

SCIENCE, CONSERVATION, AND BLACK RHINOS

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The study of adaptive traits rarely has been applied toward the conservation of biodiversity. Fields such as evolution, biogeography, behavioral ecology, population biology, and genetics have facilitated conservation goals, but only partially and only for a few taxa. Among the world's most endangered mammalian families is the Rhinocerotidae whose five species are being exterminated for their horns. Numerous conservation actions have been applied to these species. The most radical, horn removal, is designed to improve the conservation of both black (*Diceros bicornis*) and white (*Ceratotherium simum*) rhinos. In this paper, I use basic and applied biology to suggest how science has or has not contributed to the in situ conservation of black rhinos. I make four points: knowledge about associations between mating systems and sexual dimorphism has helped illuminate the evolution of secondary sexual traits; relationships between behavioral responses of black rhinos to dangerous predators and subsequent mortality are of basic interest, but this knowledge has not abetted rhino conservation; prior literature indicates that the young of horned mothers regularly are maimed by dangerous predators (if horns have utility as defensive structures, then phenotypic alterations of female horns should increase the susceptibility of young to predation, a prediction with empirical support from a Namib Desert population); because wild populations of black rhinos have been depleted in the past 25 years by 97%, it makes little sense to plan how to conserve genetic diversity over the next 500. Science will continue to play a critical role in the future conservation of small, heavily managed populations. However, it is less likely to be of major significance in the in situ conservation of rhinos until sociological, economic, and political issues are effectively resolved.

Key words: conservation, science, predation, mating systems, black rhinos, spotted hyenas, Africa

The diversity of survival strategies employed by different species of animals is truly amazing. Egg-producing anteaters, annual migrations in excess of 5,000 km by caribou (*Rangifer tarandus*) and monarch butterflies (*Danaus plexippus*) (Brower and Malcolm, 1989; Fancy et al., 1989), moisture acquisition from desert fog by tenebrionid beetles (Seely and Hamilton, 1976), and large body size (Owen-Smith, 1988) are but four of an array of evolved survival tactics. Size seems to have a fascination all its own, but, as we progress through the next century, it will be auspicious if many of the world's large wild mammals will persist. Bison (*Bos bison*) were exterminated last century for tongues, hides, and political

reasons, Pere David's deer (*Elaphurus davidianus*) and Przewalski horses (*Equus przewalski*) occur only in fenced reserves, and places like Yellowstone National Park are too small for burgeoning herds of bison and elk (*Cervus elaphus*). Although most species will be lost due to habitat destruction and fragmentation, we have the misfortune of witnessing the eradication of wild black rhinos as this century closes. In all of Africa, only a single unfenced population with >100 individuals now exists—that in Namibia's northern Namib Desert. From the Sudan and Somalia to Angola and South Africa, black rhinos have been killed for their horns, structures valued in traditional Asian medicines and as ceremonial

dagger handles in Yemen (Western, 1987; Western and Vigne, 1985).

In this paper, I describe some of the contributions made by science toward the conservation of black rhinos. Specifically, I point to information in diverse areas—evolutionary theory, genetics, behavioral biology, and ecology—and describe: 1) where theory and natural-history observations have enhanced an understanding of utility of horns; 2) how conceptual gains in conservation genetics have not aided in the formulation of realistic plans to protect populations in the wild; 3) what little is known of relationships between individuals. The first part of this paper outlines some key concepts; the second part summarizes data gathered by my colleagues and myself about behavioral and demographic responses of males and females to dangerous non-human predators and to poachers. I conclude by presenting results of a de facto experiment, dehorning, and suggest several research areas that will be increasingly important in the future.

EVOLUTION AND ADAPTIVE TRAITS

Evolutionary patterns often are viewed in three contexts, time, space, and fitness, all of which contribute to the study of conservation (Frankel and Soulé, 1981). For instance, John Eisenberg once said "If I can have only one parameter to interpret the life-history strategy of a fossil mammal, give me body size. It is a powerful predictor of so many things" (MacFadden, 1992: 269), and body size has been of value in recreating paleofaunas and community patterns (Van Valkenburgh, 1988). So why have attempts to apply information from the fossil record to conservation been so limited? For the Rhinoceratidae, the reason is excellent. Although extant rhinos are killed for their horns, 90% of the extinct rhinoceratids were hornless (Prothero, 1987). Does it logically follow that the link between the application of historical knowledge and the horns of extant rhinos is tenuous at best? I would argue no.

Evolutionary patterns regularly are used to test hypotheses about functional design using both morphology and behavior (Mayr, 1982; Reeves and Sherman, 1993). Among many mammals and other vertebrates, sexual dimorphism is most pronounced in polygynous species (Clutton-Brock et al., 1982). Both body size and secondary sexual characteristics such as horns, tusks, and canines (Geist, 1966) are related to the breeding system in ungulates, pinnipeds, and primates (Alexander et al., 1979; Harvey et al., 1978). Studies of behavioral ecology now demonstrate that such traits have an intrasexual function where males may increase their access to female mates (Clutton-Brock et al., 1982). Given sufficient knowledge about a species' morphology, it should, therefore, be possible for scientists to predict how different traits may be used even when that species has never been studied.

What is known of horn function in rhinoceratids? Little other than horns are used in combat (Owen-Smith, 1975). Horns evolved independently several times in numerous ungulate lineages of the Oligocene and Miocene (Geist, 1966), but the major proliferations of horns occurred among radiations of African bovids during the Pliocene (Janis, 1982). Rhinos are the only extant horned perissodactyls, the first, *Diceratherium*, having appeared with paired nasal appendages during the Miocene. Another armored line, the Chalicotheres, became extinct during the Pleistocene (Munthe and Coombs, 1979). The major hypotheses for conspicuous armament in ungulates is that horned structures 1) function intrasexually in combat, 2) serve in mate choice, and 3) deter predators. The first two hypotheses are related to mate acquisition while the last concerns defense from predators.

There are five species of extant rhinoceroses, two in Africa (black and white) and three in Asia (greater one-horned, *Rhinoceros unicornis*; Javan, *R. sondaicus*; Sumatran, *Dicerorhinus sumatrensis*). All are

TABLE 1.—Summary of selected behavioral, demographic, and life-history features in three extant rhinoceratids. Sample sizes in parentheses.

| Feature | Rhinoceratid | | |
|-----------------------------------|---|--|--|
| | Black | White | Greater one-horned |
| Dimorphism | | | |
| Body | — | + | — |
| Horn | — ^b | + | — |
| Other | — | Necks larger in male | Enlarged incisors in males |
| Adult sex ratio | Even ^c | Female biased | Female biased |
| Mating system | Polygynous | Polygynous | Polygynous |
| % deaths from combat ^d | 53 (39) ^d | 20 (40) ^e | 47 (15) |
| References | Freeman and King, 1969 Hitchens, 1968 Hitchens and Anderson, 1983 | A. J. Hall-Martin and K. Hillman, in litt. Hillman-Smith, 1986 Owen-Smith, 1988 | Dinerstein, 1991 Dinerstein and Price, 1991 |

^a As a function of known deaths, which include starvation, drought, fighting, predation, fire, and accidents.

^b With effects of age removed, sexual differences in anterior length of horn (ALH) or basal diameter (BD) were not evident; $ALH = 0.83X_1 - 3.83X_2 + 30.89$, $r^2 = 0.57$, $F = 23.28$ (d.f. = 2,35; $P < 0.001$) where X_1 = age and X_2 = sex; partial r : $X_1 = 0.70$ ($P < 0.001$), $X_2 = -0.20$ ($P > 0.05$); $BD = 0.19X_1 - 1.90X_2 + 15.28$, $r^2 = 0.49$, $F = 16.71$ (d.f. = 2,35; $P < 0.001$); partial r : $X_1 = 0.60$ ($P < 0.001$), $X_2 = -0.30$ ($P > 0.05$).

^c In the absence of poaching, sex ratios were equal (see Fig. 2).

^d Data combined from Uhuhluwe Complex and Etosha National Park.

^e Data combined from Uhuhluwe and Pilansberg reserves (South Africa).

thought to be polygynous, although only three have been studied in detail (Table 1). Classic models of mammalian sexual selection (Clutton-Brock et al., 1982; Packer, 1983; Ralls et al., 1980) predict sexual dimorphism in either horns or body size, or both, patterns that both greater one-horned and white rhinos appear to fit (Dinerstein, 1991; Owen-Smith, 1988). Males compete for access to mates often through combat and territorial defense, the species are polygynous, and either body size or secondary sexual traits are dimorphic. White rhino males are up to 30% larger than females and have larger horns (Kock and Atkinson, 1993; Owen-Smith, 1988). Despite monomorphism in lengths of horn and body in greater one-horned rhinos, males have enlarged incisors, and nearly 50% die in fights. (Dinerstein, 1991; Dinerstein and Price, 1991). Because of asymmetries in the horns of male and female white rhinos and none evident in greater one-horned rhinos, horn function would be expected to differ in these two species. Nevertheless, that both

species have conspicuous, although different, secondary sexual traits (Table 1) is consistent with paradigms based on sexual selection.

Why the other three rhinoceratids appear monomorphic is uncertain. Adults generally are immune from extant predators due to large body size alone, so perhaps horns evolved for defense against predators that already are extinct or the horns may have current utility; tigers (*Panthera tigris*) regularly kill young of greater one-horned rhinos (Dinerstein and Price, 1991). Knowing the underlying evolutionary impetus for horns seems moot from a conservation perspective, but ascertaining the current utility is not.

BIOLOGY AND CONSERVATION: CONSEQUENCES OF SEX AND HORNS

Behavior, dimorphism, and demography.—Darwin (1871) first noted that exaggerated structures including cranial ornamentation had survival costs. Contemporary evidence from sexually dimorphic primates

(Rajpurohit and Sommer, 1991), marsupials (Dickman and Braithwaite, 1992), ungulates, and pinnipeds (Owen-Smith, 1993; Ralls et al., 1980) now suggests that males experience greater mortality than females. The cause(s) of sex differences in mortality of adults is rather unclear. Whereas proximate events such as high parasite load, predation, or fighting can be readily assessed, ultimate causation such as intermale competition cannot (Trivers, 1985). However, the behavior of each sex can be studied to determine the extent to which some mortality risks are avoided. For instance, female ungulates often are more vigilant and likely to flee from predators than males (Berger, 1991; Prins and Iason, 1989), but whether the behavioral responses of one sex exacerbates its chances of death has been unclear. Here, using information on body and horn size from the prior section and data that C. Cunningham and I gathered in Namibia in 1991–1993, I explore how knowledge of sex differences in behavior may bear on population phenomena. I then question the application of such knowledge to conservation.

Recall that, despite monomorphism, black rhinos are polygynous (Table 1) and both sexes tend to be solitary (Owen-Smith, 1988). In the absence of young or conspecifics, females should not differ from males in their responsiveness to predators such as lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*). Solitary females, by definition, would not be involved in the protection of kin, and, by virtue of their large size, neither sex should differ in their vulnerability to predators. However, based on 193 witnessed interactions, we found that solitary females were more likely to respond actively to potentially dangerous predators than were males. The differences between sexes also persisted when rhinos encountered humans. On average, females ran 4.2 km in riverine habitat, whereas males fled <1.5 km (J. Berger and C. Cunningham, pers. obser.). Given that females were more sensitive than males in their in-

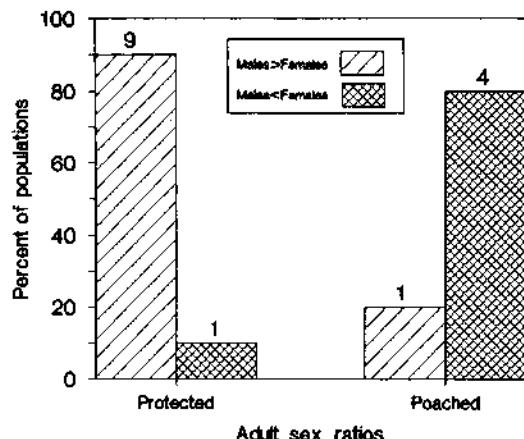


FIG. 1.—Relationships between shifts in adult sex ratios of black rhinos in protected and non-protected populations from Kenya, Tanzania, Zambia, Zimbabwe, Namibia, and South Africa. Sample sizes as indicated (above bars). Sources of populations from J. Berger and C. Cunningham (pers. comm.).

teractions with dangerous predators, males should be killed by poachers more often than females. We tested the proposition by comparing sex ratios of adults in protected and poached populations from Kenya, Tanzania, Zimbabwe, Zambia, South Africa, and Namibia (Fig. 1). In nine of 10 protected areas, adult males outnumbered females but, once poaching began, females were more abundant ($P = 0.017$; Fisher's exact test).

These results suggest that: in the absence of human predation, black rhinos deviate from the well-known pattern of male-biased mortality in polygynous mammals; despite similarities in size, females respond more strongly to potential predators than males; knowledge about why females outlive males once poaching begins has little relevance to conservation. From a biological perspective, the differences between sexes in behavior imply that females may have more to lose than males by remaining in proximity to predators, but the idea cannot be examined without comparative data on the reproductive success of each sex. What would have conservation pertinence is

knowing whether natural variation in size of horn affects maternal abilities to protect young.

Horns, spotted hyenas, and the maiming of rhino young.—One of the most radical actions in biological conservation has been the removal of horns from black rhinos in an attempt to render them valueless to poachers. The tactic had been debated in Kenya >10 years ago (Western, 1982); it is still contested in Tanzania (R. Faust, pers. comm.), and it has been practiced and continues in three countries, Namibia, Zimbabwe, and Swaziland, with the first two dehorning both species of African rhinos. Dehorning occurred as a last resort (Kock and Atkinson, 1993; Lindeque, 1990) and without the luxury of years to study potential effects. Two biological uncertainties exist: do horned individuals have advantages over hornless ones and are hornless mothers able to defend their young from dangerous carnivores. With respect to the first, the issue is generally moot because dehorning operations target all animals in the same area. However, the second issue is not; if horns have defensive utility, then the young of hornless females may be more susceptible to dangerous carnivores (Berger and Cunningham, in press *a*).

Some a priori information on predation is available. Adult rhinos are virtually immune from carnivores due to their large size, but evidence of predation on young animals by spotted hyenas and lions exists (Elliot, 1987; Goddard, 1967; Kruuk, 1972). Also, earless and tailless animals have been reported throughout much of Africa. Initially, it was suspected that earlessness was congenital (Goddard, 1969), but more recent work indicates that 97% of the "maiming" of young results from unsuccessful predation attempts (Hitchins, 1986, 1990). For instance, in Kenya's Aberdare Mountains, four of nine young were attacked by spotted hyenas; three were either scarred or missing ears or tails (Sillero-Zubiri and Gottelli, 1991). Although the incidence of mortality of the young remains un-

known, in part because during their first 6 months, young do not regularly accompany their mothers (Berger, 1993), it is possible to examine the extent to which hyenas maim young.

Using existing literature and unpublished data, I compared the incidence of maiming with the density of spotted hyenas (Table 2). Most (92%) variation in maiming (Y) is explained by the simple regression $1.30 + 23.18X$ ($P < 0.01$) where X is density of hyenas. At two Namibian sites lacking predators, Doros Crater and Waterberg Plateau Park (only one was included in the regression), no rhinos were maimed. However, the sample is small ($n = 5$), and the accuracy of some density estimates is somewhat questionable. Therefore, I performed a more conservative test and simply contrasted the frequency of maiming in areas with and without hyenas boosting the sample size to 10. The effects were nearly as strong ($P = 0.022$; Fisher's exact test) and indicate that hyenas do indeed affect the young. These results must underestimate the magnitude of effects of hyenas because young that survived attacks are detectable but those who died are not.

The findings are noteworthy for two reasons. First, horned mothers are not always successful in preventing attacks by hyenas. Second, in Africa as well as on other continents, the biomass of predators and prey are highly correlated (East, 1981; Schonewald-Cox, 1983) suggesting that, on a per capita basis, prey are not necessarily more available in herbivore-rich areas such as Ngorongoro Crater than in spartan environments like the Namib Desert. Why maiming is more frequent at greater densities of hyenas is unclear. Because clan size is larger in areas with higher prey biomass (Henschel and Tilson, 1988; Mills, 1990), perhaps bigger clans are bolder and more likely to attack young of rhinos than are small ones. It may be that the per capita risks of injury to attacking hyenas are low. Another possibility is that rhinos may be attacked more than other species in areas where rhin-

TABLE 2.—Summary of locations and frequency of maimed (missing ears or tails or having body scars associated with predator attacks) young of black rhinos and respective densities of spotted hyenas. Sample sizes in parentheses; + indicates presence of hyenas or maimed young.

| Location | Percentage of maimed young | Hyenas /km ² | Reference |
|--------------------------------|----------------------------|-------------------------|---|
| Aberdares, Kenya | 33 (9) | 1.34 | Sillero-Zubiri and Gottell, 1991 |
| Amboseli, Kenya | + | + | Goddard, 1969 |
| Tsavo East, Kenya | + | + | Goddard, 1969 |
| Tsavo West, Kenya | + | + | Goddard, 1969 |
| Ngorongoro Crater, Tanzania | + | 1.70 | Goddard, 1969; Kruuk, 1972 |
| Umfalozi Complex, South Africa | 3.9 ^a (36) | 0.36 | Hitchins and Anderson, 1983; Hitchins, 1986, 1990; Whateley, 1981 |
| Etosha, Namibia | 10 (10) | 0.20 | Gasaway et al., 1989; present study |
| Central Kaokoveld, Namibia | 3.4 (58) ^b | 0.002 ^c | Present study |
| Waterberg Park, Namibia | 0 (29) ^b | 0 | P. Erb, pers. comm. |
| Doros Crater, Namibia | 0 (12) ^b | 0 | Present study |

^a Mean of values given in Hitchins (1990); evidence offered for 36 young although the total number of intact ones is unclear.

^b Reflects total number of different animals observed, adults included.

^c Calculated as 10 hyenas within a 4,500-km² area.

^d Number of animals in population.

nos constitute a larger proportion of prey biomass. Whatever the cause(s) for the greater amount of maiming in areas with higher densities of hyenas, it is reasonable to expect that hyenas have the capacity to affect recruitment of young when mothers are horned; effects might be even greater when female rhinos are dehorned.

Variation in horn size and survival of young.—If horn size affects the outcome of successful maternal defense, then a relationship should exist between horns and maternal behavior. We tested this prediction using study sites in Namibia with dehorned and horned rhinos in areas with and without dangerous predators. Horn size was estimated with a photogrammetric device that averages ca. 98% in accuracy (Berger and Cunningham, in press *b*). First, we relied on natural variation in horn size to determine if an association existed between horn size and maternal responses to lions and hyenas in Etosha National Park. Our results demonstrated that mothers with smaller than average-sized anterior horns were no more likely to run from dangerous predators than from mothers with large horns. What affected maternal response was size of the young; mothers with young offspring were

significantly more likely to flee than those with older young, although the cause of this relationship is uncertain (Berger et al., 1993).

We also predicted that if horn size affects the outcome of maternal defense, then maternal horn size and maiming in young should be related. We tested this idea by contrasting mean anterior horn lengths (MAHL) between mothers with intact and maimed young. Differences were not detectable (for intact young, MAHL = 43.0 ± (SE) 1.1 cm, *n* = 30; for maimed calves, MAHL = 37.6 ± 5.0 cm; *n* = 5; *t* = 1.56; not significant; *d.f.* = 33). However, given the small sample of mothers with maimed young, the probability of accepting a false null hypothesis (type II error; Cohen, 1977) is high, 0.72. For example, assuming a 90% probability that the 95% confidence interval in maternal horn size is ≤4 cm, a total of 173 mothers, 142 of them (with the observed mean anterior horn size of 37.6 cm) having maimed young, would be required to show significance at the *P* < 0.05 level. Given the difficulty of obtaining sufficiently large samples, all that can reasonably be concluded is that the hypothesis that horns

are important in defense of young cannot be rejected.

Another way to examine relationships between horn size and the defense of young is by relying on evidence gathered from areas where animals have been dehorned to protect them from poachers. Given the correlation between density of hyenas and maiming (Table 2), young in the Namib Desert should be at low risk to predation because densities of hyenas at sites of dehorned and horned mothers were exceptionally low, $0.002/\text{km}^2$. However, the previous discussion was about horned mothers. The dehorned mothers at our northern Namib site were less capable of effective defense; the three dehorned females that lived sympatrically with hyenas lost young born 3 years after horn removal. Although horns regrow (Berger et al., 1993), the females that lost young had horns that averaged only 47% of the size of intact horns of females. Length of horn was significantly less for mothers whose young perished than for those with either maimed or intact young ($F = 15.71$; $d.f. = 2,35$; one-way analysis of variance with Student Newman-Keuls test; $P < 0.01$). Although comparisons across multiple study sites may obscure important ecological differences, these results are consistent with the idea that horns of females have current utility.

CONCLUSIONS: RESEARCH, SCIENCE, AND PRACTICALITY

Theory and common sense.—Conservation has both practical and theoretical components, with the former often having little to do with science or biology. Education shapes attitudes, a sympathetic populace lobbies government, regulations are instituted, and, where possible, land is set aside as reserves. In cases where areas have become too small or human influences too great, management and research are proving useful. Conversely, conceptual advances often are rare when research is narrowly focused in spite of scientific rigor. For instance, study of the food habits of deer in

county A might reveal slight differences from those in county B, but new insights about feeding habits of deer are unlikely. However, inquiries aimed at issues in biogeography, population biology, genetics, and evolution often have, but not always, proved valuable when applied to practical conservation.

Consider the study of small populations. Considerable effort has been directed at understanding components of extinction such as habitat fragmentation, insularization, and mating with relatives (Clark and Seebeck, 1990; Soulé, 1986). Small populations are expected to retain less genetic diversity than large ones (Falconer, 1960), and projected losses can be minimized by maintaining effective populations of 50–500 individuals (Frankel and Soulé, 1981). For organisms with generation times approximating 10–12 years such as black rhinos, most genetic diversity could be retained over 500 years with large populations (Fig. 2). Is such a goal realistic? It probably is not. In <25 years, $>95\%$ of Africa's black rhinos have been killed (Fig. 2), and, as pointed out by Leader-Williams (1993), genetic management has little relevance to the conservation of wild rhinos. Obviously, the conservation of genetic diversity is important (Ashley et al., 1989; Merenlender et al., 1989) and a regular feature of planning for small captive populations (Foose, 1993). However, if wild populations are to survive, other issues must take precedence; keeping animals alive, reintroducing them to existing reserves, and accelerating the growth of captive groups are of critical importance (Hall-Martin, 1988; Martin, 1993; Smith and Read, 1992).

The protection of rhinos from poaching has little to do with science. The population crashes that result from illegal horn markets in Asia (Milner-Gulland et al., in press) or the continued use of ceremonial dagger handles in Yemen are issues that cannot be solved at the local level by countries with remaining rhinos. Extinction has been resisted by the establishment of small popu-

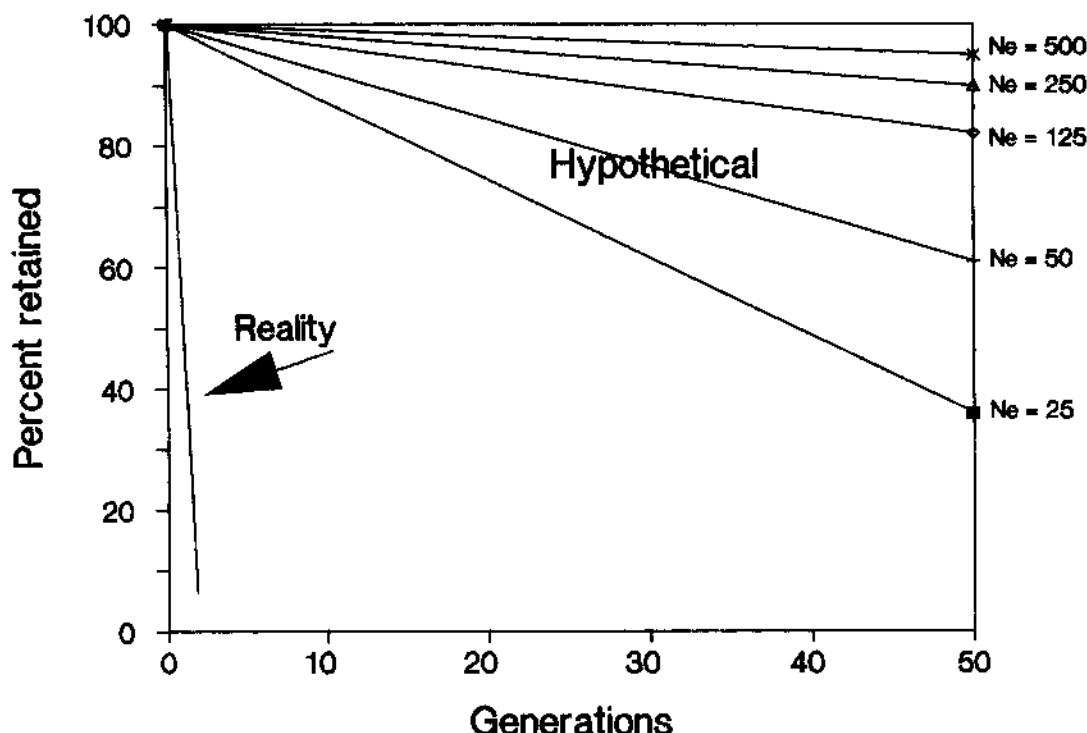


FIG. 2.—Relationships between numerical proportion of either genetic (effective populations size, N_e) diversity or population size retained and number of generations of black rhinos. The expected (designated Hypothetical) percentage of genetic diversity retained varies according to N_e . The slope indicated by the arrow Reality shows the actual 95% decrease in population size from 65,000 rhinos during the past 2.5 generations (modified from Leader-Williams, 1993).

lations in guarded, fenced sanctuaries, but problems associated with recovery still exist. About 75% (20 of 27) of the reserves in Kenya, Namibia, and South Africa have <50 animals (Brett, 1990; Brooks, 1989). If we assume that the sanctuaries will be safe, then science can play an increasingly central role in conservation because of knowledge gained about metapopulation dynamics, demographic modelling, and behavior (Brett, 1990; Ryder, 1993).

The future.—Mammals ranging from rhinos and tigers to pandas and musk deer are killed illegally for their body parts although the primary cause of biotic impoverishment today will continue to be habitat fragmentation and degradation. Biological knowledge is less likely to help in the short-term conservation of declining charismatic species than is social, economic, and politi-

cal reform. Already, it is too late for unfenced black rhinos; in all of Africa, the Namib Desert population is the last remaining with >100 individuals. Nevertheless, the harsh realities of dwindling populations should not diminish the efforts of scientists or new social approaches to future conservation efforts.

African rhinos have been translocated into reserves in many countries. If the two species are to survive, they will do so in guarded sanctuaries that inevitably will have to be managed as metapopulations, a situation no different from what currently exists for other species in many North American and European zoos. Nonetheless, there is room for optimism. Community-based conservation seems to be working in the northern Namib Desert (Bonner, 1993; Owen-Smith and Jacobsohn, 1989), popu-

lation growth has been robust in many South African reserves (Hall-Martin, 1988), and reproduction is improving in Kenyan sanctuaries (Brett, 1990).

Among the many imminent challenges for *in situ* conservation, two stand out; re-introduction and enhancing existing populations. First, because combat-related mortality among black rhinos tends to be high and is exacerbated when individuals are unfamiliar with one another (Hall-Martin and Penzhorn, 1977; Hofmeyr, 1975), future research should focus on finding ways to minimize mortality. This raises practical problems. What are the best ways to add additional animals once a new population has been established? Should dehorned animals continue to form the basis for founding new populations, as in both Namibia and Zimbabwe? Because anterior and posterior horns grow at ca. 6 and 3 cm/year in both black and white rhinos (Berger et al., 1993; Kock and Atkinson, 1993), should animals be introduced with their horns intact when residents have only partially regrown ones, or should all animals be dehorned regularly so that horn asymmetries between resident and newly introduced animals no longer exist? Clearly, a challenge will be to find ways to minimize fatal fighting.

Because most rhinos will be managed in small reserves, an attempt should be made to enlarge population size by increasing "carrying capacity." For rhinos and other territorial species, social factors, rather than food, often diminish population density (Dinerstein, 1993). Therefore, another potentially fruitful area for research concerns reducing the potential for intraspecific aggression so that more animals can be accommodated (and, hence, protected) in a smaller area. It is widely known that interspecific aggression by black rhinos toward humans is rapidly reduced by habituation, and it seems prudent to ask whether rhinos also can become less aggressive to one another? Evidence from at least one asocial, normally aggressive tropical rodent, the

paca (*Agouti paca*), suggests that the formation of tolerant social groups may be possible (Smythe, 1991). As conservation programs continue to be called on to pay for themselves and if the marketing of rhino horns becomes legal, it will be critical to determine whether black rhinos can be socialized to live in groups without increasing mortality.

Problems of a biological nature can be studied scientifically. For conservation prospects to improve via science, managers, biologists, natural historians, and reserve keepers involved in management of rhinos will have to be more diligent, reporting both their successes and failures. But, as all of us know, practical conservation requires symbiotic approaches. Before wild rhinos can be truly rescued, the more mammoth task lies in resolving social, economic, and political issues.

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LITERATURE CITED

ALEXANDER, R. D., J. L. HOOGLAND, R. D. HOWARD, K. M. NOONAN, AND P. W. SHERMAN. 1979. Sexual dimorphism and breeding systems in pinnipeds, un-

gulates, primates and humans. Pp. 402–435, in *Evolutionary biology and human social behavior: an anthropological perspective* (N. A. Chagnon and W. Irons, eds.). Duxbury Press, North Scituate, Massachusetts, pp.

ASHLEY, M. V., D. J. MELNICK, AND D. WESTERN. 1990. Conservation genetics of the black rhinoceros (*Diceros bicornis*), I. Evidence from mitochondrial DNA of three populations. *Conservation Biology*, 4: 71–77.

BERGER, J. 1991. Pregnancy incentives, predation constraints, and habitat shifts: experimental and field evidence for wild bighorn sheep. *Animal Behaviour*, 41:61–77.

—. 1993. Dissociations between black rhinoceros mothers and young calves: ecologically variable or, as yet, undetected behaviour? *African Journal of Ecology*, 31:261–264.

BERGER, J., AND C. CUNNINGHAM. In press a. Horns, hyenas, and black rhinos. *Research and Exploration*. —. In press b. *Bison: mating and conservation in small populations*. Columbia University Press, New York.

BERGER, J., C. CUNNINGHAM, A. GAWUSEB, AND M. LINDEQUE. 1993. "Costs" and short-term survival of hornless black rhinos. *Conservation Biology*, 7:920–924.

BONNER, R. 1993. *At the hands of man*. Knopf, New York, 322 pp.

BRETT, R. A. 1990. The black rhino sanctuaries of Kenya. *Pachyderm*, 13:31–34.

BROOKS, P. M. 1989. Proposed conservation plan for the black rhino, *Diceros bicornis*, in South Africa, the TBVC states, and Namibia. *Koedoe*, 32:1–31.

BROWER, L. P., AND S. B. MALCOLM. 1989. Endangered phenomena. *Wings*, 14:3–9.

CLARK, T. W., AND J. H. SEEBECK (EDS.). 1990. *Management and conservation of small populations*. Chicago Zoological Society, Chicago, 316 pp.

CLUTTON-BROCK, T. H., F. E. GUINNESS, AND S. A. ALBON. 1982. *Red deer: behavior and ecology of two sexes*. University of Chicago Press, Chicago, 378 pp.

COHEN, J. 1977. *Statistical power analysis for the behavioral sciences*. Academic Press, New York, 474 pp.

DARWIN, C. R. 1871. *The descent of man and selection in relation to sex*. John Murray, London, United Kingdom, 475 pp.

DICKMAN, C. R., AND R. W. BRAITHWAITE. 1992. Post-mating mortality of males in the dasyurid marsupial, *Dasyurus paranechimetus*. *Journal of Mammalogy*, 73:143–147.

DINERSTEIN, E. 1991. Sexual dimorphism in the greater one-horned rhinoceros (*Rhinoceros unicornis*). *Journal of Mammalogy*, 72:450–457.

—. 1993. Greater one-horned rhinoceros populations in Nepal. Pp. 196–207, in *Rhinoceros biology and conservation* (O. A. Ryder, ed.). San Diego Zoological Society, San Diego, California, 368 pp.

DINERSTEIN, E., AND L. PRICE. 1991. Demography and habitat use by the greater one-horned rhinoceros in Nepal. *The Journal of Wildlife Management*, 55: 401–411.

EAST, R. 1981. Species-area curves and populations of large mammals in African savanna reserves. *Biological Conservation*, 21:111–126.

ELLIOT, F. W. 1987. Possible predation of black rhinoceros calf by a lion. *Lammergeyer*, 36:68.

FALCONER, D. S. 1960. *Introduction to quantitative genetics*. Ronald Press, New York, 365 pp.

FANCY, S. G., L. F. PANK, K. R. WHITTEN, AND W. L. REGELEN. 1989. Seasonal movements of caribou in Arctic Alaska as determined by satellite. *Canadian Journal of Zoology*, 67:644–650.

FOOSE, T. J. 1993. Global management of rhinos. Pp. 32–47, in *Rhinoceros biology and conservation* (O. A. Ryder, ed.). San Diego Zoological Society, San Diego, California, 368 pp.

FRANKEL, O. H., AND M. E. SOULE. 1981. *Conservation and evolution*. Cambridge University Press, Cambridge, United Kingdom, 327 pp.

FREEMAN, G. H., AND J. M. KING. 1969. Relations amongst various linear measurements and weight for black rhinoceros in Kenya. *East African Wildlife Journal*, 7:67–72.

GASAWAY, W. C., K. T. MOSSESTAD, AND P. E. STANDER. 1989. Demography of spotted hyenas in an arid savanna, Etosha National Park, Southwest Africa/Namibia. *Madoqua*, 16:121–127.

GEIST, V. 1966. The evolution of horn-like organs. *Behaviour*, 27:175–214.

GODDARD, J. 1967. Home range, behaviour, and recruitment rates of two black rhinoceros populations. *East African Wildlife Journal*, 5:133–150.

—. 1969. A note on the absence of pinnae in the black rhinoceros. *East African Wildlife Journal*, 7: 179–180.

HALL-MARTIN, A. 1988. Conservation of the black rhino. The strategy of the National Parks Board of South Africa. *Rhino and Elephant Journal*, 1:12–17.

HALL-MARTIN, A. J., AND B. L. PENZHORN. 1977. Behaviour and recruitment of translocated black rhinoceros *Diceros bicornis*. *Koedoe*, 20:147–162.

HARVEY, P. H., M. J. KAVANAGH, AND T. H. CLUTTON-BROCK. 1978. Sexual dimorphism in primate teeth. *Journal of Zoology (London)*, 186:475–485.

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.

HILLMAN-SMITH, K. 1986. Notes on dentition, cranial and body measurements of the northern white rhino. *Journal of Zoology (London)*, 210:377–379.

HITCHINS, P. A. 1968. Live weights of some mammals from Hluhluwe Game Reserve, Zululand. *Lammergeyer*, 9:26–28.

—. 1986. Earlessness in the black rhinoceros—a warning. *Pachyderm*, 7:8–10.

—. 1990. Census and marking systems for black rhinoceros *Diceros bicornis* with special reference to the Zululand Game Reserves. *The Game Ranger*, 1:1–12.

HITCHINS, P. M., AND J. L. ANDERSON. 1993. Reproductive, population, characteristics, and management of the black rhinoceros *Diceros bicornis minor* in the Hluhluwe/Corridor/Umfolozi game reserve complex. *South African Journal of Wildlife Research*, 13:78–85.

HOFMEYR, J. M. 1975. The adaptation of wild animals translocated to new areas in South West Africa. Pp. 126-131, in Proceedings of the third world conference on animal production (R. Reid, ed.). Sydney University Press, Sydney, Australia.

JANIS, C. M. 1982. Evolution of horns in ungulates: ecology and paleoecology. *Biological Review*, 57: 261-318.

KOCK, M. D., AND M. ATKINSON. 1993. Report on dehorning of black (*Diceros bicornis*) and white (*Ceratotherium simum*) rhinoceroses in Zimbabwe. Department of National Parks and Wildlife Management, Harare, Zimbabwe, 90 pp.

KRUUK, H. 1972. *The spotted hyena*. University of Chicago Press, Chicago, 335 pp.

LEADER-WILLIAMS, N. 1993. Theory and pragmatism in the conservation of rhinos. Pp. 69-81, in Rhinoceros biology and conservation (O. A. Ryder, ed.). San Diego Zoological Society, San Diego, California, 368 pp.

LINDEQUE, M. 1990. The case for dehorning the black rhinoceros in Namibia. *South African Journal of Science*, 86:226-227.

MACFADDEN, B. J. 1992. *Fossil horses: systematics, paleobiology, and the evolution of the family Equidae*. Cambridge University Press, Cambridge, United Kingdom, 369 pp.

MARTIN, R. B. 1993. Rhino population dynamics, illegal hunting and law enforcement in the lower Zambezi Valley in Zimbabwe. Pp. 10-31, in Rhinoceros biology and conservation (O. A. Ryder, ed.), San Diego Zoological Society, San Diego, California, 368 pp.

MAYR, E. 1982. *The growth of biological thought. Diversity, evolution, and inheritance*. Harvard University Press, Cambridge, Massachusetts, 974 pp.

MERENLENDER, A. M., D. S. WOODRUFF, O. A. RYDER, R. KOCK, AND J. VAHALA. 1989. Allozyme variation and differentiation in African and Indian rhinoceroses. *Journal of Heredity*, 80:377-382.

MILLS, M. G. L. 1990. *Kalahari hyenas: comparative behavioural ecology of two species*. Unwin Hyman, London, United Kingdom, 304 pp.

MILNER-GULLAND, E. J., N. LEADER-WILLIAMS, AND J. R. BEDDINGTON. In press. Is dehorning African rhinos worthwhile? *Pachyderm*.

MUNTHE, J., AND M. C. COOMBS. 1979. Miocene dome-skulled Chalicotheres (Mammalia, Perissodactyla) from the western United States: a preliminary discussion of a bizarre structure. *Journal of Paleontology*, 53:77-91.

OWEN-SMITH, G., AND M. JACOBSON. 1989. Involving a local community in wildlife conservation: a pilot project at Purros, southwestern Kaokoland, SWA/Namibia. *Quagga*, 27:21-28.

OWEN-SMITH, R. N. 1975. The social ethology of the white rhinoceros. *Zeitschrift für Tierpsychologie*, 38:377-384.

—. 1988. *Megaherbivores*. Cambridge University Press, Cambridge, United Kingdom, 369 pp.

—. 1993. Comparative mortality rates of male and female kudus: the costs of sexual size dimorphism. *The Journal of Animal Ecology*, 62:428-440.

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

PRINS, H. H. T., AND G. R. IASON. 1989. Dangerous lions and non-chalant buffalo. *Behaviour*, 108:262-296.

PROTHERO, D. R. 1987. The rise and fall of the American rhino. *Natural History*, 87:26-33.

RAJPUROHIT, L. S., AND V. SOMMER. 1991. Sex differences in mortality among langurs (*Presbytis entellus*) of Jodhpur, Rajasthan. *Folia Primatologica*, 56: 17-27.

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 Commission, Special Report*, 2:223-243.

REEVES, H. K., AND P. W. SHERMAN. 1993. Adaptation and the goals of evolutionary research. *The Quarterly Review of Biology*, 68:1-32.

RYDER, O. A. (ED.). 1993. *Rhinoceros biology and conservation*. San Diego Zoological Society, San Diego, California, 368 pp.

SCHONEWALD-COX, C. M. 1983. Conclusions: guidelines to management: a beginning attempt. Pp. 414-445, in *Genetics and conservation. A reference for managing wild animal and plant populations* (C. M. Schonewald-Cox, S. M. Chambers, B. Macbride, and W. L. Thomas, eds.). The Benjamin/Cummings Publishing Company, Menlo Park, California, 722 pp.

SEELY, M. K., AND W. J. HAMILTON, III. 1976. Fog catchment sand trenches constructed by tenebrionid beetles from the Namib Desert. *Science*, 193:4552-4555.

SILLERO-ZUBIRI, C., AND D. GOTTELLI. 1991. Threat to Aberdare rhinos: predation versus poaching. *Pachyderm*, 14:37-38.

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.

SMYTHE, N. 1991. Steps toward domesticating the paca (*Agouti = Cuniculus paca*), and prospects for the future. Pp. 202-216, in *Neotropical wildlife use and conservation* (J. G. Robinson and K. H. Redford, eds.). University of Chicago Press, Chicago, pp.

SOULÉ, M. E. (ED.). 1986. *Conservation biology. The science of scarcity and diversity*. Sinauer Associates, Sunderland, Massachusetts, 584 pp.

TRIVERS, R. L. 1985. *Social evolution*. The Benjamin/Cummings Publishing Company, Menlo Park, California, 462 pp.

VAN VALKENBURGH, B. 1988. Trophic diversity in past and present guilds of large predatory mammals. *Paleobiology*, 14:155-173.

WESTERN, D. 1982. Dehorn or not dehorn? *Swara*, 5: 22-23.

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

WESTERN, D., AND L. VIGNE. 1985. The deteriorating status of African rhinos. *Oryx*, 19:215-220.

WHATELEY, A. 1981. Density and home range of spotted hyenas in Umtolozzi Game Reserve, Natal. *Lammergeyer*, 31:15-20.