

CORRELATES OF MALE MATING STRATEGIES IN WHITE RHINOS (*CERATOTHERIUM SIMUM*)

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Territoriality is a common male reproductive strategy exhibited by polygynous ungulates, and mature male white rhinos (*Ceratotherium simum*) establish and defend year-round territories. One-third of adult males in the study population in Matobo National Park, Zimbabwe, delimited territories that occupied most available space; other adult males were relegated to following a nonterritorial strategy. Correlates of male territoriality included age and body size. Testosterone levels also differed significantly between territorial and nonterritorial males but were not related to age. Overall patterns of association with adult females did not differ with male status. However, territorial males spent significantly more time with females of higher reproductive value. These results suggest that reproductive consequences of the two male strategies may not be equal.

Key words: *Ceratotherium simum*, rhinos, reproductive strategies, testosterone, territoriality, mating behavior

Reproductive strategies are shaped by natural selection favoring individuals with the greatest lifetime reproductive success. However, not all individuals adopt the same reproductive strategies (Gross, 1996); when competition for access to mates is severe, young reproductive individuals sometimes opt for alternative mating behaviors (Caro and Bateson, 1986; Rubenstein, 1980). This may be especially prevalent in species in which growth continues after sexual maturation and competitive ability is related to age. For example, in a variety of large mammals including elephant seals (*Mirounga angustirostris*—Le Boeuf, 1974), red deer (*Cervus elaphus*—Clutton-Brock et al., 1982), and horses (*Equus caballus*—Berger, 1986), older males defend harems, but young males do not. Instead, young males attempt to copulate with females surreptitiously or may defer reproduction.

Even when male mating behavior appears to be influenced by age, not all mature individuals follow the same pattern. Envi-

ronmental or demographic factors may constrain the number of males able to employ the most successful strategy, and force other mature males into "making the best of a bad job" (Dawkins, 1980). Variation in individual characteristics that lead to competitive asymmetries also may affect the age at which males switch from a less successful reproductive strategy to a more successful or optimal one (Clutton-Brock et al., 1979; Gross, 1996; Koprowski, 1993).

Among polygynous ungulates, territorial behavior is almost exclusively a male trait believed to function primarily as a reproductive strategy to secure mates (Gosling, 1986; Owen-Smith, 1977). Increases in population density and shifts in the operational sex ratios (Emlen and Oring, 1977) may alter the intensity of male-male competition in territorial species. Under elevated levels of intrasexual competition, costs of territory maintenance may be so great that alternative mating strategies are favored, even among mature males.

Adult male white rhinos (*Ceratotherium simum*) perform scent-marking behaviors, and their expression is related to a system of exclusive space use and space-correlated dominance (Owen-Smith, 1988; Pienaar et al., 1993). However, only some adult males in a population mark and defend such territories, and other adult males follow a non-territorial strategy (Owen-Smith, 1975; Rachlow et al., in press). To gain an understanding of factors influencing mating strategies of male white rhinos, we asked two questions: how do territorial and nonterritorial males differ and what are the potential reproductive consequences of these two male mating strategies? We contrasted age, body size, and testosterone levels of territorial and nonterritorial adult males. Sociality and association behavior with adult females were examined for males following each strategy.

MATERIALS AND METHODS

Our study was conducted during 1994–1995 in Matobo National Park, a 425-km² protected area in southwestern Zimbabwe. The Park is situated in the Matobo Hills that consist of granite domes and kopjes interspersed with grassland valleys and riparian areas (Wilson, 1969). Most of the white rhinos in Matobo Park ($n = 43$) inhabit a 105-km² fenced reserve, and an additional nine animals exist within the Park boundaries but outside of the fenced area. Individual adults and subadults were identified by ear-notching patterns and natural markings, and ages were known or estimates available from previous monitoring work in Matobo Park (Rachlow, 1997). We classified animals ≥ 6 years of age as adults. The youngest age at first reproduction for females in this population was 6.5 years (Rachlow and Berger, 1998). Males also appear to become sexually mature at ca. 6 years of age, although they may not breed successfully for several years after attaining this age (Bertschinger, 1994; Owen-Smith, 1988).

We collected measurements of body size from rhinos immobilized for radiocollaring. Total body length was measured along the spine from the base of the tail to the back of the skull. Chest girth was measured around the body behind the forelimbs and across the sternum. Neck girth

was measured around the neck at the smallest circumference, passing just behind the ears.

We collected fecal samples from known individuals after observation of defecation and analyzed these samples for concentrations of steroid hormones. Samples were kept frozen until thawed for laboratory analyses. A total of 0.5 g from each sample was extracted with 10 ml of ethyl acetate-hexane (3:2 v/v). The organic phase from each extraction was decanted and air-dried at 37°C for 2–3 h. The resulting residue was resuspended in 1.0 ml of phosphate buffer and frozen until assayed. We air-dried and weighed remaining fecal material from each extraction; concentrations were indexed to dried fecal weights, and results are reported in nanograms per gram of dried feces (ng/g). A commercial testosterone radioimmunoassay kit (Diagnostic Products Corp., Los Angeles, CA) was used to determine concentrations of testosterone in feces of males. Sample extracts from females were analyzed for progesterone metabolites using enzyme immunoassays following Munro and Stabenfeldt (1984) and Berkeley et al. (1997).

Females potentially will vary in receptivity to males at different times during their reproductive cycles. Mean interval between calves for 9 multiparous females in the study population ranged from 2.3 to 3.3 years (Rachlow and Berger, 1998) and given a gestation period of 16–17 months (Owen-Smith, 1988), females with young calves (<10 months) are unlikely to conceive. Analyses of fecal samples were used to identify pregnancy in females without calves and those accompanied by older calves (Berkeley et al., 1997; Rachlow, 1997). Pregnant females and females with young calves were classified as having low reproductive value to males because they were unlikely to conceive in the near future; non-pregnant females without calves or with calves >10 months old were classified as females with high reproductive value.

We conducted behavioral observations between 0500 h–1900 h, concentrating on the early morning and late afternoon periods when rhinos were most active. We located rhinos either by radiotracking or by following spoor with the help of scouts from the Zimbabwe National Parks. Activity patterns were quantified for focal groups with scan-samples collected at 5-min intervals (Altmann, 1974). Associations were recorded if individuals were ≤ 75 m (ca. 25 body lengths) from each other when first sighted, re-

TABLE 1.—*Body size of territorial and nonterritorial male white rhinos in Matobo National Park, Zimbabwe ($\bar{X} \pm SE$).*

Measurement (cm)	n	Territorial	n	Nonterritorial	Mann-Whitney U	P
Body length	5	263.2 \pm 8.8	4	250.0 \pm 4.7	14.0	0.327
Chest girth	5	298.0 \pm 11.8	4	254.0 \pm 3.6	20.0	0.014
Neck girth	5	179.6 \pm 4.0	3	159.3 \pm 2.4	15.0	0.024

ardless of their activities during the observation period. Groups were identified when individuals were ≤ 45 m (15 body lengths) from each other and exhibited synchronized activity patterns and cohesive behavior. Associations consisted of one or more groups, and patterns of association were analyzed based on proximity at first sighting to remove the potential bias of length of observation period. Following Owen-Smith (1975), we classified individuals that were sighted consistently together for periods of ≥ 1 month as a stable group, and groups that persisted for shorter periods as temporary groups. Observations were suspended if rhinos were disturbed by our presence and exhibited increased vigilance behavior for >5 min, or when a focal group was out of sight for >5 min. Nonparametric statistics were used to analyze data when sample sizes were too small to meet or adequately test for the assumptions required for parametric tests (Zar, 1984). Mean values are reported $\pm SE$.

RESULTS

Territorial males performed scent-marking behaviors that consisted of kicking with the rear legs immediately before and after defecation and spray-urination, often after scraping the rear feet across the ground (Owen-Smith, 1975, 1977). Territorial males always defecated and urinated in this fashion, but nonterritorial males did not scatter their dung and urinated in a stream like females. Territorial males in Matobo Park used areas that were exclusive of other territorial males, but nonterritorial males used areas that overlapped widely with all other males (Rachlow et al., in press). Within the fenced reserve of Matobo Park, one-third of adult males held territories that covered most of the available area.

Territorial males tended to be older, although overlap existed among ages. Mean

age for territorial males ($n = 3$) within the fenced reserve was 16.0 ± 4.7 years (range = 9–25 years) at the onset of the study. Following the death of the oldest male (25 years of age), who was killed in a fight and establishment of a new territorial male, mean age of territorial males ($n = 3$) in the fenced area was 11.7 ± 1.5 years (range = 9–13 years). The mean age of the nonterritorial males ($n = 8$) was 8.8 ± 0.7 years (range = 6–12 years). The only adult male in the group outside of the fenced reserve was 30 years old.

Growth continued after sexual maturation in white rhinos, and age-graded differences in body size existed between territorial and nonterritorial males. Body length in males increased with age and approached an asymptote at ca. 14 years, but chest girth approached an asymptote at ca. 20 years of age (Rachlow, 1997). No significant difference was observed in body length between territorial and nonterritorial males, but territorial males had significantly larger neck and chest girths (Table 1).

Territoriality among adult male rhinos was related positively to levels of fecal testosterone. Among adult males (≥ 6 -years old), fecal testosterone was not related significantly to age (Fig. 1). However, fecal testosterone levels were significantly higher (Mann-Whitney $U = 3.0$; $P = 0.028$) in territorial ($\bar{X} = 54.2 \pm 5.6$ ng/g, $n = 5$) than in nonterritorial (31.3 ± 4.0 ng/g, $n = 6$) adult males.

Association behavior with females differed in a subtle way between territorial and nonterritorial males. Although territorial males spent a greater percentage of time solitary, frequency of association with all

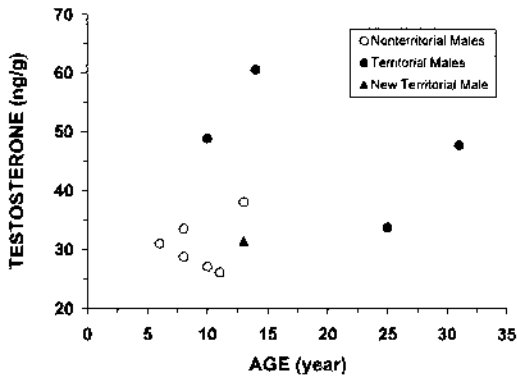


FIG. 1.—Relationship between fecal testosterone (ng/g dry feces) and age in white rhino males. Levels of fecal testosterone did not increase significantly with age among adult males ($F = 0.904$, $P = 0.367$, $n = 11$). The new territorial male began to establish a territory ca. 2 months prior to collection of the fecal sample.

adult females did not differ significantly between territorial and nonterritorial males (Fig. 2). Likewise, the number of different females observed in association with each male did not differ significantly with male status (territorial, $\bar{X} = 3.4 \pm 0.3$ females, $n = 5$; nonterritorial, 2.8 ± 0.6 females, $n = 8$; Mann-Whitney $U = 10.5$; $P = 0.150$). However, territorial males spent a significantly greater percentage of time with females of high reproductive value (Fig. 2).

The tendency for territorial males to associate with females with higher reproductive potential also was apparent in analyses of stable group formation (groups persisting for ≥ 1 month). Nonterritorial males rarely associated with reproductively valuable females for periods of ≥ 1 month. Territorial males ($n = 5$) formed stable groups with a significantly higher number of reproductively valuable females ($\bar{X} = 1.0 \pm 0.3$ females) than nonterritorial males (0.25 ± 0.03 females, $n = 8$) during this study (Mann-Whitney $U = 8.0$, $P = 0.043$). Although our measure of female reproductive value was somewhat crude, our data suggest that territorial males distinguished among females based on their reproductive

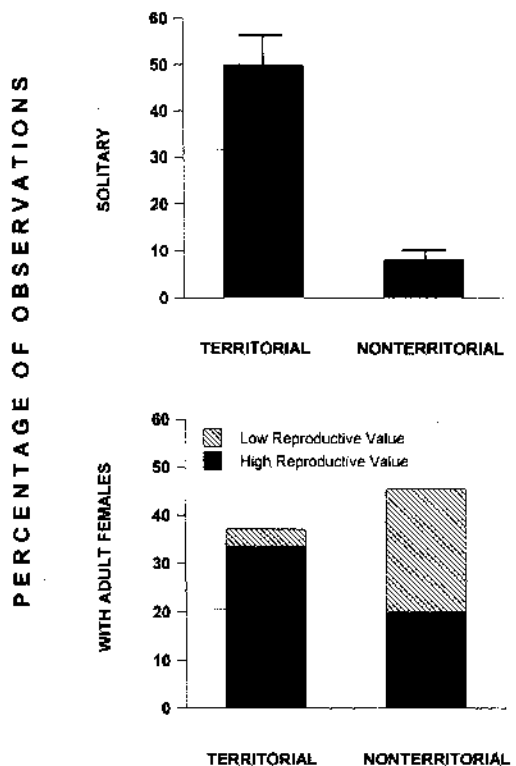


FIG. 2.—Patterns of association differed between territorial and nonterritorial adult males. Territorial males ($n = 5$) were observed solitary more frequently ($\bar{X} = 50.0 \pm 5.2\%$) than nonterritorial males ($8.1 \pm 3.6\%$, $n = 8$; Mann-Whitney $U = 0.0$, $P = 0.003$). Percentage of observations in which males were observed in association with any adult female of high or low reproductive value did not differ (Mann-Whitney $U = 22.0$, $P = 0.770$) between territorial males ($\bar{X} = 37.1 \pm 7.2\%$, $n = 5$) and nonterritorial males ($45.4 \pm 12.2\%$, $n = 8$). For territorial males, a greater percentage of all female associations occurred with females of high reproductive value (territorial, $\bar{X} = 90.9 \pm 6.2\%$; nonterritorial, $44.0 \pm 13.0\%$; Mann-Whitney $U = 5.0$, $P = 0.027$).

status and directed greater effort toward potentially valuable females.

DISCUSSION

Male mating strategies among polygynous sexually dimorphic mammals often are associated with age-graded or size-graded variation in mating success (Clutton-

Brock et al., 1982; Koprowski, 1993; Owen-Smith, 1993). White rhinos are a sexually dimorphic species in which males exhibit differing mating strategies. As in other polygynous ungulates, variation in patterns of male behavior is expected to result in variation in mating success. Owen-Smith (1977) hypothesized that territorial white rhinos achieve greater reproductive success than nonterritorial adult males. Our research represents the first detailed study of male mating strategies in this species and identifies correlates and potential consequences of male behavior.

Differences in scent-marking behaviors were useful in classifying adult male rhinos according to their territorial status. Territorial males marked and used ranges that excluded other males displaying territorial behavior (Rachlow et al., in press). In Umfolozi-Hluhluwe Reserve, South Africa, dominant territorial males were observed sharing territories with subordinate or "beta" males (Owen-Smith 1975). Although spatial overlap among territorial and nonterritorial males was high in our study, we did not observe cohabitation of a single territory by more than one male (Rachlow et al., in press), and patterns of behavior clearly differed between territorial and nonterritorial males.

Territorial males tended to be older than nonterritorial males. The age-structure of males in the fenced reserve was skewed toward younger animals because several older males were removed during the 1970s and 1980s due to fighting, and the oldest male was killed in a fight during our study (Rachlow, 1997). Despite the skewed age-structure, older males secured territories more often than did younger adult males.

Age differences between territorial and nonterritorial males were correlated with body size but not with testosterone levels. Body girth continued to increase with age, and territorial males had larger neck and chest circumferences than nonterritorial, younger males. These measurements likely reflect differences in body mass between

the two classes of males. Testosterone levels were significantly higher in fecal samples collected from territorial males than in those from nonterritorial males. However, fecal testosterone levels were not related to age, suggesting that territorial status and not just maturity is related to androgen levels.

The relationship between fecal testosterone and territoriality establishes a link between physiology and territorial behavior in male white rhinos. Similar correlations have been reported in other species of ungulates. Among white-tailed deer (*Odocoileus virginianus*), levels of serum testosterone were correlated with both male dominance and scent-marking behavior (Millar et al., 1987). Territorial behavior and testosterone also were correlated in a study of male Grevy's zebra (*Equus grevyi*), which documented significantly higher levels of testosterone in the urine of territorial males than in nonterritorial males (Chaudhury and Ginsberg, 1990). Furthermore, levels of urinary testosterone were related positively to reproductive behavior and reproductive status in male African elephants (*Loxodonta africana*—Poole et al., 1984). Numerous studies of birds also have established associations between territoriality, aggressive behavior, and levels of testosterone in males (Wingfield et al., 1990). Although causal relationships between androgen levels and reproductive behavior of males have not been fully explored, the link between territorial behavior, testosterone levels, and reproduction in male birds and mammals appears to be widespread.

Males should defend territories only when benefits outweigh costs (Brown, 1964; Davies, 1978), and the cost of territoriality in white rhinos is potentially high. In addition to energy expended during territory establishment and maintenance, territory defense and competition among male white rhinos may result in fight-related injuries. Fighting among males is believed to be the leading cause of mortality for male white rhinos in Kruger National Park, South Africa (D. J. Pienaar, pers. comm.). Injuries

sustained during fighting also were a frequent cause of death identified in populations of translocated white rhinos (Anderson, 1993) and were the source of highest mortality in free-ranging black rhinos (*Diceros bicornis*—Berger, 1994). During our study, one territorial male was killed in a fight with a neighboring territory holder. Although serious fights rarely are observed, defense of a territory is a potentially risky venture.

Young males should be more likely to follow an alternative mating strategy than older males for at least two reasons. First, they have a longer period of potential reproduction and should be less likely to take the risks associated with territory establishment. Males in polygynous species tend to have higher rates of mortality than females (Owen-Smith, 1993). Aside from fight-related mortality, survivorship of adult rhinos is high in areas where human predation is not prevalent (Owen-Smith, 1988). Second, although body length reaches an asymptote at ca. 14 years of age, chest girth, which is related to mass, continues to increase for several more years (Rachlow, 1997). In addition to having more social experience, older males are likely to be heavier than young adults. Thus, young adult males may be competitively disadvantaged in fights with prime-age males, as shown among numerous other long-lived mammals (Berger and Cunningham, 1994; Clutton-Brock et al., 1982; Le Boeuf, 1974; Poole, 1989). Although overlap in ages existed between the male classes, males following a nonterritorial strategy usually were younger.

Given that territoriality is potentially very costly, relatively large reproductive benefits are to be expected if territorial behaviors occur. Although a complete analysis of the payoffs of alternative reproductive strategies requires data about survivorship and lifetime reproductive success, an assessment of behavioral correlates of mating success can be useful in approximating relative reproductive payoffs for males following different strategies (Pemberton et al.,

1992). Patterns of association with adult females may indicate that the relative mating success of territorial and nonterritorial strategies is not equal. Territorial male rhinos in our study appeared to evaluate reproductive potential of females and expend more effort toward females that were more likely to mate and conceive (Fig. 2). Similarly, male bison (*Bison bison*) discriminate among females, and older males spend less total time with females but concentrate their efforts on those with the highest reproductive potential (Berger, 1989).

The degree to which female choice plays a roll in mate selection in rhinos is unknown. In other resource-defending ungulates, spatial distribution of females was influenced by female choice for territory quality (Carranza, 1995) and also male phenotype (Balmford et al., 1992). The tendency for non-pregnant female rhinos to associate with territorial males also may have been influenced by female choice for high-quality resources within territory boundaries or high-quality mates. Although the mechanism for mate selection is not clear, associations between territorial males and females with high reproductive potential may indicate that relative mating success is higher for males following the territorial strategy. However, observed patterns of sexual behaviors may not be correlated with absolute patterns of paternity (Amos et al., 1993; Ginsberg and Huck, 1989). Ultimately, genetic analyses are needed to test hypotheses about reproductive success and reproductive consequences of male mating strategies in white rhinos.

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LITERATURE CITED

- ALTMANN, J. 1974. Observational study of behavior: sampling methods. *Behaviour*, 49:227–267.
- AMOS, B., S. TWISS, P. P. POMEROY, AND S. S. ANDERSON. 1993. Male mating success and paternity in the grey seal, *Halichoerus grypus*: a study using DNA fingerprinting. *Proceedings of the Royal Society of London, (B)*, 252:199–207.
- ANDERSON, J. L. 1993. Management of translocated white rhino in South Africa. *Proceedings of the Third International Conference on Rhinoceros Biology and Conservation*, 287–293.
- BALMFORD, A., A. M. ROSSER, AND S. D. ALBON. 1992. Correlates of female choice in resource-defending antelope. *Behavioral Ecology and Sociobiology*, 31:107–114.
- BERGER, J. 1986. Wild horses of the Great Basin: social competition and population size. The University of Chicago Press, Chicago, Illinois, 326 pp.
- . 1989. Female reproductive potential and its apparent evaluation by male mammals. *Journal of Mammalogy*, 70:347–358.
- . 1994. Science, conservation, and black rhinos. *Journal of Mammalogy*, 75:298–308.
- BERGER, J., AND C. CUNNINGHAM. 1994. Bison: mating and conservation in small populations. Columbia University Press, New York, 330 pp.
- BERKELEY, E. V., J. F. KIRKPATRICK, N. E. SCHAFER, W. M. BRYANT, AND W. R. THRELFALL. 1997. Serum and fecal steroid analysis of ovulation, pregnancy, and parturition in the black rhinoceros (*Diceros bicornis*). *Zoo Biology*, 16:121–132.
- BERTSCHINGER, H. J. 1994. Reproduction in black and white rhinos: a review. *Proceedings of a Symposium on Rhinos as Game Ranch Animals*, 1:122–161.
- BROWN, J. L. 1964. The evolution of diversity in avian territorial systems. *The Wilson Bulletin*, 76:160–169.
- CARO, T. M., AND P. BATESON. 1986. Organization and ontogeny of alternative tactics. *Animal Behaviour*, 34:1483–1499.
- CARRANZA, J. 1995. Female attraction by males versus sites in territorial rutting red deer. *Animal Behaviour*, 50:445–453.
- CHAUDHURY, M., AND J. R. GINSBERG. 1990. Urinary androgen concentrations and social status in two species of free-ranging zebra (*Equus burchelli* and *E. grevyi*). *Journal of Reproduction & Fertility*, 88:127–133.
- CLUTTON-BROCK, T. H., F. E. GUINNESS, AND S. D. ALBON. 1982. Red deer: the behavior and ecology of two sexes. The Chicago University Press, Chicago, Illinois, 378 pp.
- CLUTTON-BROCK, T. H., S. D. ALBON, R. M. GIBSON, AND F. E. GUINNESS. 1979. The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus*). *Animal Behaviour*, 27:211–225.
- DAVIES, N. B. 1978. Ecological questions about territorial behaviour. Pp. 317–367, in *Behavioural ecology: an evolutionary approach* (J. R. Krebs and N. B. Davies, eds.). Blackwell Science, Oxford, United Kingdom, 494 pp.
- DAWKINS, R. 1980. Good strategy or evolutionarily stable strategy. Pp. 331–367, in *Sociobiology: beyond nature/nurture?* (G. W. Barlow and J. Silverberg, eds.). Westview Press, Inc., Boulder, Colorado, 627 pp.
- EMLEN, S. T., AND L. W. ORING. 1977. Ecology, sexual selection and the evolution of mating systems. *Science*, 197:215–223.
- GINSBERG, J. R., AND U. W. HUCK. 1989. Sperm competition in mammals. *Trends in Ecology and Evolution*, 4:74–79.
- GOSLING, L. M. 1986. The evolution of mating strategies in male antelopes. Pp. 244–281, in *Ecological aspects of social evolution: birds and mammals* (D. I. Rubenstein and R. W. Wrangham, eds.). Princeton University Press, Princeton, New Jersey, 551 pp.
- GROSS, M. R. 1996. Alternative reproductive strategies and tactics: diversity within the sexes. *Trends in Ecology and Evolution*, 11:92–98.
- KOPROWSKI, J. L. 1993. Alternative reproductive tactics in male eastern gray squirrels: "making the best of a bad job." *Behavioral Ecology*, 4:165–171.
- LE BOEUF, B. J. 1974. Male-male competition and reproductive success in elephant seals. *American Zoologist*, 14:163–176.
- MILLAR, K. V., R. L. MARCHINTON, K. J. FORAND, AND K. L. JOHANSEN. 1987. Dominance, testosterone levels, and scraping activity in a captive herd of white-tailed deer. *Journal of Mammalogy*, 68:812–817.
- MUNRO, C. J., AND G. STABENFELDT. 1984. Development of a microtiter plate enzyme immunoassay for the determination of progesterone. *Journal of Endocrinology*, 101:41–49.
- OWEN-SMITH, R. N. 1975. The social ethology of the white rhinoceros *Ceratotherium simum* (Burchell 1817). *Zeitschrift für Tierphysiologie*, 38:337–384.
- . 1977. On territoriality in ungulates and an evolutionary model. *The Quarterly Review of Biology*, 52:1–38.
- . 1988. Megaherbivores: the influence of very large body size on ecology. Cambridge University Press, Cambridge, United Kingdom, 369 pp.
- . 1993. Age, size, dominance and reproduction among male kudus: mating enhancement by attrition of rivals. *Behavioral Ecology and Sociobiology*, 32:177–184.
- PEMBERTON, J. M., S. D. ALBON, F. E. GUINNESS, T. H. CLUTTON-BROCK, AND G. A. DOVER. 1992. Behavioral estimates of male mating success by DNA fingerprinting in a polygynous mammal. *Behavioral Ecology*, 3:66–75.
- PIENAAR, D. J., J. DU P. BOTHMA, AND K. G. THERON. 1993. White rhinoceros range size in the south-west-

- ern Kruger National Park. *Journal of Zoology* (London), 229:641–649.
- POOLE, J. H. 1989. Mate guarding, reproductive success and female choice in African elephants. *Animal Behaviour*, 37:842–849.
- POOLE, J. H., L. H. KASMAN, E. C. RAMSAY, AND B. L. LASLEY. 1984. Musth and urinary testosterone concentrations in the African elephant (*Loxodonta africana*). *Journal of Reproduction & Fertility*, 70: 255–260.
- RACHLOW, J. L. 1997. Demography, behavior, and conservation of white rhinos. Ph.D. dissertation, The University of Nevada, Reno, 126 pp.
- RACHLOW, J. L., AND J. BERGER. 1998. Reproduction and population density: trade-offs for the conservation of rhinos *in situ*. *Animal Conservation*, 2:37–42.
- RACHLOW, J. L., J. G. KJE, AND J. BERGER. In press. Territoriality and spatial patterns of white rhinoceros in Matobo National Park, Zimbabwe. *African Journal of Ecology*.
- RUBENSTEIN, D. J. 1980. On the evolution of alternative mating strategies. Pp. 1–44, in *Limits to action: the allocation of individual behavior* (J. E. R. Staddon, ed.). Academic Press, New York, 308 pp.
- WILSON, V. J. 1969. The large mammals of the Matopos National Park. *Arnoldia*, 4:1–32.
- WINGFIELD, J. C., R. E. HEGNER, A. M. DUFTY JR., AND G. F. BALL. 1990. The "challenge hypothesis": theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. *The American Naturalist*, 136:829–846.
- ZAR, J. H. 1984. *Biostatistical analysis*. Prentice-Hall, Englewood Cliffs, New Jersey, 718 pp.

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