interval of 18 months, as was reported for other rhinoceros species.” It should be noted that interbirth intervals reported for African (only documented) species in the wild are smaller (Owen-Smith 1975; Rachlow and Berger 1998; Hrabar and du Toit 2005; Skinner et al. 2006; Ferreira et al. 2011; Patton et al. 2012; Law et al. 2013) than those for Indian rhinoceros (Table 1). In some populations of black rhinoceros, the interbirth intervals are affected by rainfall (Hrabar and du Toit 2005; but see Law et al. 2013). Although we could not test this factor in our study, it is unlikely that it affects interbirth intervals in Indian rhinoceros, which inhabit flood savannah areas surrounding large rivers. Thus, if the interbirth intervals of Indian rhinos in zoos were slightly prolonged as to approaching the interval lengths observed in the wild (Table 1) rather than shortened as suggested by Hermes et al. (2014), this could improve the management of the captive population. In this way, the number of offspring from genetically over-represented females could be reduced, which would benefit the preservation of genetic diversity (Foose and Wiese 2006).
This could be carried out by the existing breeding programs such as European Endangered Species Programme or the Species Survival Plan in North America. The manager of the breeding program can thus issue more frequent breeding recommendations to genetically under-represented pairs and less frequent recommendations to over-represented pairs. In addition, extending interbirth intervals in the captive population of Indian rhinoceros might prove beneficial for the welfare of the animals such as it approaches the reproductive pattern observed in the wild (Table 1).

Although senescence of reproductive performance was suggested for wild Indian rhinoceros (Dinerstein and Price 1991), 2 females in Dudhwa gave birth at the age of 33 years (1 of them successfully reared the offspring) and 2 captive females gave birth and reared offspring when they were at the age of 31 and almost 32 years, respectively. Therefore, our findings do not support reproductive senescence in this species. Nevertheless, since our data set remains very limited, future research is necessary to verify or refute if reproductive senescence occurs in Indian rhinoceros.

By using a large dataset from the captive population and data from 1 wild population, we showed that in Indian rhinoceros, the interbirth intervals were affected by the age of the mother and the infant mortality was associated with mother’s parity but not with interbirth interval length. Since interbirth intervals in the wild populations of Indian rhinoceros are longer than those in captive ones, we suggest that interbirth intervals in captive Indian rhinoceros could be slightly prolonged up to 45 months to improve the welfare of the animals as this would be more similar to the situation observed in the wild without effect on infant mortality. Finally, we demonstrated that the use of data from a wild and a captive population as well as the verification of previously reported scientific findings may be very important tools to prevent errors when applied to the captive management of an endangered species.

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