
Phenotypic Alterations, Evolutionarily Significant Structures, and Rhino Conservation

JOEL BERGER
CAROL CUNNINGHAM

Program in Ecology, Evolution, and Conservation Biology
University of Nevada
1000 Valley Road
Reno, NV 89512, U.S.A.

Abstract: *To slow the impending loss of wild black (Diceros bicornis) and white (Ceratotherium simum) rhinos, three African countries have resorted to dehorning, a practice designed to remove the incentive for poachers to kill the hornless animals. The efficacy of this controversial conservation action remains unknown, in part because much uncertainty exists about the functional significance of rhino horns. We assessed the current utility of horns in Namibian black rhinos from phenotypically altered and intact populations in the Namib Desert, and we collated data on mortal fighting among horned females living in Etosha National Park. Infant mortality was 100% when dehorned mothers were sympatric with spotted hyenas (Crocuta crocuta). In contrast, infant survival was 100% for both horned mothers living with hyenas and occasional lions (Panthera leo) and 100% for dehorned mothers in the absence of dangerous carnivores. These data suggest that female horns can have direct fitness benefits in terms of calf survival. However, because lethal wounding due to fighting may account for up to 33% of the mortality of horned females, dehorning may improve adult survivorship. Our results (1) suggest that, where the aim of conservation programs is to improve population viability through juvenile recruitment, dehorning is unlikely to be a prudent strategy if practiced in areas with dangerous predators, and (2) illustrate the value of experimental approaches to onerous problems in conservation.*

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Alteraciones fenotípicas, estructuras evolutivamente significativas y conservación de rinocerontes

Resumen: *Para retardar la inminente pérdida de los rinocerontes salvajes negros (Diceros bicornis) y blancos (Ceratotherium simum), tres países Africanos han recurrido a la extracción de los cuernos, una práctica destinada a eliminar el incentivo de los cazadores furtivos para matar animales sin cuernos. La eficacia de esta controversial medida de conservación es aún desconocida en parte porque existen muchas dudas acerca de la significancia funcional de los cuernos de los rinocerontes. Nosotros evaluamos la utilidad corriente de los cuernos en los rinocerontes negros de Namibia a partir de poblaciones alteradas fenotípicamente y poblaciones intactas en el Desierto de Namibia y reunimos datos sobre peleas mortales entre hembras con cuernos en el Parque Nacional de Etosha. La mortalidad infantil fue del 100% cuando las madres sin cuernos vivían en simpatria con hienas moteadas (Crocuta crocuta). En forma opuesta, la supervivencia infantil fue del 100% tanto para madres con cuernos que vivían con hienas y ocasionalmente con leones (Panthera leo) como para madres sin cuernos en ausencia de carnívoros peligrosos. Estos datos sugieren que los cuernos de las hembras pueden tener un beneficio directo sobre el fitness en términos de la supervivencia de los becerros. Sin embargo, dado que el 33% de la mortalidad de hembras con cuernos es debida a heridas mortales por peleas, la extracción de los cuernos mejoraría la supervivencia de los adultos. Nuestros resultados 1) sugieren que cuando el objetivo de los programas de conservación es el mejoramiento de la viabilidad poblacional a través del reclutamiento de juveniles, la extracción de cuernos no sería una estrategia prudente si se practica en áreas con predadores peligrosos y 2) ilustran el valor de aproximaciones experimentales para problemas de conservación onerosos.*

Introduction

The study of adaptive traits is at the core of evolutionary theory (Mayr 1982; Reeve & Sherman 1993), and recent attention has focused on relationships between morphological structures and individual fitness—particularly the experimental alteration of avian ornaments (Anderson 1982; von Schantz et al. 1989; Jones & Montgomery 1992). Rarely has such inquiry been directed toward the conservation of taxa confronted by problems of rapid depletion. Among the world's most endangered mammals are the Rhinocerotidae, whose five species are killed for their horns (Western 1987; Ryder 1993). Although numerous controversial conservation strategies have been proposed, perhaps the most contentious has been that of horn removal (Western 1982), a tactic first adopted for black rhinos in Namibia in 1989 and followed subsequently by Swaziland and Zimbabwe (Lindeque 1990; Kock & Atkinson 1993). While the assumption that horn removal will reduce poaching pressure remains untested, it is known that horn regenerates rapidly and poachers show little discrimination among horn sizes (Bigalke 1945; Berger et al. 1993). To determine whether dehorning has a chance to be effective biologically requires information about the current utility of horns. The prevailing model for the significance of mammalian secondary structures such as antlers or horns is sexual selection in which access to mates is enhanced through male-male competition (Geist 1966; Ralls et al. 1980; Clutton-Brock 1982). For at least two species of rhinocerotids, Indian and white, sexual selection may adequately explain why males have enlarged incisors or bodies relative to females (Dinerstein 1991; Dinerstein & Price 1991; Owen-Smith 1988). However, for black rhinos, sexual selection appears to be an inappropriate paradigm because the sexes are equal in both horn and body sizes (Hitchins 1968; Freeman & King 1969; Berger 1994). Other models predict that horns function in mate choice and predator defense (Geist 1966; Packer 1983; Kiltie 1985), but in the absence of data concerning the current utility of horns it has been impossible to gauge whether the dehorning of rhinos is likely to conserve rhinos effectively. Here we report our three-year findings concerning the demographic effects of dehorning wild black rhinos. We make two points: (1) hornless females suffer lower reproductive success than their horned conspecifics when the former live sympatrically with spotted hyenas; and (2) among horned females about 33% of the deaths resulted from lethal wounds. These data are important because they suggest a current utility for horns, and they offer only mixed support for the idea that dehorning is a prudent conservation strategy.

Background and Methods

We studied black rhinos from 1991 through 1993 in two areas of Namibia: (1) Etosha National Park (ENP;

19°S, 14°40'–17°E) is a 22,000-km² reserve with only horned rhinos that coexist with potentially dangerous predators, spotted hyenas and lions, and (2) a region of the northern Namib Desert (NND; about 19°S70'–20°80'S, 13°80'–14°20'E) of about 7000 km² of unprotected land with three geographically distinct populations of dehorned and horned rhinos, all in exceptionally xeric areas receiving an average of less than 100 mm of precipitation annually. The Namibian government dehorned females and males, and for security we refer to our NND study areas as *A*, *B*, and *C*. The status of large carnivores and year of dehorning is as follows: *Area A*—horned rhinos with spotted hyenas and occasional lions; *Area B*—hornless rhinos without lions or spotted hyenas (1991); *Area C*—hornless rhinos with spotted hyenas only (1989). Evidence of interchange between areas does not exist. A country-length veterinary cordon fence isolates *Area A* from *B* and *C*, although breakage by elephants has resulted in limited short-term movements by two male rhinos between *A* and *C*. Females have not moved between areas. A total of 104 individuals were identified by ear tears and notches or by lip wrinkles, and horns and data were gathered on 248 interactions between rhinos and dangerous predators on 202 nights using night-vision equipment (Berger & Cunningham 1994a).

Horn size was calculated for rhinos observed at night by using a Mitutoyo (500 Series) Photogrammetric Digital Caliper attached to a 300-mm Nikon lens (Jacobsen 1986), equipment which estimates with 98% accuracy the size of known morphological structures. Horns were scaled on photographs using a Jandel Scientific Digitizer. The procedure involves measuring to the nearest 0.01 mm the degree of ring extension on the focused telephoto lens. The device loses accuracy if the subject is more than 37 meters distant. Animals of the Kunene Province were photographed with a 500-mm Nikon lens during the day from within 70 meters, estimated by a Leitz rangefinder, a distance where the average error of morphological features is not more than 5%. Possible sources of bias in our estimates include darkroom procedures and the crispness of photos, problems for which we attempted to correct by avoiding commercial laboratories and by only one of us (C. Cunningham) performing the darkroom work using standardized enlarger heights. Horn mass (Y) on live animals was estimated by $Y = 15.49X - 0.21$ ($r^2 = 0.83$; $p < 0.0001$), where X is horn length times circumference, a relationship derived by measurements obtained from 104 horns confiscated by the Namibian government.

Body condition was assessed by gauging the degree of rib, spine, and pelvic prominence by ranking individuals categorically with scores from 1 (poor) to 5 (best) following suggestions of Keep (1971). A relation between horn length (cm) and age (years) was derived from 37

skulls whose sex had been previously recorded or was known to us through either on-site investigation or examination of sex differences in pelvises. Age was estimated according to Hitchins (1978) based on tooth wear and eruption. Our estimates should not differ by a maximum of more than 4 years for those animals calculated to be 37 years old; for younger animals, the absolute error will be less.

Like most nocturnal, asocial mammals occurring at low densities (Norton 1990; Matsson & Reid 1991), rhinos are difficult to study. Mothers with neonates are exceptionally secretive, and the dyads may be separated by up to 19 km when mothers go to water (Berger 1993). Our evidence on calf mortality therefore requires explanation. At night, calves younger than 6 months are generally alone and stationary and are re-joined by their mothers after the latter have satiated their thirst. This is rare during the day (Berger 1993). We recorded deaths when known mothers were re-sighted without calves. While it is possible that calves may have been elsewhere, this is unlikely. Of our daytime observations ($n = 139$) of 19 calves older than 6 months and 39 sightings of six calves younger than 6 months of age, 100% were of mothers with young. This strong association between mothers and young calves suggests that calves may be dead or injured when not with their mothers. To further substantiate the absence of calves after a known mother had been found, we relied on two other criteria. First, because mothers nurse young for at least 18 and perhaps up to 30 months, the absence of udders or pendulous teats indicates that milk production has ceased. So if a solitary mother who had been known to have a young calf was not parous, we deduced that the calf had died. Second, we used a professional tracker (A. Gawuseb), and together all of us searched for small footprints. We assumed a mortality if after a minimum of 4 days calf signs were not detected.

We also inferred a calf mortality if mothers had enlarged or receding teats but had been observed calfless multiple times, simply because all female mammals have teats and because rhino mothers and young associate (see above). It is possible, however, that we might wrongly assign a putative calf to a female that had not been lactating. To check the possibility of error, we evaluated our accuracy in identifying parity using unlabeled night photographs (Fig. 1) when lactational status was previously known through observations: 100% of 11 females were correctly assigned to nonlactating and 95% (19 of 20) to lactating categories. Had a female mistakenly been assigned nonparous status when she had been lactating, we would have failed to conclude that a calf had been born. Alternatively, had we erred by claiming that a nonlactating female had a calf when she did not, our mistake would have added a mortality. Obviously the latter is the more serious error biologically.

Fortunately, despite our 97% (30/31) accuracy, any error would not result in the claim of an additional calf mortality. And appraising parity during the day (when our work was done in the NND) is far easier than at night (ENP) as in the above exercise (see Fig. 1).

Results

If maternal horn size influenced calf protection, then calves of smaller-horned mothers should be maimed (missing ears or tails) or die more frequently as the result of dangerous predators. In Waterberg Reserve, an area where lions and spotted hyenas have been eliminated, none of the rhinos were missing ears or tails ($n = 29$) (P. Erb, personal communication), but maiming in ENP and the NND was about 4.6% ($n = 194$) and 3.4% ($n = 58$), respectively. Mothers of maimed calves had anterior horns that did not differ statistically in length from those of mothers with living, nonmaimed calves ($t = 1.56$, $df = 33$, NS; Fig. 2). The possibility of a Type II error cannot be dismissed due to the small sample of mothers of maimed calves. Similarly, horn mass (anterior and posterior combined) did not vary between maternal categories ($t = 1.39$, $df = 33$, NS). Although the foregoing suggests little association between maternal horn size or mass with calf protection, data from the NND reveal striking demographic effects.

All calves of mothers in *Area C* (dehorned females, hyenas present) died within one year of birth, whereas calf survival was 100% in the dehorned population living without dangerous predators (*Area B*) and 100% for horned mothers sympatric with hyenas and occasional lions (Fig. 3). Despite the small sample, differences in recruitment among areas exist ($p = 0.017$ Fisher's [3×2] Exact Test; *B* versus *C*, $p = 0.05$; *A* versus *C*, $p = 0.029$) and suggest that female horns have current utility.

Our evidence on calf mortality requires further explanation. Two mother/young dyads were initially observed in 1992, but subsequent observations revealed the same females without calves. The presence in 1992 of a third calf was deduced because another female with enlarged teats had been observed calfless. If, to be conservative, we assume only two births and deaths, then the probability that two calves would die by chance from *Area C* relative to calves in the dehorned control or horned populations approaches significance ($p = 0.10$ to 0.067 , respectively). Based on the foregoing evidence, however, it is more likely that three calves had been born. By early 1993 none were living in *Area C*. Not only do our data indicate that dehorned mothers lost calves, but they also suggest that mothers cannot safely protect their neonates for at least three years after horn removal, a period when the mean size of regrown anterior horns is about 47% the length of those of horned mothers whose calves survived (Fig. 2).

These results imply that hyena predation may be responsible for poor calf recruitment, but other explanations exist. First, food may have been limited in *Area C*. If so, this should be reflected by variation in body condition. For instance, body condition in NND populations was poorer than it was in ENP populations ($F_{1,18} = 63.78$; $p < 0.001$; nonparametric two-way ANOVA), indicating that our crude condition measures could detect regional variation. But within-site variation at the NND sites was lacking ($F_{2,9} = 1.80$, NS).

Second, because infant mortality is greater in primiparous mothers than in other ungulates (Clutton-Brock et

al. 1982), it may be that the dehorned females who lost their calves were simply young. If so, then age by itself might explain the deaths. This proposition is doubtful. Two of the three females had had prior calves. Also, female age and anterior horn size are related ($Y_{age} = 13.26 + 1.97X$, where X is horn size in cm; $r^2 = 0.63$; $p < 0.02$; standard error estimate = 8.58), and all of the mothers who experienced calf mortality were estimated to be between 15 and 25 years old. Because mothers generally first reproduce before the age of 10 years (Smith & Read 1992), it appears unlikely that the third female was primiparous.

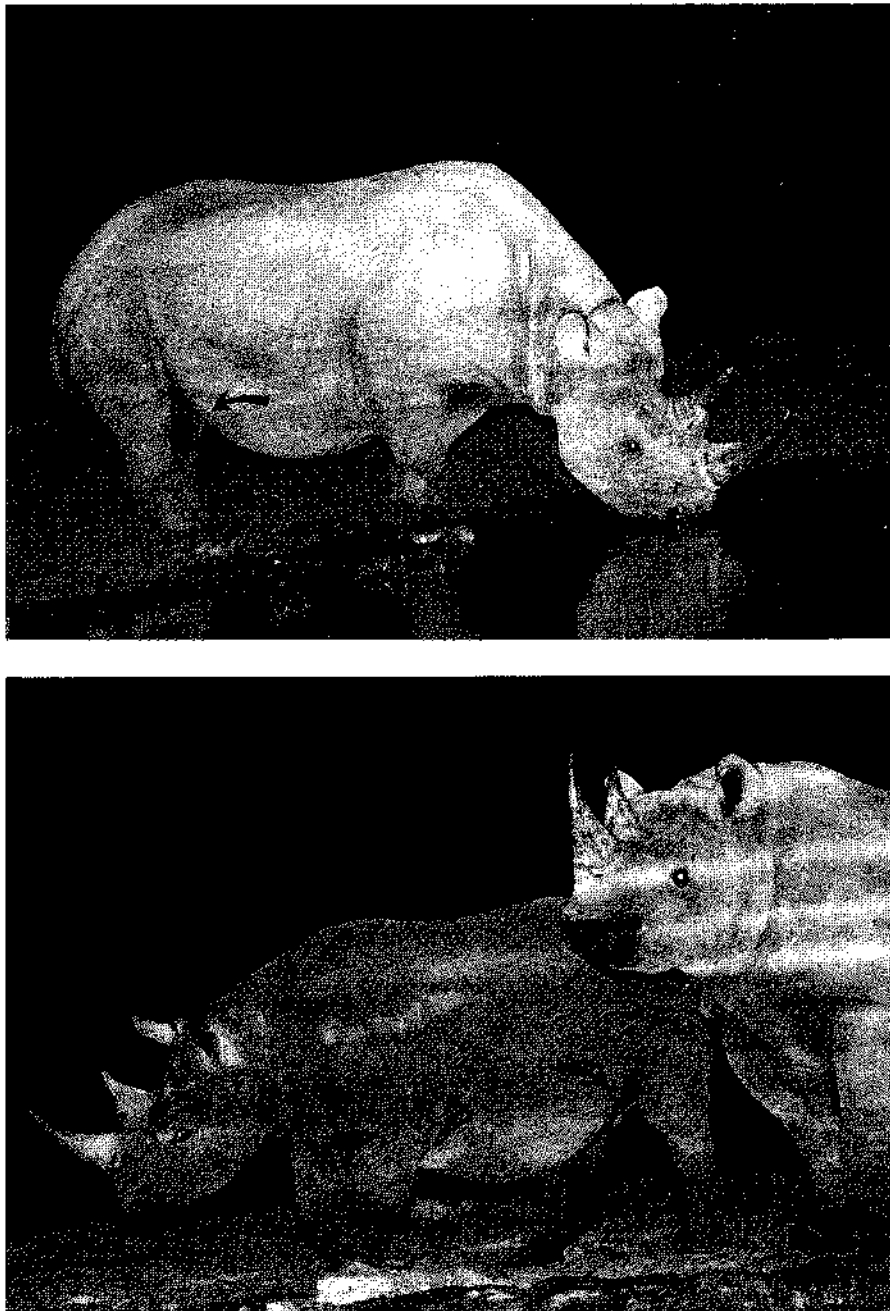


Figure 1. Lactating (top, note distended teats and udder) and nonlactating (bottom) females.

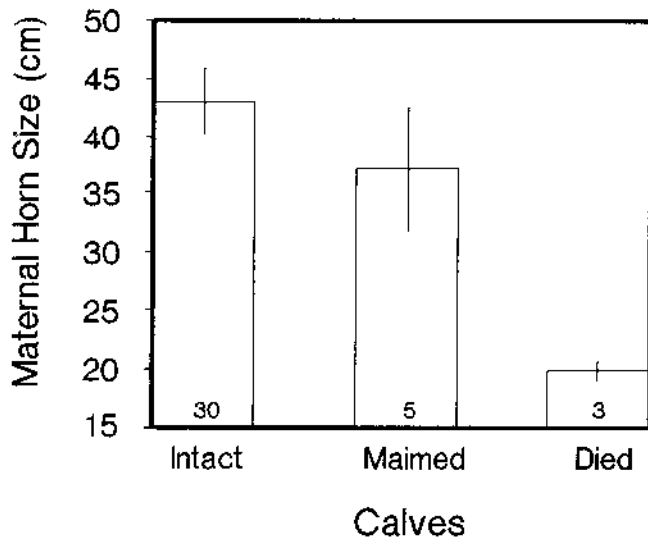


Figure 2. Mean (\pm SD) anterior horn length (AHL) of mothers with calves of differing status. Maternal AHL is less for dead calves than in the other two categories ($F_{2,35} = 15.71$, $p < 0.001$; one-way ANOVA), neither of which differs from the other (Newman Keul's Test). Sample sizes as indicated.

Third, calf age and year of dehorning could be confounded because calves in Area B were up to 18 months old prior to dehorning. But because predators were absent from Area B, calf age in itself should have little bearing on survivorship.

Fourth, at least two females from Area C, and more likely three, all produced calves that survived prior to dehorning in 1989 (G. Owen-Smith, P. Erb, J. Berger, &

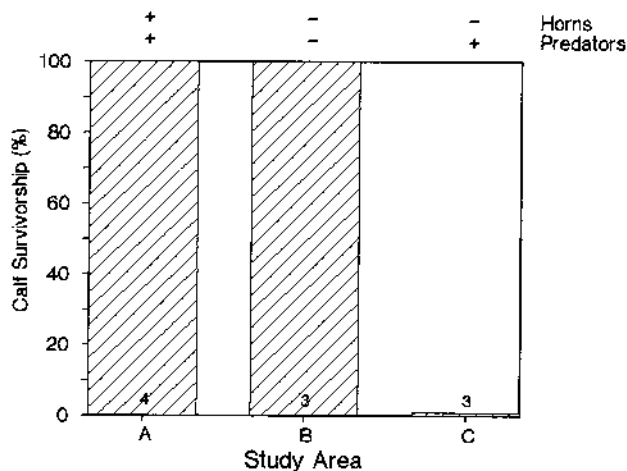


Figure 3. Calf survivorship (to 12 months) of dehorned and horned mothers at Namib Desert sites varying in dangerous carnivores. Area A—lions and spotted hyenas; Area B—no dangerous carnivores; Area C—spotted hyenas only.

C. Cunningham, unpublished). The probability of achieving these differences in neonate survival before and after dehorning by chance alone are as follows: for five calves (three survived; two died) $p = 0.10$; for six calves (three survived, three died) $p = 0.05$ (Fisher's Exact Test).

The best evidence in support of the notion that horns affected calf survival is the contrast among study areas A, B, and C. Despite striking differences in calf survival before and after dehorning at the same site, the comparison is not strictly valid. Precipitation recorded 30–50 kilometers to the north also differed, averaging 67 mm and 42 mm per year for the 6 years prior to and 3 years after dehorning, respectively (G. Owen-Smith, unpublished). Whether these differences in precipitation caused the temporal variation in calf mortality association with dehorning is uncertain. Nevertheless, the data do anything but support the argument that dehorning enhances population viability.

DISCUSSION

Horns, Maiming, and Mortality

Our findings offer the first empirical support that mammalian horns have current utility in females, a find with clear relevance to conservation. We do not know whether the horns of female black rhinos evolved as defensive structures to thwart predators that may now be extinct or for other purposes. Nevertheless, horned females are more aggressive to predators than are males; females with attendant young are the most likely to attack (Berger & Cunningham 1994a). It is clear, however, that horns carry a biological cost. Lethal wounding may result in exceptional mortality among subadult and adult female black rhinos. For instance, 33% (7 of 21) of female deaths in Etosha and South Africa's Ululuwe reserve resulted from fighting (data were pooled from Hitchins & Anderson 1983; Etosha National Park files, our findings). Although male black rhinos and males of other species die from mortal combat (Ralls et al. 1980) and even one female Indian rhino perished from lethal wounds (Dinerstein 1991), black rhino females may be unique among the Mammalia in that combat-caused deaths appear to be a regular feature of their life history. These results illustrate two points with relevance to conservation, one predicated on evolutionary theory, the other unanticipated.

First, hornless females appear disadvantaged when protecting their young from dangerous predators, suggesting that horns have functional significance as defensive structures. Our data on calf mortality emanate from the Namib Desert, however, an area at the extreme margin of black rhino range. Drought is a characteristic feature of this area, and during early 1993 it resulted in the

reduction of large herbivore biomass (kudu, springbok, zebra, gemsbok, giraffe, and ostrich) by about 85% (Berger, unpublished). For unknown reasons spotted hyenas remained, and it is plausible that they preyed on alternative food—rhino calves.

The existence of a significant relationship between the density of spotted hyenas and the proportion of maimed calves in five horned black rhino populations throughout Africa (Berger & Cunningham 1994b) strengthens the idea that dehorned mothers may be less than capable of calf defense. Why maiming is more frequent at higher hyena densities is not clear. Clan size is larger in areas of higher primary productivity (Henschel & Tilson 1988; Mills 1990), so perhaps large clans are more likely than small ones to attack mothers with calves. Perhaps where rhinos constitute a larger proportion of potential prey biomass, they are attacked more frequently. It may also be that maternal behavior varies in relation to horn size, although observations of 27 interactions between mothers and hyenas in ENP suggests that maternal defense is more closely aligned to calf age rather than to horn size (Berger et al. 1993). Whatever the cause(s), our inability to know more about the relationships among calf maiming in horned populations, prey biomass, and hyena densities does not mean that low-density populations of spotted hyenas, such as at our northern Namib site C (about 0.002/km²), are incapable of killing calves of hornless females.

From a conservation perspective, the claim can always be made that calf mortalities are unpredictable when the timing of herbivore migration is unknown. But any sound conservation plan must account for potential uncertainty. Drought is but one of many possible ecological crunches, some of which are more pressing. In Zimbabwe, for instance, dehorned black and white rhino populations have been decimated by poachers in part because funding for vital antipoaching measures failed (Begley 1993). In the absence of other protective measures, dehorning appears not to be a sound, long-term conservation tactic.

On the other hand, the relatively high frequency of combat-related mortality among horned females, based in part on prior findings (Hitchins & Anderson 1983), was unanticipated. Viewed in this context, dehorning is likely to enhance adult female survival once populations can be protected from poachers.

Implications for the Future

Dehorning has been viewed as a mixed bag. Initially, the tact was thought of as a one-time preemptive measure for low-density populations when adequate protection was not possible (Lindeque 1990). Horn removal has now been practiced in at least six discrete Namibian

black and white rhino populations and even more in Zimbabwe (Kock & Atkinson 1993). Dehorning might be acceptable as a long-term tactic when calf mortality is exceeded by the number of adult females that survive rather than die in combat and then produce calves that live to reproduce. Where the aim is to improve population viability via juvenile recruitment, however, dehorning may be imprudent unless practiced in areas where dangerous carnivores no longer exist or are removed. Given that predation can limit herbivore populations under some conditions, the removal of species such as lions or spotted hyenas to protect the young of dehorned rhinos is likely to have substantial ecosystem-level effects. Still, few would contest that the African ecosystems that retain viable rhino populations have not already been heavily affected by humans. And, except for Namibia, most of the areas where black rhino populations have increased are already small, guarded sanctuaries (Brett 1990; see also Ryder 1993) where system-wide disturbances have been anything but mild.

With respect to horn removal, biological, social, and political uncertainties lie ahead. There is a need to know much more about demographic effects and correlates including pregnancy rates, interbirth intervals, interactions with dangerous carnivores, and home-range shifts among rhinos. If dehorning continues not for biological reasons but to generate sustainable revenue, optimal harvesting strategies can be met only by considering demographic management in a metapopulation context with requisite attention focused on the social milieu. For instance, when should small, existing populations be supplemented with new individuals? Are the immigrants and/or residents to be horned or dehorned, and over what time frame? To what extent do individuals know each other, and what is the potential for fatal aggression? Is fight-related mortality associated with horn asymmetries? It is important that these and other questions relating to horns, behavior, and reproduction are answered, but this can only be accomplished when host governments are open and willing to accept both pleasant and unpleasant results.

Economically, dehorning might be a reasonable long-term measure if it were supported financially by non-government interests, practiced at frequent intervals, and occurred in fenced reserves with effective antipoaching protection. The critical factor here is adequate protection. In the absence of high levels of funding, rhino populations plummet (Leader-Williams & Albon 1988). If support is unavailable, then dehorning by itself will be a poor way to improve population viability (Milner-Gulland et al. 1993). One way to garner monies in support of rhino conservation is to allow rhinos to pay for themselves. Proponents of dehorning suggest that legalization of the horn trade will accomplish this, an issue that is destined to remain contentious.

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Literature Cited

- Andersson, M. 1982. Female choice selects for extreme tail length in a widowbird. *Nature* 299:818–820.
- Begley, S. 1993. Killed by kindness. *Newsweek* April 12:50–56.
- Berger, J. 1993. Disassociations between black rhinoceros mothers and young calves: Ecologically variable or, as yet, undetected behaviour? *African Journal of Ecology* 31:261–264.
- Berger, J. 1994. Science, conservation, and black rhinos. *Journal of Mammalogy* 75:298–308.
- Berger, J., and C. Cunningham. 1994a. Predation, sex, and sensitivity: Why black rhinoceros females outlive males. *Behavioral Ecology* 5: in press.
- Berger, J., and C. Cunningham. 1994b. Horns, hyenas, and black rhinos. *Research and Exploration* 10:241–244.
- Berger, J., C. Cunningham, A. Gawuseb, and M. Lindeque. 1993. "Costs" and short-term survivorship of hornless black rhinos. *Conservation Biology* 7:920–924.
- Bigalke, R. 1945. The regeneration of the anterior horn of black rhinoceros, *Diceros bicornis* (Linn.). *Proceeding of Zoological Society of London* 115:323–326.
- Brett, R. A. 1990. The black rhino sanctuaries of Kenya. *Pachyderm* 13:31–34.
- Clutton-Brock, T. H. 1982. The function of antlers. *Behaviour* 79:109–125.
- Clutton-Brock, T. H., F. E. Guinness, and S. D. Albon. 1982. Red deer: Ecology and behavior of two sexes. University of Chicago Press, Chicago, Illinois.
- Dinerstein, E. 1991. Sexual dimorphism in the greater one-horned rhinoceros (*Rhinoceros unicornis*). *Journal of Mammalogy* 72:450–457.
- Dinerstein, E., and L. Price. 1991. Demography and habitat use by greater one-horned rhinoceros in Nepal. *Journal of Wildlife Management* 55:401–411.
- Freeman, G. H., and J. M. King. 1969. Relations among various linear measurements and weight for black rhinoceros in Kenya. *East African Wildlife Journal* 7:67–72.
- Geist, V. 1966. The evolution of horn-like organs. *Behaviour* 27:175–214.
- Henschel, J. R., and R. L. Tilson. 1988. How much does a spotted hyena eat? Perspectives from the Namib Desert. *African Journal of Ecology* 26:247–255.
- Hitchins, P. A. 1968. Live weights of some mammals from Hluhluwe Game Reserve, Zululand. *Lammergeyer* 9:26–28.
- Hitchins, P. A. 1978. Age determination of the black rhinoceros (*Diceros bicornis* Linn.) in Zululand. *South African Journal of Wildlife Research* 8:71–80.
- Hitchins, P. A., and J. L. Anderson. 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* 13:78–85.
- Jacobsen, J. 1986. A digital photogrammetric scaling device. Typescript. Humboldt State University, Arcata.
- Jones, I. L., and R. Montgomerie. 1992. Least auklet ornaments: Do they function as quality indicators? *Behavioral Ecology and Sociobiology* 30:43–52.
- Keep, M. E. 1971. Observable criteria for assessing the physical condition of the white rhinoceros *Ceratotherium simum simum*. *Lammergeyer* 13:25–28.
- Kiltie, R. A. 1985. Evolution and function of horns and horn-like organs in female ungulates. *Biological Journal of Linnean Society* 24:299–320.
- Kock, M., and M. Atkinson. 1993. Report on dehorning of black and white rhinoceroses in Zimbabwe. Zimbabwe Department of National Parks and Wildlife Management, Harare, Zimbabwe.
- Leader-Williams, N., and S. D. Albon. 1988. Allocation of resources for conservation. *Nature* 336:533–535.
- Lindeque, M. 1990. The case for dehorning the black rhinoceros in Namibia. *South African Journal of Science* 86:226–227.
- Mattson, D. J., and M. M. Reid. 1991. Conservation of the Yellowstone grizzly bear. *Conservation Biology* 5:364–372.

Mayr, E. 1982. *The growth of biological thought*. Harvard University Press, Cambridge, Massachusetts.

Milner-Gulland, E. J., N. Leader-Williams, and J. R. Beddington. 1993. Is dehorning African rhinos worthwhile? *Pachyderm* 17:52-58.

Norton, P. 1990. How many leopards? A criticism of Martin and de Meulenaer's population estimates for Africa. *South African Journal of Science* 86:218-220.

Owen-Smith, N. O. 1988. *Megaherbivores*. Cambridge University Press, Cambridge, England.

Packer, C. 1983. Sexual dimorphism: The horns of African antelope. *Science* 221:1191-1193.

Ralls, K., R. Brownell, and J. Ballou. 1980. Differential mortality by sex and age in mammals with specific reference to the sperm whale. Report of the International Whaling Commission 2:223-243.

Reeve, H. K., and P. W. Sherman. 1993. Adaptation and the goals of evolutionary research. *Quarterly Review of Biology* 68:1-32.

Ryder, O. A., editor. 1993. *Rhinoceros biology and conservation*. Zoological Society of San Diego, San Diego, California.

Smith, R. L., and B. Read. 1992. Management parameters affecting the reproductive potential of captive, female black rhinoceros, *Diceros bicornis*. *Zoo Biology* 11:375-383.

von Schantz, T., G. Goransson, G. Andersson, I. Froberg, M. Grahn, A. Helgee, and H. Wittzell. 1989. Female choice selects for a viability-based male trait in pheasants. *Nature* 337:166-169.

Western, D. 1982. To dehorn or not dehorn? *Swara* 5:22-23.

Western, D. 1987. Africa's elephants and rhinos: Flagships in crisis. *Trends in Ecology and Evolution* 2:343-346.

