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Article

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 interbith 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 rhinoceros 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.

Rhinoceroses represent one of the most endangered groups of mammals. Four out of 5 extant species including Indian or greater one-horned rhinoceros (*Rhinoceros unicornis* L., 1758) are classified as threatened (Indian rhinoceros is categorized as "Vulnerable B1ab") according to The IUCN Red List of Threatened Species (Talukdar et al. 2008). Although wild populations of several rhinoceros species have increased in numbers in recent decades (Amin et al. 2006; Martin and Vigne 2012), poaching or political instability represent considerable threats as they can eliminate large wild populations very quickly (Mills et al. 2006; Biggs et al. 2013), as reported for Indian rhinoceros in Manas National Park, Assam, India (Martin and Vigne 1996; Barman et al. 2009). Moreover, in recent years, the rate of rhinoceros poaching has increased sharply, mostly in Africa (Knight 2013a, 2013b; Talukdar 2013). This increase has also affected the Indian rhinoceros, although less severely, (Subedi et al. 2013; Talukdar and Sinha 2013; Thapa et al. 2013), which inhabits not more than 3 reserves in Nepal (Bardia, Chitwan, and Suklaphanta) and 8 in India (Dudhwa, Gorumara, Jaldhapara, 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 (Swaisgood 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 Iason 1986; Berteaux 1993), the social rank of the mother (Lloyd and Rasa 1989) or caused by external factors, such as infanticide (Lewison 1998; Pluháček and Bartoš, 2000, 2005), or interspecific aggression (Hanzlíková et al. 2014). Other important factors, such as predation (Berger et al. 1993; Brain et al. 1999), environmental factors (Monard et al. 1997), or human-induced mortality (poaching) cannot be considered in captivity. It should be noted that even in closely related species, different factors may vary in their relative impact on infant mortality (Ibáñez et al. 2013; Law et al. 2013).

In addition, the interbirth interval in non-seasonally reproducing ungulates is associated with various social and reproductive factors including the sex of the young (White et al. 2007; Barnier et al. 2012), male infanticide (Lewison 1998), age of the mother (Cameron et al. 2000; Law et al. 2013; but see Penzhorn 1985; Monard et al. 1997; Barnier et al. 2012), mother's parity (Bercovitch et al. 2009), or social rank of the female (Cassinello and Alados 1996; Pluháček et al. 2006). The effect of infant mortality on interbirth intervals (shorter interbirth interval after the death of young) has been reported in many studies (ungulates: Lee and Moss 1986; Lewison 1998; Bercovitch et al. 2004; but see Bercovitch et al. 2009; other mammals: Silk 1990; Balme and Hunter 2013), whereas the opposite effect (higher probability of infant mortality after longer interbirth intervals), has been suggested (Hermes et al. 2014), but not been demonstrated to our knowledge. Nevertheless, Law et al. (2013) noted that the longest interbirth interval they recorded in a reintroduced wild black rhinoceros *Diceros bicornis* population, which was also the final interbirth interval for that female, resulted in calf mortality.

Infant mortality of Indian rhinoceros has been the subject of several studies in the past. In the wild, researchers identified the main causes of infant mortality to be mostly poaching, predation by tigers *Panthera tigris*, and male infanticide (Laurie 1982; Laurie et al. 1983; Dinerstein et al. 1988; Dinerstein 1991; Dinerstein and Jnawali 1991; Talukdar and Bora 1998). In the captive population, parity (Baur and Studer 1995; Zschokke et al. 1998), mother's origin (wild/captive (Baur and Studer 1995), inbreeding (Baur and Studer 1995; Zschokke and Baur 2002), and outbreeding (Zschokke and Baur 2002) were reported as the main factors affecting infant mortality in this species. However, later it was documented that the methodology in one of the studies (Zschokke and Baur 2002) was problematic and that inbreeding, mother's origin, and outbreeding have no effect on infant mortality in Indian rhinoceros (Pluháček et al. 2007). Instead, it was found that parity and mother's age were the determinants of infant mortality (Pluháček et al. 2007). Recently, Hermes et al. (2014) confirmed the effect of parity and reported that infant mortality may be caused by tumors in the female's reproductive tract. They also showed that the earlier a female started to reproduce, the shorter the interbirth intervals in that respective female, which resulted in a higher number of surviving calves in these females than would be expected simply due to their longer reproductive lifespan. They also suggested that pregnancies could delay the development of reproductive tract tumors and that extending interbirth intervals for any period may impact on the female's reproduction by increasing the probability of abortions and stillbirths (Hermes et al. 2014; page 8–9). 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 live(d) with a male and weaned the last offspring were longer than those of females that cannot/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 rhinoceroses born at various zoos 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-caught 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 ≥ 7 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 (d), 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)

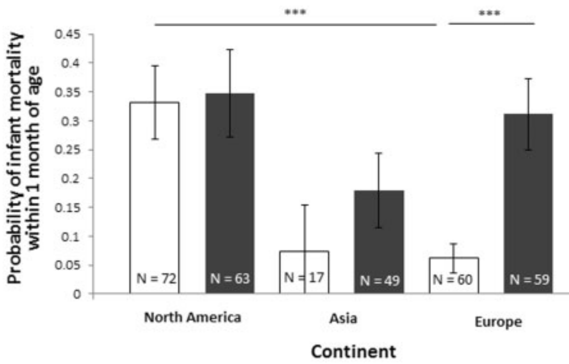

Figure 1. Probability of infant mortality in captive Indian rhinoceros within the first month of life according to the mother's breeder category (early breeders = mothers that bred for the first time until the age of 7 years; late breeders = mothers that bred for the first time when 8 years old or older) and continent where the zoo was. Open bars represent early breeders and solid bars late breeders.

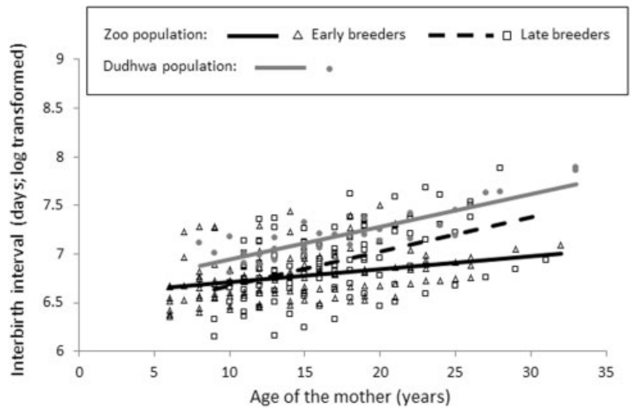

Figure 2. The association between interbirth interval and the age of the mother according to population (Dudhwa and zoo) and mother's breeder category within the zoo population (early breeders = mothers that bred for the first time until the age of 7 years, late breeders = mothers that bred for the first time when 8 years old or older).
Intervals were logarithmically transformed.

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 ($\chi^2_1 = 8.09$, $P = 0.0044$), 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 ($\chi^2_1 = 3.75$, $P = 0.0429$). When considering only the captive population, infant mortality within 1 month of age was affected by parity ($\chi^2_1 = 9.34$, $P = 0.0022$), breeder ($\chi^2_1 = 4.26$, $P = 0.0390$), continent ($\chi^2_2 = 9.40$, $P = 0.0091$), and by the interaction between breeder and continent ($\chi^2_2 = 6.68$, $P = 0.0354$, 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%, $n = 35$, $\chi^2_1 = 14.03$, $P = 0.0002$) and in inbred ones (12.5%, $n = 24$), than in non-inbred (9.1%, $n = 22$, $\chi^2_1 = 4.04$, $P = 0.0443$).

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 ($\chi^2_1 = 11.77$, $P = 0.0006$; 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"; $\chi^2_1 = 0.03$, $P = 0.8707$, 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 ($\pm SD$) 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 ($F_{1,184} = 6.17$, $P = 0.0139$).

In the captive population, the length of the interbirth interval was affected by breeder ($F_{1,150} = 9.50$, $P = 0.0012$), age of the mother ($F_{1,150} = 32.15$, $P < 0.0001$), individual zoo ($F_{40,150} = 1.82$, $P = 0.0054$), and by the interaction between breeder and the age of the mother ($F_{1,150} = 8.62$, $P = 0.0038$). The length of interbirth intervals increased with increase in age of the mother and this increase was steeper in late breeders than in early breeders (Figure 2). No other factor including the type of interval was significant. Similarly, in the Dudhwa population, the interbirth intervals increased with increasing age of the mother ($F_{1,24} = 7.81$, $P = 0.0101$; Figure 2).

When only last intervals were considered, the length of interbirth intervals either in captivity ($F_{1,29} = 0.16$, $P = 0.6938$, ns) or in Dudhwa ($F_{1,8} = 0.62$, $P = 0.4531$, ns) was not associated with the potential breeding.

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 greater 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 km^2 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 km^2, 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 oestrous, 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).

Table 1. The interbirth intervals length of various populations of Indian rhinoceros *Rhinoceros unicornis*

Interbirth interval length (in months)		Sample size	Population	Reference
Average ± SD	Range			
49.13 ± 23.02	20–121	35	Dudhwa NP, India	this study
34.61 ± 18.78	15–138	230	Zoos	this study
45.6 ± 1.8	34–51	13	Chitwan RP, Nepal	Dinerstein and Price 1991; Dinerstein and Jnawali 1991
60.9 ± 3.4	48–88	12	Chitwan RP, Nepal	Dinerstein and Price 1991
42 (median = 34)	? –50	42	Chitwan RP, Nepal	Laurie 1982
52	48–58	4	Bardia RP, Nepal	Jnawali 1995

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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References

Amin R, Okita-Ouma B, Adcock K, Emslie RH, Mulama M et al., 2006. An integrated management strategy for the conservation of eastern black rhinoceros *Diceros bicornis michaeli* in Kenya. *Int Zoo Yb* **40**:118–129.

Ballou J, Ralls K, 1982. Inbreeding and juvenile mortality in small populations of ungulates: a detailed analysis. *Biol Cons* **24**:239–272.

Balme GA, Hunter LTB, 2013. Why leopards commit infanticide. *Anim Behav* **86**:791–799.

Barman R, Choudhury B, Talukdar A, Ashraf NVK, Menon V, 2009. Return of the greater one-horned rhinoceros to Manas National Park. *Oryx* **43**:325.

Barnier F, Grange S, Ganswindt A, Ncube H, Duncan P, 2012. Inter-birth interval in zebras is longer following the birth of male foals than after female foals. *Acta Oecol* **42**:11–15.

Baur B, Studer P, 1995. Inbreeding in captive Indian rhinoceros. *Int Zoo Yb* **34**:205–211.

Bercovitch FB, Bashaw MJ, Penny CG, Rieches RG, 2004. Maternal investment in captive giraffes. *J Mammal* **85**:428–431.

Bercovitch FB, Loomis CP, Rieches RG, 2009. Age-specific changes in reproductive effort and terminal investment in female Nile lechwe. *J Mammal* **90**:40–46.

Berger J, Cunningham C, Gawuseb AA, Lindeque M, 1993. "Costs" and short-term survivorship of hornless black rhinos. *Cons Biol* **7**:920–924.

Berteaux D, 1993. Female-biased mortality in a sexually dimorphic ungulate - feral cattle of Amsterdam island. *J Mammal* **74**:732–737.

Biggs D, Courchamp F, Martin R, Possingham HP, 2013. Legal trade of Africa's rhino horns. *Science* **339**:1038–1039.

Brain C, Forge O, Erb P, 1999. Lion predation on black rhinoceros *Diceros bicornis* in Etosha National Park. *Afr J Ecol* **37**:107–109.

Cameron EZ, Linklater WL, Stafford KJ, Minot EO, 2000. Aging and improving reproductive success in horses: declining residual reproductive value or just older and wiser? *Behav Ecol Sociobiol* **47**:243–249.

Cassinello J, 2005. Inbreeding depression on reproductive performance and survival in captive gazelles of great conservation value. *Biol Cons* **122**:453–464.

Cassinello J, Alados CL, 1996. Female reproductive success in captive *Ammotragus lervia* (Bovidae, Artiodactyla): study of its components and effects of hierarchy and inbreeding. *J Zool* **239**:141–153.

Clutton-Brock TH, 1985. Birth sex ratios and reproductive success of sons and daughters. In: Greenwood PJ, Harvey PH, Slatkin M, editors. *Evolution: Essays in Honor of John Maynard Smith*. Cambridge: Cambridge University Press, 221–235.

Clutton-Brock TH, Iason GR, 1986. Sex-ratio variation in mammals. *Quart Rev Biol* **61**:339–374.

Dinerstein E, 1991. Sexual dimorphism in the greater one-horned rhinoceros *Rhinoceros unicornis*. *J Mammal* **72**:450–457.

Dinerstein E, 2003. *Return of the Unicorns*. New York: Columbia University Press.

Dinerstein E, Jnawali SR, 1991. Greater One-horned Rhinoceros Populations in Nepal. *International Rhino Conference* San Diego (CA): Zoological Society of San Diego, 196–207.

Dinerstein E, Price L, 1991. Demography and habitat use by greater one-horned rhinoceros in Nepal. *J Wildl Manag* **55**:401–411.

Dinerstein E, Wemmer C, Mishra H, 1988. Adoption in greater one-horned rhinoceros *Rhinoceros unicornis*. *J Mammal* **69**:813–814.

Ferreira SM, Greaver CC, Knight MH, 2011. Assessing the population performance of the black rhinoceros in Kruger National Park. *South Afr J Wildl Res* **41**:192–204.

Foose TJ, Wiese RJ, 2006. Population management of rhinoceros in captivity. *Int Zoo Yb* **40**:174–196.

Hanzlíková V, Pluháček J, Čulík L, 2014. Association between taxonomic relatedness and interspecific mortality in captive ungulates. *Appl Anim Behav Sci* **153**:62–67.

Hermes R, Göritz F, Saragusty J, Stoops MA, Hildebrandt TB, 2014. Reproductive tract tumours: the scourge of woman reproduction ails Indian rhinoceroses. *PLoS ONE* **9**(3):e92595.

Hrabar H, du Toit JT, 2005. Dynamics of a protected black rhino *Diceros bicornis* population: Pilanesberg National Park, South Africa. *Anim Cons* **8**:259–267.

Hurlbert SH, 1984. Pseudoreplication and the design of ecological field experiments. *Ecol Monogr* **54**:187–211.

Ibáñez B, Moreno E, Barbosa A, 2013. Parity, but not inbreeding, affects juvenile mortality in two captive endangered gazelles. *Anim Cons* **16**:108–117.

Jnawali SR, 1995. *Population Ecology of Greater One-horned Rhinoceros Rhinoceros unicornis with Particular Emphasis on Habitat Preference, Food Ecology and Ranging Behaviour of A Reintroduced Population in Royal Bardia National Park in lowland Nepal*. Ås Norway: Agricultural University of Norway.

Johanson JM, Berger PJ, 2003. Birth weight as a predictor of calving ease and perinatal mortality in Holstein cattle. *J Dairy Sci* **86**:3745–3755.

Knight M, 2013a. African Rhino Specialist Group report. *Pachyderm* **54**:8–27.

Knight M, 2013b. African Rhino Specialist Group report. *Pachyderm* **53**:7–24.

Lang EM, Leutenegger M, Tobler K, 1977. Indian rhinoceros *Rhinoceros unicornis* births in captivity. *Int Zoo Yb* **17**:237–238.

Laurie A, 1982. Behavioural ecology of the greater one-horned rhinoceros *Rhinoceros unicornis*. *J Zool* **196**:307–341.

Laurie WA, Lang EM, Groves CP, 1983. Rhinoceros unicornis. *Mamm Species* **211**:1–6.

Law PR, Fike B, Lent PC, 2013. Mortality and female fecundity in an expanding black rhinoceros *Diceros bicornis minor* population. *Eur J Wildl Res* **59**:477–485.

Lee PC, Moss CJ, 1986. Early maternal investment in male and female African elephant calves. *Behav Ecol Sociobiol* **18**:353–361.

Lewison R, 1998. Infanticide in the hippopotamus: evidence for polygynous ungulates. *Ethol Ecol Evol* **10**:277–286.

Liang KY, Zeger SL, 1986. Longitudinal data analysis using generalized linear models. *Biometrika* **73**:13–22.

Linklater WL, 2003. Science and management in a conservation crisis: a case study with rhinoceros. *Cons Biol* **17**:968–975.

Lloyd PH, Rasa OAE, 1989. Status, reproductive success and fitness in Cape mountain zebras *Equus zebra zebra*. *Behav Ecol Sociobiol* **25**:411–420.

Martin E, Vigne L, 1996. Numbers of great Indian rhinos continue to rise. *Oryx* **30**:163–165.

Martin E, Vigne L, 2012. Successful rhino conservation continues in West Bengal, India. *Pachyderm* **51**:27–37.

Metrione L, Eyres A, 2014. *Rhino Husbandry Manual*. Fort Worth (TX): International Rhino Foundation.

Mills A, Morkel P, Amiyo A, Runyoro V, Borner M et al., 2006. Managing small populations in practice: black rhino *Diceros bicomis michaeli* in the Ngorongoro Crater, Tanzania. *Oryx* **40**:319–323.

Monard AM, Duncan P, Fritz H, Feh C, 1997. Variations in the birth sex ratio and neonatal mortality in a natural herd of horses. *Behav Ecol Sociobiol* **41**:243–249.

Nix JM, Spitzer JC, Grimes LW, Burns GL, Plyler BB, 1998. A retrospective analysis of factors contributing to calf mortality and dystocia in beef cattle. *Theriogenology* **49**:1515–1523.

Owen-Smith NR, 1975. The social ethology of the white rhinoceros *Ceratotherium simum* (Burchell 1817*). *Zeitschrift für Tierpsychologie* **38**:337–384.

Patton FJ, Campbell PE, Genade A, Ayiko R, Lutalo G, 2012. Dispersal and social behaviour of the three adult female white rhinos at Ziwa Rhino Sanctuary in the immediate period before, during and after calving. *Pachyderm* **52**:66–71.

Penzhorn BL, 1985. Reproductive characteristics of a free-ranging population of Cape mountain zebra. *J Repr Fert* **73**:51–57.

Pluháček J, Bartoš L, 2000. Male infanticide in captive plains zebra *Equus burchelli*. *Anim Behav* **59**:689–694.

Pluháček J, Bartoš L, 2005. Further evidence for male infanticide and feticide in captive plains zebra *Equus burchelli*. *Folia Zool* **54**:258–262.

Pluháček J, Bartoš L, Čulík L, 2006. High-ranking mares of captive plains zebra *Equus burchelli* have greater reproductive success than low-ranking ones. *Appl Anim Behav Sci* **99** 315–329.

Pluháček J, Sinha SP, Bartoš L, Šípek P, 2007. Parity as a major factor affecting infant mortality of highly endangered Indian rhinoceros: evidence from zoos and Dudhwa National Park, India. *Biol Cons* **139**:457–461.

Rachlow JL, Berger J, 1998. Reproduction and population density: trade-offs for the conservation of rhinos *in situ*. *Anim Cons* **1**:101–106.

Rookmaaker LC, 2002. Historical records of the rhinoceros *Rhinoceros unicornis* in northern India and Pakistan. *Zoos' Print J* **17**:923–929.

Silk JB, 1990. Sources of variation in interbirth interval among captive bonnet macaques *Macaca radiata*. *Am J Phys Anthropol* **82**:213–230.

Sinha SP, Sawarkar VB, 1991. Management of the reintroduced greater one-horned rhinoceros *Rhinoceros unicornis* in Dudhwa National Park Uttar Pradesh, India. International Rhino Conference.

Sinha SP, Sawarkar VB, Singh PP, 2004. Twenty years of Rhino Reitroduction Programme in Dudhwa National Park/ Tiger Reserve, Uttar Pradesh, India (1984–2004): a report. Dehra Dun: Wildlife Institute of India.

Sinha SP, Sinha BC, Sawarkar VB, 2010. Twenty five years of Rhino Reintroduction Programme in Dudhwa National Park / Tiger Reserve, Uttar Pradesh, India (1984–2010) with management implications. Dehradun: Wildlife Institute of India.

Skinner JD, Dott HM, Matthee A, Hunt L, 2006. Captive breeding of the white rhinoceros *Ceratotherium simum* and the Cape buffalo *Syncerus caffer*. *Onderstepoort J Vet Res* **73**:237–239.

Stokes ME, Davis CS, Koch GG, 2012. *Categorical Data Analysis using SAS*, 3rd edn. Cary (NC): SAS Institute Inc.

Subedi N, Jnawali SR, Dhakal M, Pradhan NMB, Lamichhane BR et al., 2013. Population status, structure and distribution of the greater one-horned rhinoceros *Rhinoceros unicornis* in Nepal. *Oryx* **47**:352–360.

Swaisgood RR, Dickman DM, White AM, 2006. A captive population in crisis: testing hypotheses for reproductive failure in captive-born southern white rhinoceros females. *Biol Cons* **129**:468–476.

Talukdar BK, 2013. Asian Rhino Specialist Group report. *Pachyderm* **54**:28–35.

Talukdar BK, Bora N, 1998. Tiger predation of rhinoceroses. *Oryx* **32**:96.

Talukdar BK, Sinha SP, 2013. Challenges and opportunities of transboundary rhino conservation in India and Nepal. *Pachyderm* **54**:45–51.

Talukdar BK, Emslie R, Bist SS, Choudhury A, Ellis S et al., 2008. *Rhinoceros unicornis*. The IUCN Red List of Threatened Species. Version 2015.1. Available from: www.iucnredlist.org.

Thapa K, Nepal S, Thapa G, Bhatta SR, Wikramanayake E, 2013. Past, present and future conservation of the greater one-horned rhinoceros *Rhinoceros unicornis* in Nepal. *Oryx* **47**:345–351.

von Houwald F, 2014. *International Studbook for the Greater One-Horned Rhinoceros*. Basel: Basel Zoo.

Wass JA, Pollard JC, Littlejohn RP, 2003. A comparison of the calving behaviour of farmed adult and yearling red deer *Cervus elaphus* hinds. *Appl Anim Behav Sci* **80**:337–345.

White AM, Swaisgood RR, Czekala N, 2007. Differential investment in sons and daughters: Do white rhinoceros mothers favor sons? *J Mammal* **88**: 632–638.

Zschokke S, Armbruster GFJ, Ursenbacher S, Baur B, 2011. Genetic differences between the two remaining wild populations of the endangered Indian rhinoceros *Rhinoceros unicornis*. *Biol Cons* **144**:2702–2709.

Zschokke S, Baur B, 2002. Inbreeding, outbreeding, infant growth, and size dimorphism in captive Indian rhinoceros *Rhinoceros unicornis*. *Can J Zool* **80**:2014–2023.

Zschokke S, Studer P, Baur B, 1998. Past and future breeding of the Indian rhinoceros in captivity. *Int Zoo News* **45**:261–276.