Natural Variation in Horn Size and Social Dominance and Their Importance to the Conservation of Black Rhinoceros

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Introduction

The importance of behavioral ecology to evolutionary theory, zoo biology, and animal husbandry is well recognized (Caro 1994; Krebs & Davies 1984), but, despite the prevalence of global biodiversity issues, its contribution to in situ conservation has been limited (Soulé 1986; Ulfstrand 1996; Clemmons & Buchholz 1997). Populations of the world's elephants and rhinoceros have been decimated by poaching; in Africa, rhino conservation measures increasingly rely on protection in heavily guarded reserves (Brett 1990). Extreme measures have included dehorning and shooting poachers. Although the case has been made that social status in black rhinos (*Diceros bicornis*) is unaffected by horn removal (Lindeque 1990), it is less than convincing because neither the inter- nor intrasexual consequences of asymmetries in horn size on dominance have been studied.

To understand horn function, models of sexual selection have been applied to dimorphic ungulates (Jarman 1983; Packer 1986; Clutton-Brock 1988), but predictions do not fit black rhinoceros because (1) the sexes are similar in horn and body size, (2) secondary sex ratios are equal, and (3) mortal fighting, the highest recorded for any mammal, results in about 50% of the males and 30% of the females dying from combat-related wounds (Berger 1994). We report field data on 52 black rhinoceros of known horn and body size and 442 dyadic encounters from three sites in northern Namibia. Our results suggest that intersexual dominance is female-biased, that intrasexual dominance is related to horn mass in males but not in females, and that where asymmetries between horned participants exceed 10 cm, larger horns confer

dominance advantages. These findings are relevant because they (1) fail to refute the possibility that female horns function interspecifically in neonatal protection from predators and (2) illustrate that nonexperimental and even limited data sets predicated on knowledge of a species' behavioral ecology contribute to conservation—in this case, why dehorning programs may inadvertently affect intrasexual relations in one gender (males) more than the other.

Background and Methods

Our analyses are based on data gathered during 1030 hours of direct observation aided by night vision systems during 197 nights (1991–1993) on three discrete subpopulations in Etosha National Park, Namibia. The sites (separated by about 70 and 200 km) are designated A, B, and C, each having 10, 26, and 16 adult rhinos, respectively. Social rank was determined by calculating the frequency of individuals displacing or being supplanted in dyadic encounters and by subsequent rankings checked by comparing results of two methods: standard matrices with the proportion of winners and losers ranked and absolute differences in dyadic outcomes (Wilson 1975; Appleby 1982); both were highly correlated (Table 1). Individuals not observed in at least 2 consecutive years and young animals were excluded. Although intraspecific interactions can result in play (Owen-Smith 1988), of the 614 witnessed, dominance was evident in 442 (72%). To evaluate the effects of horns, we estimated horn and head size photogrammetrically, which yields greater than 95% accuracy (Rachlow & Berger 1997), and removed potential age effects by partial correlation (Table 2) because age and head size are correlated (Goddard 1970).

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Table 1.   Descriptive summary of study areas, anterior horn and head (± SE), and the Spearman rank (r_s) correlation coefficients and probability values (in parentheses) between two methods of rank-assessed dominance.[a]

| | Study area[b] | | | | | |
| | A | | B | | C | |
Trait	females (5)	males (5)	females (12)	males (14)	females (8)	males (8)
Anterior horn length (cm)	25.7 (3.47)	28.5 (3.17)	28.3 (1.84)	28.4 (1.80)	36.9 (2.80)	28.6 (2.85)
Basal width (cm)	10.8 (0.37)	13.0 (0.87)	12.1 (0.51)	11.8 (0.28)	12.7 (0.48)	13.2 (1.24)
Head size (cm)[c]	16.4 (0.24)	16.6 (0.69)	16.9 (0.41)	16.5 (0.26)	19.8 (0.88)	19.7 (1.09)
Dominance	0.90 (0.10)	0.97 (0.02)	0.77 (0.01)	0.98 (0.001)	0.70 (0.10)	0.66 (0.10)

[a] Rank-assessed dominance (bottom row) was determined by comparing standard matrices with the proportion of winners and losers ranked and absolute differences in dyadic outcomes (Wilson 1975; Appleby 1982).
[b] N is in parentheses after sex.
[c] Distance from eye to nostril. The relationship between head size (occipital condyle to tip of nose) and distance of eye to nostril is $y = 2.722x + 2.458$; $p < 0.0001$; $r^2 = 0.98$ (n = 46).

A problem in working with large-bodied species is that sample sizes will be low. For instance, a majority of the world's rhinos are confined to areas with fewer than 50 individuals (Ryder 1993). So, despite our sample of 52 individually known adults, irrespective of gender the number of adults in any of our study areas varied from 10 to 26, limiting statistical power. To reduce the possibility of a Type II error (that is, failing to reject the null hypothesis when false; Cohen 1988), we raised the alpha level to 0.10. We also used three discrete study areas and checked whether the effects of horns and gender on dominance were similar across sites.

Results and Discussion

If horns play equally important roles in females and males, with other factors equal, larger horns should confer social advantages. The data fail to support this prediction. At all sites, females dominated males (Fig. 1). Despite the similarity of female and male horn masses (Berger et al. 1993; Berger & Cunningham 1995), intersexual dominance might arise because females with young are more aggressive. This explanation is untena-

ble, however, because even nonparous females were dominant to males. If horn size were important, females should dominate in encounters when their horns are larger, not the converse. This was not the case. Independent of horn size, nonparous females dominated intersexual encounters, displacing males 81% of the time when horns were larger and 74% when smaller ($n = 16$, 23, respectively). The lack of difference ($p = 0.447$) suggests that gender affects intersexual dominance more than horn size.

Intrasexually, two lines of evidence indicate that horns are associated with dominance for one gender but not the other. First, in 128 male-male interactions, individuals with larger horns dominated 65% of the encounters, but among females, bigger-horned individuals won in only 20% of 46 interactions; the effects of horn asymmetries on outcomes of dyadic encounters were greater in males than in females ($G = 29.16$; $p < 0.001$). Second, with the effects of age removed, male horn mass and rank were positively associated at all sites (Table 2). Although statistical power at study site A is low because only five males were resident, the existing partial rank order coefficient ($xy.z = 0.52$) would achieve significance with one more male. In contrast, for females a positive relationship between horns and rank existed in

Table 2.   Relationships between dominance in adult female and male black rhinoceros at three sites in Etosha National Park and anterior horn mass, head size (age), and effects of head size removed (partial correlation, $T_{xy.z}$).[a]

Site	n[b]	Horn mass	Head size	$T_{xy.z}$	Minimum[c]
Females					
A	5	0.000 (0.50)	0.359 (0.19)	0.459 (0.20<)	+3
B	12	−0.349 (0.06)	−0.114 (0.30)	−0.372 (0.10<)	none
C	8	−0.077 (0.39)	−0.039 (0.45)	0.067 (<0.50)	100
Males					
A	5	0.527 (0.10)	0.222 (0.29)	0.519 (0.20<)	+1
B	14	0.379 (0.03)	0.068 (0.37)	0.384 (0.05)	none
C	8	0.692 (0.01)	0.593 (0.02)	0.451 (0.10<)	none

[a] All values are for Kendall's tau, with probability in parentheses.
[b] Sample size per site.
[c] The required sample size to achieve $p < 0.10$, given the existing partial correlation and the assumption that horns are associated with dominance.
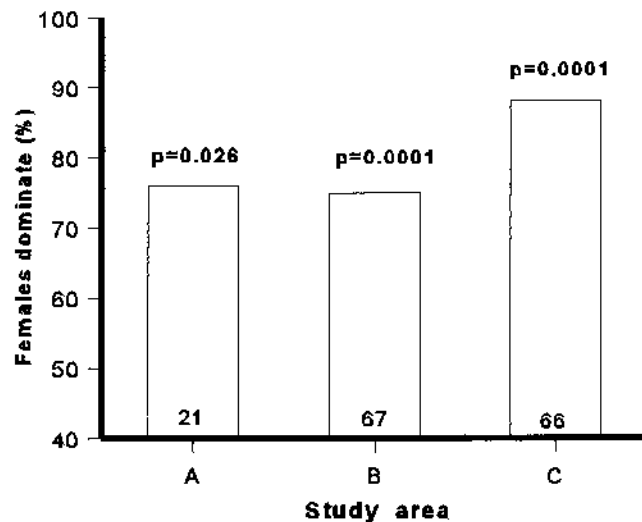
Figure 1. Proportion of contact encounters in which adult black rhino females dominated males at three sites within Etosha National Park. The p values are based on binomial distribution to determine the probability of deviation from an expected 50:50 outcome. Sample sizes as indicated within the bars.

only one area. At site C a sample of at least 100 additional females would be required to detect statistical significance given the existing partial correlation, yet, given the small size of most remaining populations, having this many rhinoceros interacting at the same site is highly improbable. At site B an inverse relationship between dominance and anterior horn existed ($xy.z = -0.37$; $p < 0.05$; Table 2).

Hence, whereas horns were consistently related to dominance in males, our analyses failed to discern a similar pattern among females. These findings suggest, in this sexually monomorphic species, that horns either play a greater intrasexual role in males than in females, or that female horns and dominance are not related in obvious ways. It is also possible that female horns, although intrasexually unimportant, function interspecifically in neonate defense against predators (Berger & Cunningham 1994, 1996), as they may in sexually dimorphic horned bovids (Packer 1986). Or, as others have suggested, female horns may simply be nonadaptive (Lindeque & Erb 1995).

Although explanation of the evolution of traits such as horns is fundamental in behavioral ecology, from a conservation perspective what is essential is the prediction of consequences of horn size asymmetries because three African countries have employed dehorning programs for black rhinoceros (Milner-Gulland et al. 1992; Cunningham & Berger 1997). Our data on inter- and intrasexual differences in dominance raise a question about the degree of variation in horn size necessary to produce consistent outcomes. Where dyads differed in horn size

by less than 10 cm, winners with larger horns did not deviate from a 50:50 win-to-loss ratio (Fig. 2). But, with asymmetries from 12 to 28 cm, smaller-horned individuals were regularly put at a disadvantage ($p = 0.0004$; Fig. 2).

These findings have direct relevance to how the study of behavioral ecology can contribute to conservation. In dehorned black rhinoceros, anterior horn regrowth averages about 6 cm/year (cumulative total for both horns = 8.7 cm/year; Berger et al. 1993). Because most black rhinoceros populations are small (Ryder 1993), extinction risks have been minimized both by developing satellite populations and by the induced migration of new individuals. A fundamental dilemma concerns the timing of adding new rhinoceros to existing populations. If all members are dehorned simultaneously but new individuals with intact horns are added 2 years later, asymmetries in horn size between dehorned residents and horned immigrants will, on average, exceed 10 cm (Table 1), so social disparities should be great (Fig. 2). Alternatively, if immigrants are dehorned but residents have been dehorned for longer than 2 years, asymmetries will still be large and immigrants are likely to be socially disadvantaged. In either case, intact black rhinoceros have the highest rate of fatal fighting known for any mammal (Berger 1994), so a potential consequence of increasing horn size asymmetries is an increase in mortal wounding. Therefore, frequent horn pruning may be necessary to minimize social disparities, fight-related mortality, and
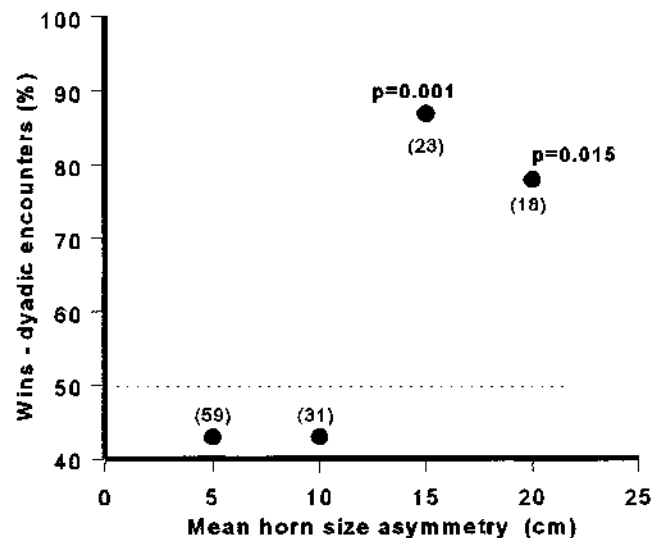

Figure 2. Relationships between asymmetries in mean anterior horn size during agonistic encounters and the proportion dominated by larger-horned individuals. Sample sizes are of events for all individuals in a single year. The probability that differences in mean anterior horn size during agonistic encounters deviates from 50:50 (dotted line) with horn size asymmetries at 5 and 10 cm is $p = 0.24$ and $p = 0.19$, respectively. Other probability values are in the figure.

perhaps poaching risks (Milner-Gulland et al. 1992; Cunningham & Berger 1997).

If interventive management via horn size manipulations is an achievable goal in the conservation of black rhinoceros, then the maintenance of minimal intrapopulation variation is likely to alter patterns of intrasexual dominance among males and to decrease fight-related mortality in both sexes of black rhinoceros. Nevertheless, to achieve maximal success, this strategy will also require intense monitoring of both individual behavior and horn regrowth, and it will necessitate risks associated with frequent immobilization. For our findings to have relevance for the conservation of the world's other rhinoceratids, an enhanced understanding of their behavioral ecology is needed. For instance, substantial sexual dimorphism exists in both greater one-horned rhinoceros (*Rhinoceros unicornis*) and white rhinoceros (*Ceratotherium simum*), with males having either tusk-like incisors (Dinerstein 1991) or larger horns and bodies than females (Owen-Smith 1988; Rachlow & Berger 1997). Thus, unlike in black rhinoceros, horn size in white rhinoceros is likely a product of sexual selection (Berger 1994), and the intrasexual outcome of horn size asymmetries, whether occurring naturally or through dehorning programs, may differ among species.

Our prior efforts to understand the consequences of dehorning were primarily concerned with interspecific encounters because intraspecific interactions among hornless black rhinoceros in the Namib Desert were not witnessed (Berger & Cunningham 1994, 1995, 1996). The data from this paper, however, allow empirically-based assessments of some of the expected social consequences of variation in horn size. Although the study of behavioral ecology continues to be guided by evolutionary theory, its use in conservation can be improved by asking direct questions about short-term consequences of anthropogenic perturbation on the biology of a species.

Acknowledgments

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