

Research article

Reproductive non-seasonality in rhinoceroses: A review of the in-situ literature and birth records of ex-situ institutions

Katharina Radeke-Auer¹, Anita Wittwer¹, Julia Aust¹, Marco Roller², Dennis W.H. Müller³, Friederike von Houwald^{4,5}, Beatrice Steck⁴, Rebecca Biddle⁶, Lars Versteeg⁷ and Marcus Clauss¹

¹Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich, Winterthurerstrasse 260, 8057 Zurich, Switzerland

²Zoological Garden of Karlsruhe, Ettlinger Str. 6, 76137 Karlsruhe, Germany

³Zoological Garden of Halle, Fasanenstrasse 5a, 06114 Halle (Saale), Germany

⁴Zoological Garden of Basel, Binningerstrasse 40, 4054 Basel, Switzerland

⁵Zoological Garden of Bern, Tierparkweg 1, 3005 Bern, Switzerland

⁶Twycross Zoo - East Midland Zoological Society, Norton Grange, Norton-Juxta-Twycross, Atherstone, Warwickshire, CV9 3PX, United Kingdom

⁷Safaripark Beekse Bergen, 5081 NJ Hilvarenbeek, The Netherlands

Correspondence: Marcus Clauss, email; mclauss@vetclinics.uzh.ch

Keywords: husbandry; rhinoceros; reproduction; seasonality

Article history:

Received: 16 Jun 2021

Accepted: 26 Jan 2022

Published online: 31 Jan 2022

Abstract

Mammals whose breeding activity is triggered by seasonal photoperiodic cues typically maintain seasonal reproduction in zoos, with births accumulating to various degrees in spring. For zoo-kept rhinoceroses, accumulation of births in autumn has been suggested, which would make this group unusual. We compare birthing (and hence conception) patterns of free-ranging rhinoceros populations from the scientific literature with those of the global zoo populations based on birth data available from Species360, to facilitate deductions on the cues that trigger rhinoceros reproduction. The patterns do not indicate a photoperiodic element in rhinoceros reproduction but suggest suppression of conception in free-ranging populations at times of resource scarcity. This is not evident in zoos. However, a slight accumulation of autumn births, due to a slight reduction in births in spring, is visible in the zoo populations. Given rhinoceros gestation periods, this is linked to reduced conceptions in November–December. The most parsimonious interpretation is management-related, as has been suggested (Roth 2006, *Int. Zoo Yb.* 40(1): 130–143): not all facilities are prepared to allow mating at times when outdoor husbandry is reduced due to weather restrictions. Given the long interbirth intervals of rhinoceroses, missed conception opportunities of 1–2 months are unlikely to affect population demographics. Nevertheless, detailed recording of approaches to facilitate mating during winter months by those zoos that achieve this may increase the general skill of rhinoceros management.

Introduction

The reproduction of mammals is mainly, but not exclusively, governed by two mechanisms that may lead to the occurrence of seasonal breeding patterns. On the one hand, nearly all mammals are subject to control of reproduction by body condition, where a low degree of body reserves will prevent conception (Bronson 2009). In environments where natural resources fluctuate in a consistent way across years, this mechanism alone may lead to a pattern of seasonal reproduction. Additionally, animals that live in environments where a fluctuation of natural resources is paralleled by a photoperiodic signal—as for example at temperate latitudes—may have evolved a photoperiodic trigger for reproduction

(Bronson 1989, 2009). Animals responding to photoperiod are classified as ‘short-day’ and ‘long-day’ breeders (Hansen 1985), depending on whether reproductive activity is triggered at the time of year when days are getting shorter or longer. Given that the adaptation of a photoperiodic trigger serves to time births in the growing season (‘spring’) of the respective hemisphere, one can use the knowledge of a species’ gestation period (and potential additional adaptations, such as delayed implantation) to estimate whether it should be a short-day or a long-day breeder (Figure 3 in Clauss et al. 2021). Animals constrained only by natural resource fluctuation in their natural habitat typically reproduce less seasonally in zoos; animals additionally subjected to a photoperiodic trigger mostly maintain a seasonal pattern of reproduction in zoos (Clauss et al. 2021).

Black *Diceros bicornis*, white *Ceratotherium simum* and greater one-horned *Rhinoceros unicornis* rhinoceroses ('rhinos' from here on) are considered to reproduce non-seasonally (Roth 2006), which matches their current distribution in the tropics of Africa and Asia and subtropical southern Africa. Many physiological studies support this view (Brown et al. 2001, Edwards et al. 2015, Hindle et al. 1992, Patton et al. 1999, Roth et al. 2016, Schwarzenberger et al. 1993, 1998, 2000, Stoops et al. 2004). Nevertheless, seasonal reproductive peaks have been reported in free-ranging rhinos that have been associated with fluctuations in resource availability due to rainfall at the time of conception (Owen-Smith 1988, Owen-Smith and Ogutu 2013).

In addition to the current geographic spread, reproductive patterns might also be related to historical distributions, as tentatively suggested for springbok *Antidorcas marsupialis* (Zerbe et al. 2012) and elephants (Hufenus et al. 2018). As the global distribution of rhinos was historically not restricted to the tropics (Rookmaaker and Antoine 2012, Roosevelt and Heller 1914), a relict seasonal photoperiodic component to their reproduction might have remained that may only become evident when large numbers of reproductive events are assessed.

To the authors' knowledge, whether the fluctuations observed in the reproductive patterns of free-ranging rhino populations are mirrored in zoos, especially concerning their occurrence

across the photoperiodic annual cycle, has not been evaluated. If a photoperiodic component remained in their reproductive physiology, one would expect some increase in births in the spring-summer period (with increasing day length), and correspondingly some increase in mating activity occurring a gestation period earlier. With gestation lengths of about 16 (*D. bicornis*, *R. unicornis*) to 17 (*C. simum*) months (Miller and Buss 2015), rhinos have the second-longest gestation times among terrestrial mammals, after elephants. Whether such long gestation periods that span more than one year, and that are typically also associated with long lactation periods, should or should not make seasonal reproduction adaptive has been debated. From the side of the mother animal, such a wide spread of moderately increased energetic requirements would, most likely, not strictly require synchrony with a seasonally fluctuating resource (Owen-Smith 1988, van Noordwijk et al. 2013). From the side of the offspring, favourable conditions around the time of birth may nevertheless be desirable and make seasonal reproduction adaptive (Clausen et al. 2021).

Given their long gestation periods, any putatively increased mating activity in rhinos should occur during the short-day period in the last months of the northern hemisphere calendar year, if there was a photoperiodic component to their reproductive physiology (Figure 1). However, a study providing data on a rhino

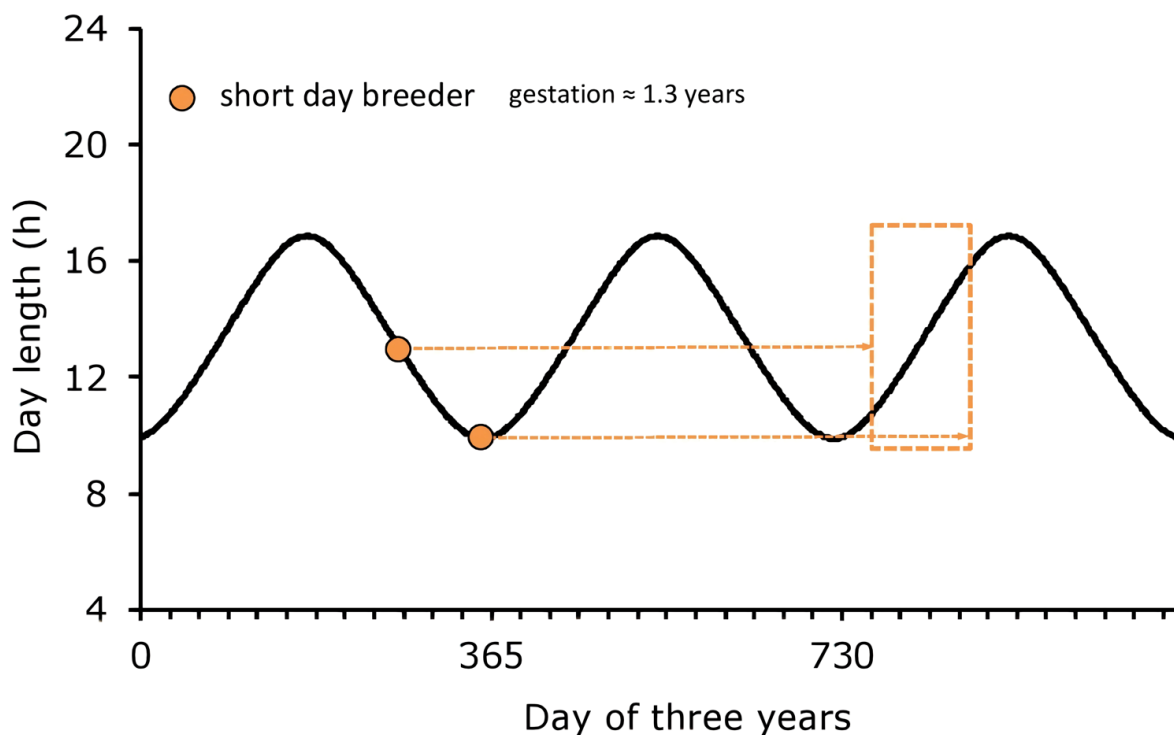


Figure 1. Schematic representation of the course of day length over several calendar years (in the northern hemisphere), the breeding season (framed by the dots) and the corresponding birth window (box) in seasonally reproducing animals with a gestation period of 1.3 years. At this gestation length, one would expect the animals to be short-day breeders (mating during shortening day lengths or around the time of the winter solstice) so that births are timed in the spring/summer.

species indicates the opposite—a reduction of conceptions in this period (Skinner et al. 2002 for *C. simum*). In many temperate zone zoos, these are the months where access to larger outdoor enclosures for both sexes at the same time is reduced. Because mating in rhinos is associated with a certain degree of agitation and aggression between the sexual partners, large spaces are generally desirable for this activity, and therefore zoos might be more reluctant to allow breeding in the mostly smaller indoor facilities. Thus, the following three potential outcomes were considered for the present study: (i) the complete absence of a seasonal pattern in zoo rhinos, suggesting that the observed reproductive seasonality in natural habitats is driven by resource availability that is not limited in zoos; (ii) a certain similarity in seasonal patterns between rhinos from zoos and in natural habitats, suggestive of a photoperiodic component in their reproductive physiology with an increase in breeding activity in autumn/winter and (iii) a reduction in breeding activity during the winter period in zoos unparalleled in natural habitats, suggestive of zoo management practices (Roth 2006; Clauss et al. 2021).

Materials and methods

Data were collected on reproductive patterns, mainly based on births, in black *D. bicornis*, white *C. simum* and greater one-horned *R. unicornis* (GOH) rhinos, based on literature review. The search engines used were Google Scholar and PubMed, and the search terms were the species names, coupled with the search terms 'reproduction', 'birth', or 'seasonality'. This search was only conducted in the English language. Additionally, literature cited in identified sources, as well as publications citing the identified sources, were screened.

If quantitative data were available, these were either copied from tabulated or numerical values in the respective publications, or digitised from graphs using the WebPlotDigitizer tool (www.automeris.io/WebPlotDigitizer/). Data on births in zoo-kept individuals were taken from the Species360 database (research data use agreement #68960) for the period from 1900 to the end of 2019. Data from Species360 were used on an anonymous basis, with only information on the hemisphere of the respective institutions—displaying the data within a hemisphere by latitude was not possible. Raw Species360 birth data typically show the artefact of a peak on 1 January (presumably from entries of births for which the real month and day information was not at hand during data entry). These entries were discarded.

Data were displayed on a per-month basis. All data from Species360 and the literature were corrected for hemisphere (aligned to the northern hemisphere seasonal cycle, Figure 1), by shifting all patterns by six months for individuals or populations from the southern hemisphere. Apart from the zoo animals, only the reconstructed conceptions are displayed, which were calculated by subtracting the corresponding gestation periods (470–475 days i.e. 16 months for black and GOH rhinos, 501 days i.e. 17 months for white rhinos) (Miller and Buss 2015). It should be noted that there may be substantial intra-specific variation in gestation length in rhinos (e.g. Patton et al. 1999).

While there is a variety of methods to quantify the degree of seasonality of animals (reviewed in Table 1 of Heldstab et al. 2021), the aim of the present data collation was not to compare the degree of seasonality of rhinos to that of other mammals. Rather, the aim was to assess whether conception peaks across studies—visually identified on graphs that displayed the available data—occurred systematically in a specific period of the year that represented days getting either shorter or longer. To determine whether a specific pattern showed a distribution of conceptions across months that was significantly different from a homogenous distribution, a chi-square goodness of fit test in R (R Core Team

2017) was applied to samples with more than 50 observations; the corresponding P values are indicated in the respective figure legends.

In the following, results are displayed in a narrative and with graphs representing the available data. Statements made by authors who did not provide supporting original data are simply paraphrased. A tabulated version that compiles the literature findings is available in the supplementary material (Table S1).

Results

Natural habitat

Diceros bicornis

Mating in black rhinos has been characterised as occurring throughout the year (Goddard 1966, Ritchie 1963, Roosevelt and Heller 1914). Five studies provided data on birthing or conception patterns (Garnier et al. 2002, Greaver et al. 2014, Hall-Martin and Penzhorn 1977, Hitchins and Anderson 1983, Hrabar and du Toit 2005); the corresponding conception months do not indicate a pattern of specific short-day or winter breeding (Figure 2). Additionally, Freeman et al. (2014) reported that in a South African population, the majority of conceptions occurred during the long-day period. A similarly increased timing of conceptions during the long-day period is noted in a report on populations in today's Namibia and Botswana (Wilhelm 1931). In most of these studies, as well as another that did not give season-specific data (Berkeley and Linklater 2010), a major finding was that breeding activity (conception) was related to the wet season.

Ceratotherium simum

White rhinos are also reported to mate throughout the year, with mating peaks occurring at times of fresh grass growth, i.e. during a wet season (Kretzschmar et al. 2004, Owen-Smith 1974, 1988, Penny 1987, Pienaar 1963, Van der Goot et al. 2015); even very clear seasonal patterns with conceptions in the wet season were described (Guerier 2012). Four studies provided data on seasonal birthing (Condy 1973, Owen-Smith 1988, Patton and Genade 2019, Ververs et al. 2017), and one on male reproductive hormone patterns (Kretzschmar et al. 2004). Again, the corresponding months of increased conceptions or hormonal activity do not indicate a pattern of specific short-day or winter breeding (Figure 3). Other descriptions of peak mating activity rather indicate a clustering of breeding during the long-day period (Penny 1987, Pienaar 1963).

Rhinoceros unicornis

The only observations of GOH rhinos stem from Chitwan National Park, Nepal, located in the northern hemisphere. Individual observations suggest breeding or increased breeding activity in the long-day period (Gee 1953, Laurie 1982). Different publications reporting on the monthly distribution of the number of births (Dinerstein and Price 1991, Laurie 1978, Subedi et al. 2017) were combined to assess the distribution of conceptions (Figure 4). No indication of increased breeding activity during the long-day or the short-day period was evident.

Zoos

In the three rhino species, zoo data indicate year-round reproductive activity, with a somewhat elevated birthing activity in autumn (Figure 5). This corresponds to a description by Skinner et al. (2002) of white rhinos in a single zoological institution. Correspondingly, there was a somewhat elevated mating activity in summer (Figure 5). In particular, a low proportion of births in spring and of conceptions in winter appears striking. For all three rhino species, the pattern was significantly different from a homogenous distribution (Figure 5).

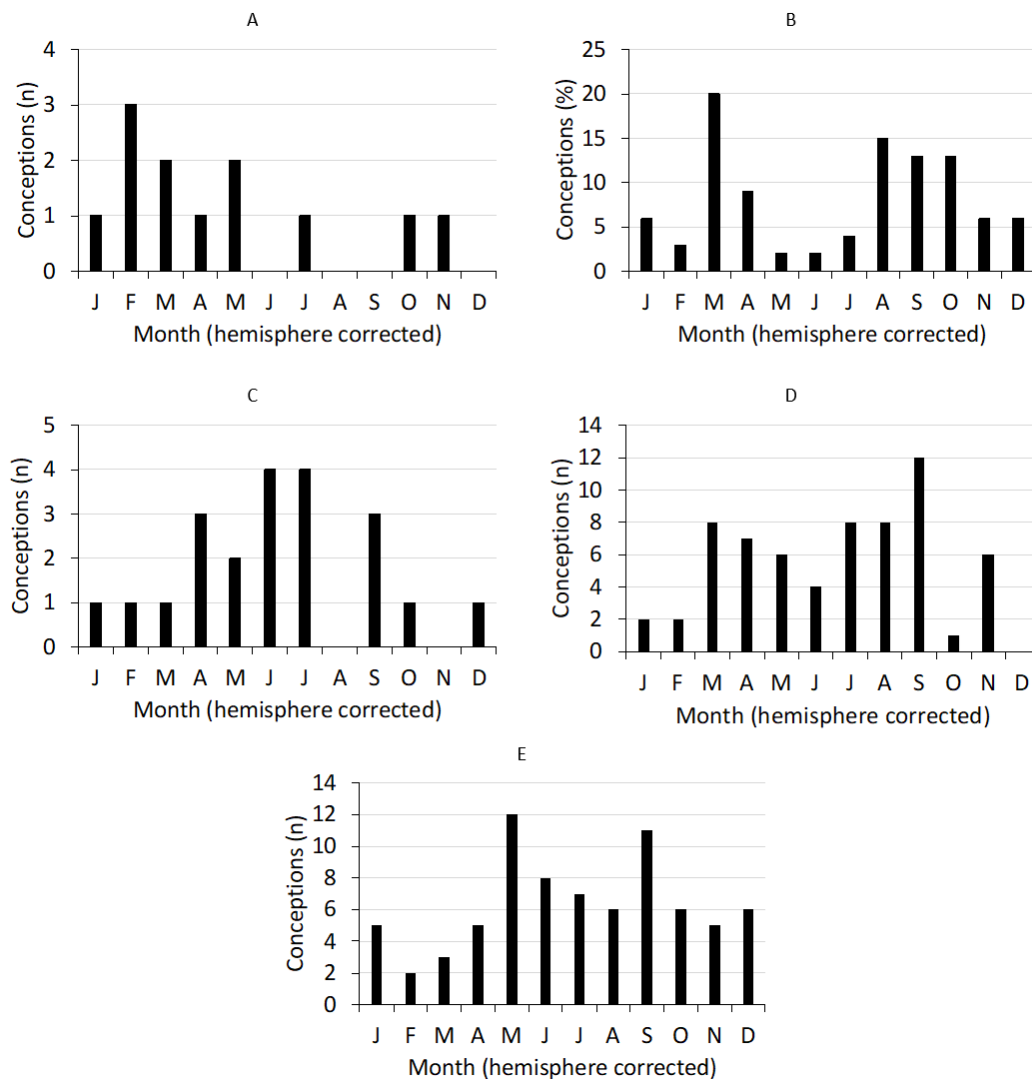


Figure 2. Distribution of conceptions in black rhinos *D. bicornis* in different populations in natural habitats reconstructed from birthing patterns and gestation period from the literature, corrected to a northern hemisphere year. (A) Addo Elephant Park, South Africa (n=12 births 1968–1977) (Hall-Martin and Penzhorn 1977); (B) Hluhluwe-Umfolozzi Game Reserve, South Africa (n=128 births, 1961–1973, $P < 0.001$) (Hitchins and Anderson 1983); (C) Save Valley Conservancy and Imire Game Ranch, Zimbabwe (n=21 births, 1994–1999) (Garnier et al. 2002); (D) Pilanesberg National Park, South Africa (n=64 conceptions, 1986–2000, $P = 0.006$) (Hrabar and du Toit 2005); (E) Ithala Game Reserve, South Africa (n=76 births, 1990–2008, $P = 0.200$) (Greaver et al. 2014). Note that even though data are corrected to a common photoperiod, there is no evident common pattern in mating activity with peaks occurring both during the long-day (spring) and the short-day (autumn) period, even within a population. P values for samples with $n > 50$ indicate whether the distribution differs significantly from an equal distribution of conceptions across all months.

Discussion

The current investigation was originally triggered by curiosity about the previously described slight increase in number of births in the autumn season in zoo-kept white rhinos (Skinner et al. 2002), which was paralleled by the pattern in the global zoo population of the present study (Figure 5). Such a pattern is unusual. Animal species that reproduce seasonally in natural environments and maintain such a pattern in zoos, i.e. species with a distinct photoperiod component in their reproduction, generally time births to occur during spring and early summer of

their respective hemisphere (Claus et al. 2021). This is because in seasonal habitats, this is the time of year when natural resources are particularly plentiful, which is not the case in autumn (Bronson 1989). For this reason alone, a photoperiod trigger would appear unlikely as an underlying cause. Comparison with the data from natural habitats additionally did not provide evidence for a common seasonal denominator of mating activity that could be linked to a photoperiod signal.

Thus, the observations corroborate what has been known for these rhino species for a long time: that they are non-seasonal breeders that do not follow a photoperiodic signal (Roth 2006).

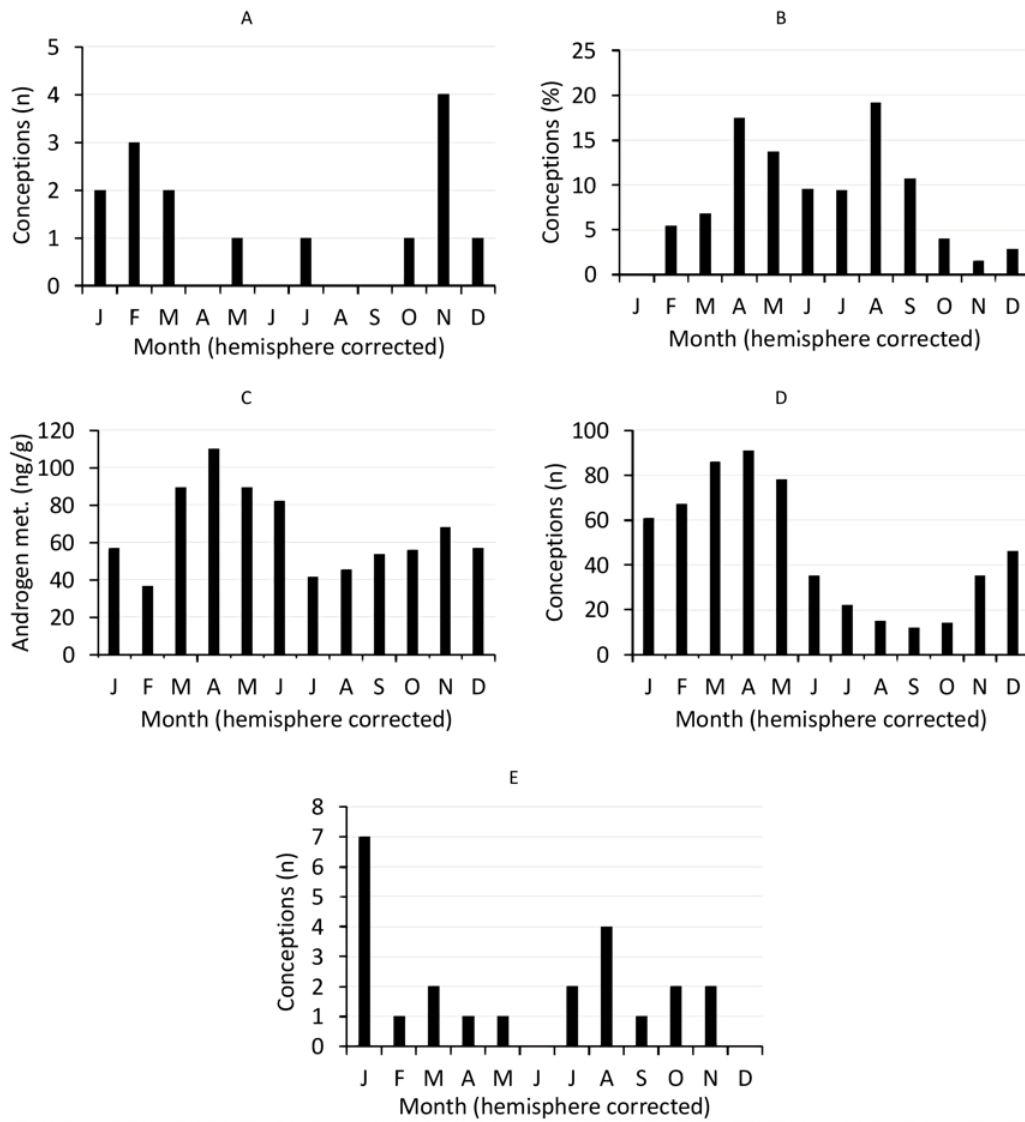


Figure 3. Distribution of conceptions in white rhinos *C. simum* in different populations in natural habitats reconstructed from birthing patterns and gestation period from the literature, corrected to a northern hemisphere year. (A) Kyle National Park, Zimbabwe (n=15 births, 1962–1972) (Condy 1973); (B) Hluhluwe-Umfolozi Game Reserve, South Africa (n=74 births, 1968–1971, P<0.001) (Owen-Smith 1988); (C) Limpopo Province game farm, South Africa (faecal androgen metabolites, n=5 males sampled repeatedly in 1997–1999) (Kretzschmar et al. 2004); (D) private game ranch, South Africa (n=562 births, 2008–2016, P<0.001) (Ververs et al. 2017); (E) Ziwa Sanctuary, Uganda (n=23, 2010–2019) (Patton and Genade 2019). Note that even though data are corrected to a common photoperiod, there is no evident common pattern in mating activity, with peaks occurring both during the long-day (spring) and the short-day (autumn) period, even within a population. P values for samples with n>50 indicate whether the distribution differs significantly from an equal distribution of conceptions across all months.

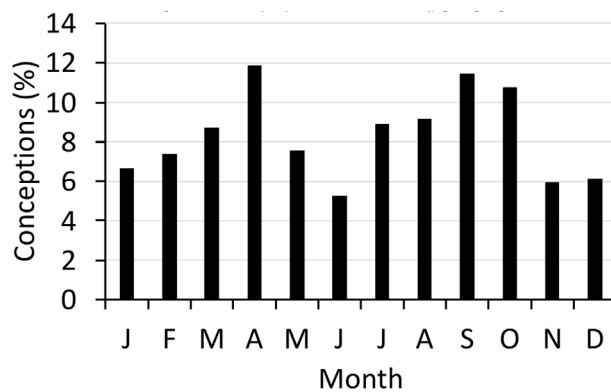


Figure 4. Distribution of conceptions in greater one-horned rhinos *R. unicornis* at Chitwan National Park, Nepal (n=185 births, 1972–1988 and 2008–2015, P=0.370) (Dinerstein and Price 1991, Laurie 1978, Subedi et al. 2017). Note that there is no evident common pattern in mating activity, with conceptions occurring both during the long-day (spring) and the short-day (autumn) period. P value indicates whether the distribution differs significantly from an equal distribution of conceptions across all months.

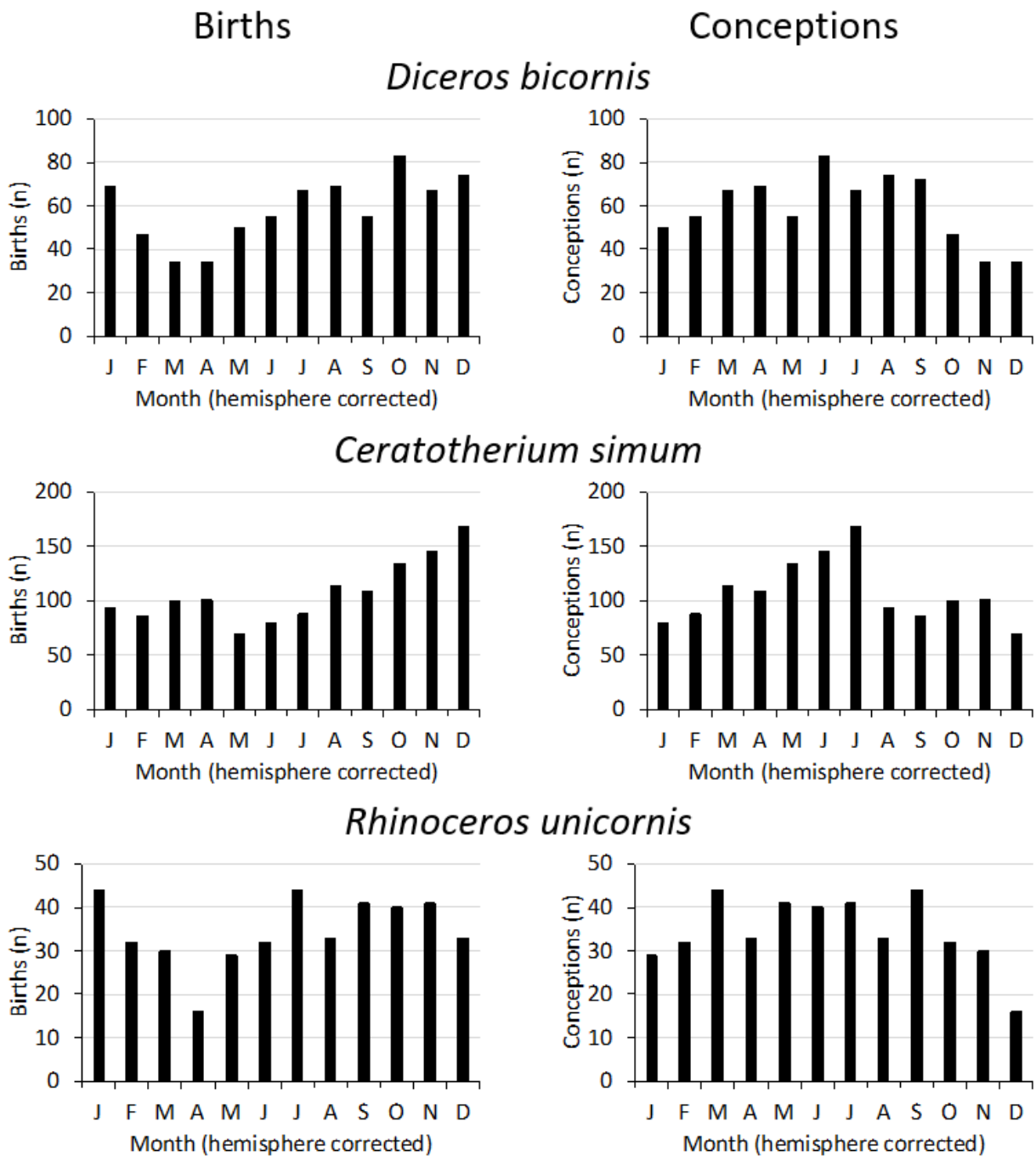


Figure 5. Distribution of births and conceptions (*Diceros bicornis* n=704, P<0.001; *Ceratotherium simum* n=1290, P<0.001; *Rhinoceros unicornis* n=415, P=0.040) in the global rhino zoo population, corrected to the northern hemisphere. P values indicate whether the distribution differs significantly from an equal distribution of conceptions across all months.

In natural environments, breeding is not so much triggered by a certain environmental cue, but rather suppressed by suboptimal conditions that may occur, e.g. during dry seasons. The fact that reproduction in the global zoo population appears less confined

to certain periods of the year than in most natural habitats is a consequence of the consistent supply of food and shelter in zoological institutions. In some cases, this provision might overshoot and lead to obesity, which may be linked to fertility or

reproductive disease (Edwards et al. 2015, Heidegger et al. 2016), although conclusive epidemiological evidence for rhinos is still lacking in this respect.

The impression of a low proportion of births in spring in global rhino zoo populations is linked to a reduced number of conceptions in December and an increase in conceptions during summer, even though globally, breeding activity did occur in all months. The lower breeding activity in December, and the higher activity in summer, is neither an old nor a recent phenomenon but has occurred rather consistently throughout rhino husbandry. In the absence of any similarity to patterns in natural habitats, this is interpreted as a management phenomenon following Roth (2006). Globally, rhino husbandry systems may not allow the same degree of mating activity when animals are more confined indoors due to climatic conditions, leading to the reduced number of conceptions in this period. Additionally, the fact that the end of the year represents a holiday period in many parts of the world, with potential reductions in staff numbers and a reduced focus on extra-routine activities, may contribute to this effect.

One could claim that ideally, mating should be evenly spread across the year in rhinos, because that would make the maximum use of female reproductive potential. Possibly, this would necessitate more widespread use of facilities that make winter mating feasible. From a population point of view, however, such an improvement is unlikely to change demographic developments. While some conception opportunities in the winter months may be missed, these are unlikely to affect population growth given the long inter-calf interval of rhinos of 2–4 years (Miller 2003). Hence, for the two rhino studbooks where no breeding restrictions are currently proposed in Europe, the black and the white rhino, a prudent choice of the timing of matings depending on the current facilities and with the aim to prevent accidents is the main priority. For the GOH rhino studbook, which aims to reduce the rate of reproduction of the European population due to a constraint in the number of GOH rhinos that can be kept in zoos, routine cessation of conceptions during the winter period is even less problematic. In such considerations of breeding management, it should also be kept in mind that interruptions in reproductive activity should not be too long, as prolonged cessation of breeding may lead to irreversible pathologies, as for example documented in GOH rhinos (Hermes et al. 2014). However, it should be kept in mind that the average interbirth intervals for GOH rhinos in zoos are still shorter than those observed in the wild (Pluháček et al. 2017) and therefore moderate prolonging of interbirth intervals appears biologically acceptable.

In conclusion, the available data and literature on the seasonal timing of reproductive activity indicate that rhinos are non-seasonal breeders that are, in their natural habitats, subjected to resource constraints. In zoos, management issues are the most likely systematic cause for reduced breeding activity in winter. Detailed reports of the management of breeding activity from those zoos that achieve winter conceptions would be welcome. It would be interesting to differentiate among winter breeding because of mild climatic winter conditions, large inside enclosures, or very experienced management under spatially constrained conditions. Given that the survival of endangered species will probably depend not only on the maintenance of in-situ, but also on ex-situ populations (Pizzutto et al. 2021), such information would help to further the global skill of the reproductive management of rhinoceros species.

Acknowledgements

This research was made possible by the worldwide information network of zoos and aquariums that are members of Species360. It is authorized by Species360 research data use and grant agreement #68960.

References

- Berkeley E.V., Linklater W.L. (2010) Annual and seasonal rainfall may influence progeny sex ratio in the black rhinoceros. *South African Journal of Wildlife Research* 40(1): 53–57.
- Bronson F.H. (1989) *Mammalian Reproductive Biology*. Chicago, Illinois: University of Chicago Press.
- Bronson F.H. (2009) Climate change and seasonal reproduction in mammals. *Philosophical Transactions of the Royal Society B* 364(1534): 3331–3340. doi:10.1098/rstb.2009.0140
- Brown J.L., Bellem A.C., Fouraker M., Wildt D.E., Roth T.L. (2001) Comparative analysis of gonadal and adrenal activity in the black and white rhinoceros in North America by noninvasive endocrine monitoring. *Zoo Biology* 20(6): 463–486. doi:10.1002/zoo.10028
- Clauss M., Zerbe P., Bingaman Lackey L., Codron D., Müller D.W.H. (2021) Basic considerations on seasonal breeding in mammals including their testing by comparing natural habitats and zoos. *Mammalian Biology* 101: 373–386. doi:10.1007/s42991-020-00078-y
- Condy P.R. (1973) *The Population Status, Social Behaviour and Daily Activity Pattern of the White Rhinoceros in Kyle National Park, Rhodesia*. MSc thesis, University of Rhodesia.
- Dinerstein E., Price L. (1991) Demography and habitat use by greater one-horned rhinoceros in Nepal. *The Journal of Wildlife Management* 55(3): 401–411. doi:10.2307/3808968
- Edwards K.L., Shultz S., Pilgrim M., Walker S.L. (2015) Irregular ovarian activity, body condition and behavioural differences are associated with reproductive success in female eastern black rhinoceros (*Diceros bicornis michaeli*). *General and Comparative Endocrinology* 214: 186–194. doi:10.1016/j.ygcen.2014.07.026
- Freeman E.W., Meyer J.M., Bird J., Adendorff J., Schulte B.A., Santymire R.M. (2014) Impacts of environmental pressures on the reproductive physiology of subpopulations of black rhinoceros (*Diceros bicornis bicornis*) in Addo Elephant National Park, South Africa. *Conservation Physiology* 2(1): cot034. doi:10.1093/conphys/cot034
- Garnier J.N., Holt W.V., Watson P.F. (2002) Non-invasive assessment of oestrous cycles and evaluation of reproductive seasonality in the female wild black rhinoceros (*Diceros bicornis minor*). *Reproduction* 123(6): 877–889. doi:10.1530/rep.0.1230877
- Gee E.P. (1953) The life history of the great Indian one-horned rhinoceros (*Rhinoceros unicornis*). *Journal of the Bombay Natural History Society* 34(2): 341–348
- Goddard J. (1966) Mating and courtship of the black rhinoceros (*Diceros bicornis*). *African Journal of Ecology* 4(1): 69–75. doi:10.1111/j.1365-2028.1966.tb00883.x
- Greaver C., Ferreira S., Slotow R. (2014) Density-dependent regulation of the critically endangered black rhinoceros population in Ithala Game Reserve, South Africa. *Austral Ecology* 39(4): 437–447. doi:10.1111/aec.12101
- Guerier A.S. (2012) *Parentage Analysis in a Free Ranging, Closed Population of Southern White Rhinoceros: Genetics, Pedigrees and Management*. MSc thesis, University of Pretoria.
- Hall-Martin A.J., Penzhorn B.L. (1977) Behaviour and recruitment of translocated black rhinoceros *Diceros bicornis*. *Koedoe* 20(1): 147–162. doi:10.4102/koedoe.v20i1.941
- Hansen P.J. (1985) Photoperiodic regulation of reproduction in mammals breeding during long days versus mammals breeding during short days. *Animal Reproduction Science* 9(4): 301–315. doi:10.1016/0378-4320(85)90059-4
- Heidegger E.M., von Houwald F., Steck B., Clauss M. (2016) Body condition scoring system for greater one-horned rhino (*Rhinoceros unicornis*): Development and application. *Zoo Biology* 35(5): 432–443. doi:10.1002/zoo.21307
- Heldstab S.A., van Schaik C.P., Müller D.W.H., Rensch E., Bingaman Lackey L., Zerbe P., Hatt J.M., Clauss M., Matsuda I. (2021) Reproductive seasonality in primates: Patterns, concepts and unsolved questions. *Biological Reviews* 96(1): 66–88. doi:10.1111/brv.12646
- Hermes R., Göritz F., Saragusty J., Stoops M.A., Hildebrandt T.B. (2014) Reproductive tract tumours: The scourge of woman reproduction ails Indian rhinoceroses. *PLoS ONE* 9(3): e92595. doi:10.1371/journal.pone.0092595
- Hindle J.E., Möst E., Hodges J.K. (1992) Measurement of urinary oestrogens and 20 α -dihydroprogesterone during ovarian cycles of black (*Diceros bicornis*) and white (*Ceratotherium simum*) rhinoceroses. *Reproduction* 94(1): 237–249. doi:10.1530/jrf.0.0940237
- Hitchins P.M., Anderson J.L. (1983) Reproduction, population characteristics and management of the black rhinoceros *Diceros bicornis minor* in the Hluhluwe/Corridor/Umfolozzi Game Reserve Complex. *South African Journal of Wildlife Research* 13(3): 78–85.

- Hrabar H., du Toit J.T. (2005) Dynamics of a protected black rhino (*Diceros bicornis*) population: Pilanesberg National Park, South Africa. *Animal Conservation* 8(3): 259–267. doi:10.1017/S1367943005002234
- Hufenus R., Schiffmann C., Hatt J.M., Müller D.W.H., Bingaman Lackey L., Clauss M., Zerbe P. (2018) Seasonality of reproduction in Asian elephants *Elephas maximus* and African elephants *Loxodonta africana*: Underlying photoperiodic cueing? *Mammal Review* 48(4): 261–276. doi:10.1111/mam.12133
- Kretzschmar P., Gansloßer U., Dehnhard M. (2004) Relationship between androgens, environmental factors and reproductive behavior in male white rhinoceros (*Ceratotherium simum simum*). *Hormones and Behavior* 45(1): 1–9. doi:10.1016/j.yhbeh.2003.08.001
- Laurie A. (1982) Behavioural ecology of the Greater one-horned rhinoceros (*Rhinoceros unicornis*). *Journal of Zoology* 196(3): 307–341. doi:10.1111/j.1469-7998.1982.tb03506.x
- Laurie W.A. (1978) *The Ecology and Behaviour of the Greater One-Horned Rhinoceros*. Doctoral dissertation, University of Cambridge.
- Miller M.A., Buss P.E. (2015) Rhinocerotidae (Rhinoceroses). In: Miller R.E., Fowler M.E. (eds.). *Fowler's Zoo and Wild Animal Medicine Vol. 8*. St. Louis, Missouri: Elsevier Saunders, 538–547.
- Miller R.E. (2003) Rhinocerotidae (Rhinoceroses). In: Fowler M.E., Miller R.E. (eds.) *Fowler's Zoo and Wild Animal Medicine. Fifth edition*. St. Louis: Missouri, Elsevier Saunders, 559–569.
- Owen-Smith R.N. (1974) The social system of the white rhinoceros. In: Geist V., Walthers F. (eds.) *The Behaviour of Ungulates and its Relation to Management*. Morges, Switzerland: IUCN, 341–351.
- Owen-Smith R.N. (1988) *Megaherbivores: The Influence of Very Large Body Size on Ecology*. Cambridge, UK: Cambridge University Press.
- Owen-Smith N., Ogutu J.O. (2013) Controls over reproductive phenology among ungulates: Allometry and tropical-temperate contrasts. *Ecography* 36(3): 256–263. doi:10.1111/j.1600-0587.2012.00156.x
- Patton F., Genade A.E. (2019) Behavioural observations of white rhinos at Ziwa Rhino Sanctuary—Analyses from 10 years of data collection. Uganda: Rhino Fund.
- Patton M.L., Swaisgood R.R., Czekala N.M., White A.M., Fetter G.A., Montagne J.P., Rieches R.G., Lance V.A. (1999) Reproductive cycle length and pregnancy in the southern white rhinoceros (*Ceratotherium simum simum*) as determined by faecal pregnane analysis and observations of mating behavior. *Zoo Biology* 18(2): 111–127. doi:10.1002/(SICI)1098-2361(1999)18:2<111::AID-ZOO3>3.0.CO;2-0
- Penny M. (1987) *Rhinos: Endangered Species*. London, UK: Christopher Helm.
- Pienaar U.de V. (1963) The large mammals of the Kruger National Park—Their distribution and present-day status. *Koedoe* 6(1): 1–37. doi:10.4102/koedoe.v6i1.810
- Pizzutto C.S., Colbachini H., Jorge-Neto P.N. (2021) One Conservation: The integrated view of biodiversity conservation. *Animal Reproduction* 18(2): e20210024. doi:10.1590/1984-3143-AR2021-0024
- Pluháček J., Steck B.L., Sinha S.P., von Houwald F. (2017) Interbirth intervals are associated with age of the mother, but not with infant mortality in Indian rhinoceroses. *Current Zoology* 63(3): 229–235. doi: 10.1093/cz/zow036
- R Core Team (2017) *R: A Language and Environment for Statistical Computing*. v3.4.1. Vienna, Austria: R Foundation for Statistical Computing <http://www.R-project.org/>
- Ritchie A.T.A. (1963) The black rhinoceros (*Diceros bicornis*). *African Journal of Ecology* 1(1): 54–62. doi:10.1111/j.1365-2028.1963.tb00178.x
- Rookmaaker K., Antoine P.O. (2012) New maps representing the historical and recent distribution of the African species of rhinoceros: *Diceros bicornis*, *Ceratotherium simum* and *Ceratotherium cottoni*. *Pachyderm* 52: 91–96.
- Roosevelt T., Heller E. (1914) *Life-histories of African Game Animals Vol. II*. New York, New York: Charles Scribner's Sons.
- Roth T.L. (2006) A review of the reproductive physiology of rhinoceros species in captivity. *International Zoo Yearbook* 40(1): 130–143. doi:10.1111/j.1748-1090.2006.00130.x
- Roth T.L., Stoops M.A., Robeck T.R., O'Brien J.K. (2016) Factors impacting the success of post-mortem sperm rescue in the rhinoceros. *Animal Reproduction Science* 167: 22–30. doi:10.1016/j.anireprosci.2016.01.019
- Schwarzenberger F., Francke R., Göldenboth R. (1993) Concentrations of faecal immunoreactive progesterone metabolites during the oestrous cycle and pregnancy in the black rhinoceros (*Diceros bicornis michaeli*). *Reproduction* 98(1): 285–291. doi:10.1530/jrf.0.0980285
- Schwarzenberger F., Walzer C., Tomasova K., Vahala J., Meister J., Goodrowe K.L., Zima J., Strauss G., Lynch M. (1998) Faecal progesterone metabolite analysis for non-invasive monitoring of reproductive function in the white rhinoceros (*Ceratotherium simum*). *Animal Reproduction Science* 53(1–4): 173–190. doi:10.1016/S0378-4320(98)00112-2
- Schwarzenberger F., Rietschel W., Vahala J., Holeckova D., Thomas P., Maltzan J., Baumgartner K., Schaftenaar W. (2000) Faecal progesterone, estrogen, and androgen metabolites for noninvasive monitoring of reproductive function in the female Indian rhinoceros, *Rhinoceros unicornis*. *General and Comparative Endocrinology* 119(3): 300–307. doi:10.1006/gcen.2000.7523
- Skinner J.D., Moss D.G., Skinner D.C. (2002) Inherent seasonality in the breeding seasons of African mammals: Evidence from captive breeding. *Transactions of the Royal Society of South Africa* 57(1–2): 25–34.
- Stoops M.A., Pairan R.D., Roth T.L. (2004) Follicular, endocrine and behavioural dynamics of the Indian rhinoceros (*Rhinoceros unicornis*) oestrous cycle. *Reproduction* 128(6): 843–856. doi:10.1530/rep.1.00328
- Subedi N., Lamichhane B.R., Amin R., Jnawali S.R., Jhala Y.V. (2017) Demography and viability of the largest population of greater one-horned rhinoceros in Nepal. *Global Ecology and Conservation* 12: 241–252. doi:10.1016/j.gecco.2017.11.008
- Van der Goot A.C., Martin G.B., Millar R.P., Paris M.C.J., Ganswindt A. (2015) Profiling patterns of faecal 20-oxopregnane concentrations during ovarian cycles in free-ranging southern white rhinoceros (*Ceratotherium simum simum*). *Animal Reproduction Science* 161: 89–95. doi:10.1016/j.anireprosci.2015.08.009
- van Noordwijk M.A., Willems E.P., Atmoko S.S.U., Kuzawa C.W., van Schaik C.P. (2013) Multi-year lactation and its consequences in Bornean orangutans (*Pongo pygmaeus wurmbii*). *Behavioral Ecology and Sociobiology* 67: 805–814. doi:10.1007/s00265-013-1504-y
- Ververs C., van Zijll Langhout M., Hostens M., Otto M., Govaere J., Durrant B., Van Soom A. (2017) Reproductive performance parameters in a large population of game-ranched white rhinoceroses (*Ceratotherium simum simum*). *PLoS One* 12(12): e0187751. doi:10.1371/journal.pone.0187751
- Wilhelm J.H. (1931) Das Wild des Okavangogebietes und des Caprivizipfels. *South-West African Scientific Society Journal* 7: 13.
- Zerbe P., Clauss M., Codron D., Bingaman Lackey L., Rensch E., Streich J.W., Hatt J.M., Müller D.W.H. (2012) Reproductive seasonality in captive wild ruminants: Implications for biogeographical adaptation, photoperiodic control, and life history. *Biological Reviews* 87(4): 965–990. doi:10.1111/j.1469-185X.2012.00238.x