Predation, sensitivity, and sex: why female black rhinoceroses outlive males

Among sexually dimorphic, polygynous mammals, adult females tend to outlive males and respond more strongly to predators than males. We asked whether a monomorphic, polygynous species virtually immune to predation due to large size (black rhinoceros, *Diceros bicornis*) conforms to this pattern. Data on 193 interactions with lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*) in two nonhabituated populations in Namibia studied from 1991 to 1993 revealed that: (1) females were more vigilant or aggressive than males to either of the potential predators; and (2) whether solitary or with calves, females attacked more often than males. Although solitary females tended to be more aggressive to lions than to hyenas, neither females with calves or males seemed to discriminate between the two carnivores. We also simulated the behavior of human predators (poachers) during 69 encounters with rhinoceroses. While both sexes abandoned local sites because of our presence, females ran farther than males, covering up to 40 km in a day. These findings implicate a behavioral mechanism to explain why secondary sex ratios favor females—males are more prone to human predation, a prediction consistent with data from 12 populations throughout Africa. Black rhinoceroses appear to be an unanticipated exception to the well-established pattern of male-biased mortality in polygynous mammals; in the absence of intense human predation (a recent event), male mortality fails to exceed that of females, suggesting that intrasexual competition in a polygynous mammal may not be the primary cause of unbalanced secondary sex ratios. Our results on the causes of sex differences in mortality and in responsiveness to different predators reinforce the relevance of behavioral ecology to conservation; such information is necessary for planning how best to minimize negative human influences on the few remaining wild African rhinos. *Key words:* conservation, endangered species, lion, monomorphism, mortality, rhinoceros, sexual selection, spotted hyena. *[Behav Ecol 6:57–64 (1995)]*

Joel Berger
Carol Cunningham
Program in Ecology,
Evolution,
and Conservation Biology,
University of Nevada,
Reno, NV 89512, USA

Why males and females differ behaviorally has been a topic of much interest (Clutton-Brock, 1991). Among mammals, far less attention has focused on how the sexes respond to potential predation, especially because natural predators are now absent from so many of the world's ecosystems. Nevertheless, determining the extent to which males and females vary behaviorally is essential for gaining a better understanding of relationships among sexual dimorphism, parental investment, and demography. For instance, Darwin (1871) first noted that exaggerated ornamentation may have survival costs, and evidence from several mammalian orders, including primates (Rajpurohit and Sommer, 1991), marsupials (Dickman and Braithwaite, 1992), and ungulates and pinnipeds (Owen-Smith, 1993; Ralls, 1976; Ralls et al., 1980), now suggests that the males of dimorphic species experience greater mortality than females. Nowhere is this pattern more striking than for African elephants for whom males, because their tusks are larger and more valuable than those of females, are the preferred trophy of poachers (Leader-Williams et al., 1990). What remains unclear, however, is whether ornaments and/or large body size per se have anything to do with the general mammalian pattern of greater male mortality particularly because sexual dimorphism and polygyny covary (Clutton-Brock, 1989).

Resolution of this problem has proved difficult because: (1) effects of sexual dimorphism cannot be separated from those polygyny without comparative data on species in which the sexes are either similar in body size or monogamous, or both; (2) the hoofed mammals that satisfy these criteria are often small, nocturnal forest dwellers or endangered, making study difficult; and (3) assessment of what, if any, role predation plays necessitates direct information on predator–prey interactions. Nevertheless, the perissodactyls, which include rhinoceroses, tapirs, and equids, may be illustrative. Unlike elephants or the majority of ruminants in which males are adorned with horns, antlers, or tusks (Clutton-Brock et al., 1982; Geist, 1966; Packer, 1983), perissodactyls lack conspicuous secondary sexual characteristics and are monomorphic in body size even though they are polygynous (Berger, 1986; Dinerstein, 1991; Eisenberg, 1981; Owen-Smith, 1988). Despite being one of the earth's most endangered mammals, black rhinoceroses (*Diceros bicornis*) offer unusually good opportunities to evaluate hypotheses about the mechanisms and causes of sex differences in mammalian mortality. Neither males nor females differ in armament or body size (see below), sex ratio data for both living and extirpated subpopulations are available, and interactions with predators can be readily observed at night.

Here, we present data on adult sex ratios in a polygynous, monomorphic mammal and evaluate possible causes for the observed variation. Specif-

Received 22 September 1992
Revised 13 September 1993
Second revision 25 January 1994
Accepted 29 January 1994
1045-2249/95/$5.00

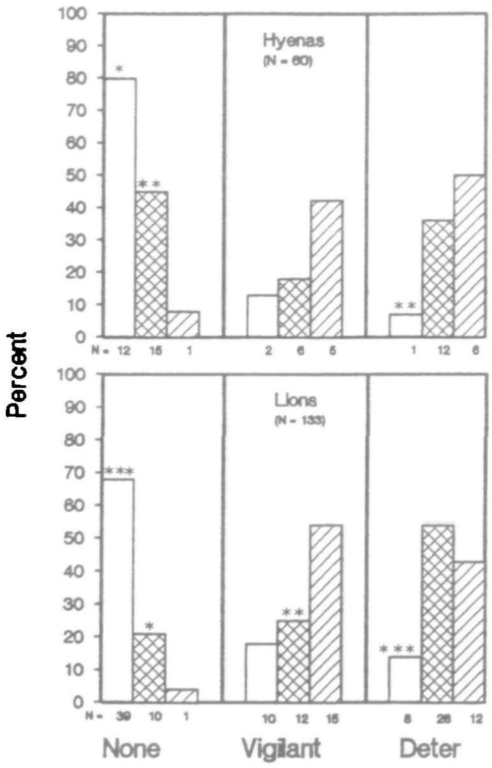

Figure 1
Percent of three increasingly responsive behaviors directed by adult black rhinos toward hyenas and lions. Bars: open, solitary males; cross-hatched, solitary females; hatched, females with calf. Asterisks refer to contrasts between the column below the asterisks and the one to its right (**p < .01, ***p < .001). Cumulative numbers of interactions with hyenas and lions are as indicated and the numbers below each bar are the sample sizes for interactions with each of the designated categories of rhinos.

ically, we: (1) first describe responses of males, females, and mothers with young to spotted hyenas (*Crocuta crocuta*) and lions (*Panthera leo*), and then to humans; (2) document patterns of mortality in the presence and absence of poaching throughout Africa; and (3) suggest how knowledge about the behavioral responses of rhinoceroses to humans is useful for understanding some aspects of spatial distribution, information that has possible bearings on conservation. Finally, we point out that although black rhinoceroses are an anomaly to the well established pattern of male-biased mortality in polygynous mammals, the rhinos differ from other perissodactyls; thus it is difficult to know whether it is the rhinoceroses or the other perissodactyls that are the exception.

METHODS

Study sites and populations

During 1991, 1992, and 1993 we spent 23 months observing black rhinos in two discrete regions of Namibia, the Kaokoveld area of the Kunene Province (latitudes 19°70′–20°80′ S, longitudes 13°80′–14°20′ E) and Etosha National Park (19° S, 14°40′–17° E), each comprising about 7,000 and 20,000 km², respectively. The former is a rugged, mountainous region bisected by open gravel plains and dry rivers extending into the Namib Desert (Joubert and Eloff, 1971; Viljoen, 1989). The area comprises the edge of the natural range of both African rhinos and elephants with corresponding low rhino densities (ca. 0.002/km²) and enormous elephant home ranges (5800–8700 km²; Lindeque and Lindeque, 1991). Our Kaokoveld study area is devoid of people, has not more than 10 lions, and contains an undetermined number of spotted hyenas. Etosha is mixed thronveld and savanna with higher densities of rhinos (about 0.02/km²) and lions (.016–.020/km²; Stander, 1991). At both sites, the study animals are unhabituated, seeing or smelling humans other than us about 6–10 times annually. However, because 20 of our 36 known Kaokoveld study animals had their horns removed (either in 1989 or 1991) to reduce the risk of poaching (Berger, 1993), we cannot discount the possibility that such actions might have affected their behavior toward humans. Nevertheless, nonimmobilized male and female rhinoceroses consistently differed in their responses to us, behaviors that were similar to those of the immobilized Kaokoveld animals (see below).

Sampling, data, and rationale

In Etosha, interactions between rhinoceroses and spotted hyenas or lions were recorded during 153 evenings using night vision equipment, or opportunistically during the day. Data were gathered most often near waterholes, where observations typically lasted from dusk until from 0001–0430 h during 8 to 19 consecutive day sequences. In the Kaokoveld, the probability of witnessing interactions between rhinoceroses and dangerous carnivores is low; during 16 all-night watches, rhinoceroses were seen only twice and never in the presence of potential carnivores. Because seeps and fountains are more widespread in the Kaokoveld than in Etosha, further night observations were not attempted in this desert environment.

The responses of adult rhinos to hyenas or lions at distances of less than 25 m were classified as none (no detected change in behavior), vigilant (head lifted, ears forward, nose movement evident), or deter (horns lowered with movement directed toward the potential predator). Eighteen of 211 interactions (8.5%) could not be categorized and were omitted from analyses; these included five cases in which calves charged predators (thus influencing the behavior of their mothers), four times when rhinos displaced cheetahs, and one instance when a leopard was supplanted. Although rhinoceroses are generally asocial (Owen-Smith, 1988), they may occur in assemblages of up to 11 animals; therefore, data on interactions with potential predators were used only when adult males or females were solitary, or when a mother was solely in the presence of her calf.

We also recorded the immediate behavioral reactions of rhinoceroses to humans in two ways. First, we noted the frequency that we were charged separating the data into night and day episodes because our methods of approach to rhinoceroses differed. At night we stalked to within 25 m of rhinoceroses to confirm individual identities by noting the locations and sizes of ear tears and notches, and horn shapes and sizes. We recorded an interaction as possible any time we were within about 50 m (measured by a Mitutoyo digital caliper attached to a telefoto lens). During the day the same criterion was used except that the distance was greater, 75 m (assessed by a Lietz range finder) because rhinoceroses appear either to see better or are more aggressive. Fortunately, the obvious difference in sampling between night and day (e.g., distance of separation between rhinoceroses and us) did not inflate the number of charges; only 4 of 393 (1%) night interactions resulted in human-directed aggression, whereas 14 of 84 (16.7%) day interactions did. Second, we recorded the frequency that rhinoceroses fled from us as we approached on foot from 100 m. The data on interactions with humans offered a more systematic way to gauge whether the sexes differed in their sensitivity to potential predators; that is, rhinoceroses might charge, remain, or flee.

At our Kaokoveld site, the responses of adult males and females to us were recorded during thirteen 5–9-day sampling trips. Animals were located by following fresh rhinoceros spoor on foot for up to 23 km. Upon discovery, animals were approached to within 40 m (estimated by range finder) and shot with a photogrammetric device attached to a camera. (As with the night photographs, these images allowed us to confirm individual identities and provided for later estimation of horn, head, and body size parameters; Berger, 1993). When animals fled before being photographed, we again followed their spoor on foot using the point at which they subsequently rested to approximate distances of flight. A Trimble Navigation Global Positioning (Ensign) System was used to plot locations. Data on flight were considered only from those rhinoceroses that had been disturbed during the day, thus assuring them the opportunity to rest; in 98.1% of 156 observations of undisturbed animals from 1030 h to 1630 h the animals were lying or standing in shade.

Our goals in determining behavioral responses of Kaokoveld rhinoceroses to potential human predators were twofold; to assess whether rhinos responded differently to predators capable of killing them (e.g., humans shoot adult rhinoceroses but there is no evidence that either lions or hyenas have killed adults) and to evaluate how animals at the edge of their range become distributed spatially after encountering humans. If a difference exists between how rhinoceroses perceived unarmed humans and real poachers, then of course it is not possible to extrapolate the possible responses of rhinos to their most dangerous predator, humans. Though we cannot say with certainty that our actions in disturbing rhinos differed from those of poachers, this prospect appears unlikely, as all of the Kaokoland data were gathered with the help of a field assistant (Damara tracker) who previously was convicted of rhinoceros poaching. Using him, we employed the same tracking methods as when he or his consorts followed rhinoceroses.

To assess whether our presence, either at temporary base camps or in searching for spoor, affected the distribution of rhinoceroses in the Kaokoveld, we estimated the probability of finding rhinoceroses per 1000 km^2. Our daily protocol was to depart base camps just after sunrise with the field assistant (tracker) sitting atop the Landrover. Each time we encountered spoor, he noted whether it was fresh (i.e., the animal had been there the previous night or that morning) or old. If fresh, we tracked the animal(s) until it was found and photographed or until those tracks proved fruitless and we looked for other fresh spoor. Identical search procedures were used from all base camps—especially driving along soft substrate when possible, a situation that favors the detection of fresh tracks.

Habitats from which animals were initially disturbed by us were classified as either gravel plains—areas with excellent visibility and little vegetation cover except for scattered acacias, boscias, and euphorbias—or dry rivers—riverine vegetation, often with poor visibility due to extensive cover, and associated mopane, camel-thorn acacia, omumborombonga (hardwood), and tamarisk trees. Eight data points were excluded when habitats could not be categorized.

Because our analyses of male and female behavior have largely been exploratory and developed retrospectively, we have not tested explicit a priori hypotheses. All statistical tests are two-tailed.

Body dimension data were extracted from the literature. The evidence indicated that neither body size nor mass differs between the sexes (Freeman and King, 1969; Hitchins, 1968), although rhinoceroses grow throughout their lives (Goddard, 1967). Thus, without taking age into account the claim that the width of male horns is greater than that for females (Pienaar and Hall-Martin, 1991) cannot be substantiated. In fact, based on the 37 anterior horns of Namibian rhinoceroses of known sex that we measured and whose ages were estimated from tooth eruption and wear (according to Hitchins, 1978), horn basal diameter and length were independent of sex (partial correlation coefficients for diameter and length, respectively, are −.20, −.30) but highly correlated with age (r = .70,.60, $p <$ 0.001 for both).

RESULTS AND DISCUSSION

Behavioral responses to potential predators

Although females of sexually dimorphic species are more vigilant and likely to flee from predators than are males (Berger, 1991; Berger and Cunningham, 1988; Prins and Iason, 1989), sex differences in responsiveness to potential predators may be a simple consequence of neonate presence, relatively small(er) body size, or group formation. For instance, because spotted hyenas, lions, and tigers have preyed on the calves of African or Asian rhinoceroses (Dinerstein and Price, 1991; Elliot, 1987; Goddard, 1967; Western, 1982), it would be surprising if parous females were *not* more vigilant than females without calves or solitary males. However, for species like black rhinoceroses that are not sexually dimorphic, body size in itself should not affect outcomes with possible predators. In the absence of offspring, we predicted that adult males and solitary nonparous females should behave similarly in the presence of spotted hyenas and lions.

Nevertheless, information on 193 encounters suggests prominent sex differences. Solitary adult females were more sensitive than males to dangerous carnivores (Figure 1); females responded to and deterred potential predators more often than did males [Fisher's exact probability test (FEPT)—hyenas: 55% versus 20% (p = .025) and 36% versus 7% (p = .031); lions: 79% versus 32% (p = .00001) and 54% versus 14% (p = .00001), respectively]. Although male behaviors did not vary in response to carnivore species (FEPT; p = .30), once solitary females became vigilant, they were more likely to charge lions than hyenas (54% versus 36%; FEPT;

Table 1
Summary of night and day responses of black rhinoceroses (percentage of interactions) to humans

	Flee	Charge	*N*
Day			
Males	33	6	36
Solitary females	58	27	26
Females with calves	59	23	22
p	.0003	.0003	
Night			
Males	13	3	39
Solitary females	26	0	19
Females with calves	33	7	42
p	.025	.39	

p is probability that males and females differ; data pooled for solitary females and females with calves.

$p = .047$, $n = 56$). Not surprisingly, mothers were more vigilant than solitary females (Figure 1), but mothers were no more responsive to lions than to hyenas (96% versus 92%; FEPT; $p = .52$) nor were they likely to charge one species over the other (43% versus 50%; FEPT; $p = .417$). These data suggest both subtle and prominent effects stemming from the presence of potentially dangerous predators. Females with young responded in predictable ways to minimize predation on their calves by being more vigilant or likely to charge than solitary females; males, on the other hand, were less likely than solitary females to display overt responses to either lions or hyenas.

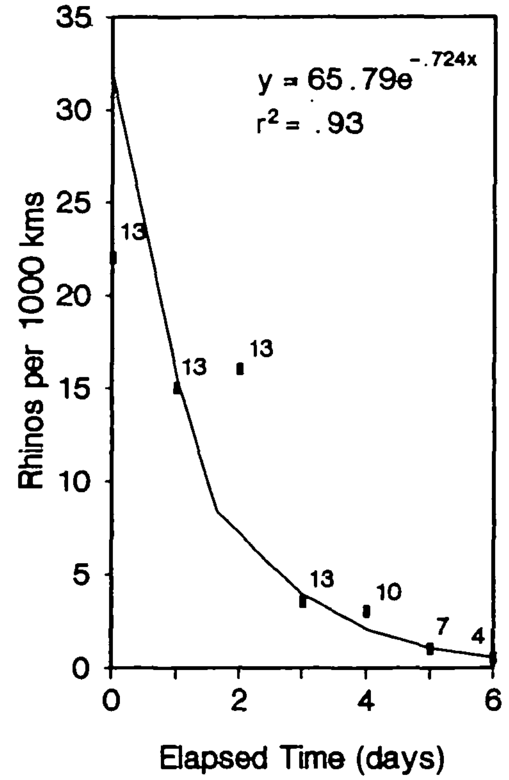

Figure 2
Relationship between the mean number of fresh rhino tracks per km and the elapsed time (days) at the same base camp expressed as a negative exponential regression (coefficient of determination as shown). Numbers are the frequency of trips lasting the indicated length of time (in days).

Behavioral responses to humans

The sex differences in behavior to dangerous predators persisted when we interacted with rhinoceroses (Table 1). For instance, males were less likely to flee than females (FEPT; day: $p = .0003$; night: $p = .025$) although differences in flight did not exist between lactating and nonparous females (FEPT; day: $p = .59$; night: $p = .34$) and females charged more often than males (day and night interactions combined; FEPT; $p = .003$). At night, less than 10% of the interactions with us resulted in aggressive behavior, and sex differences in human-directed aggression were not evident (FEPT; $p = .39$).

These data on behavioral reactions to humans appear similar to those with hyenas and lions, but it is not possible to compare directly the probability of fleeing from humans with those of non-humans because the data were recorded differently. Thus, whereas female rhinoceroses with calves fled from lions or hyenas six times, all but two occurred when the mothers were more than 50 meters away. On the other hand, solitary male and female rhinoceroses never fled from lions or hyenas, but they did flee from us during the night and day (Table 1: males, 13% and 33%; females, 26% and 58%).

Given that solitary rhinoceroses are more apt to flee from humans than from other potential predators, do they experience local site abandonment? That is, do rhinoceroses leave the immediate areas they are in and how far do they move? We evaluated this idea in three ways. First, we found that the frequency of encountering fresh tracks decreased daily, by a magnitude of 60 times from 21 (day 1) to 0.33 (day 7) per 1000 km^2 (Figure 2). Exponential regression of elapsed time in an area explained 93% of the variance in rhino presence. The possibility that the observed reduction in rhinos arose as an artifact of sampling appears untenable for at least two reasons: (1) Quasi-experimental evidence points to a similar inverse relationship between the number of rhinoceroses detected and length of human occupancy of an area. In our absence, government or nongovernment fieldworkers visited our Kaokoveld study areas on three occasions, remaining for up to 6 days. Whereas they detected at least 9, 5, and 5 individuals, none of our visits (all occurring within 6 days of theirs), produced evidence of animals in the area. The differences between what we should have found on average in the absence of human disturbance and what we actually found differs (t test; $t = 4.59$; df $= 14$; $p < .001$). (2) The routes we traversed to and from the base camps were the same and search procedures did not vary among areas (see Methods).

Second, assuming human presence had no influence on the spatial and temporal distribution of rhinoceroses, the frequency with which springs or seeps were used should remain unaltered. This was not the case; visitation to water differed strikingly between the first 3 and last 3 days we were in an area (16 to 4; $p = .028$; binomial probability). Unfortunately, only in rare instances was it possible to gauge how far rhinos shifted. Two females independently moved more than 40 km in 24 h, another more than 30 km; two males independently moved in excess of 23 km.

Third, we assessed whether males and females differed in the distances they fled after disturbance, predicting that because females displayed greater behavioral sensitivities than males to potentially dangerous predators, females should move greater distances. Irrespective of habitat, females moved farther than males (Figure 3) with sex exerting a stronger effect on flight distance than habitat [two-way ANOVA; $F_{1,65}$(sex) = 16.41, $p < .001$; F (habitat) = 5.12; $p < .05$; interaction ns]. These distances of flight before resting represent the most extreme known to us for terrestrial mammals. Although bison have run as far as 86 km in a single day, they had first been chased by wolves for several km and occur in groups (Carbyn et al., 1993) whereas the rhinos who fled from us had presumably only smelled us and were, of course, solitary. They were not chased. Irrespective of the causes, the above three lines of evidence are consistent with the tenet that some degree of local site abandonment occurred in unhabituated black rhinos.

Human predation and sex differences in mortality

Because females were more sensitive to hyenas and lions (Figure 1) and fled farther from humans than did males (Figure 2), were females killed less frequently? The proposition is difficult to evaluate. Numbers can be approximated only crudely even under the best of conditions unless details of individuals are known (Hitchins and Anderson, 1983; Leader-Williams, 1988) and the subpopulations of many endangered species, rhinoceroses included, have such prohibitively few individuals that to gain statistical reliability in the assessment of sex ratios is a serious problem. (Only 2 of 22 areas exceeded 75 adults; Table 1.) Sample sizes cannot even be bolstered by using information derived from confiscated trophies because sex cannot be determined from horn size (Freeman and King, 1969; Goddard, 1970). Despite these caveats, data from Namibia and five other countries allow evaluation of vulnerability to poachers.

In western Etosha a poaching epidemic during 1987–1989, which included the slaughter of 23 animals in less than 3 weeks, resulted in the identification of 18 male and 9 female carcasses (Cilliers A, personal communication). The number of adult males (18) and females (21) remaining alive in the population and poached adults differs, approaching significance (FEPT; $p = .081$). More pertinent, however, is that about 100 additional rhinoceroses lived at that time in western Etosh (Cilliers, personal communication), thus the sample of living adults was really a subsample of a larger population. Assuming that the adult sex ratio of these rhinos was 50:50 (the average based on 19 studies with, or before, minimal human predation is .525 males : .475 females; Table 2) prior to the poaching deluge, then the disproportionate taking of males is exaggerated ($p = .069$). Similar patterns occurred in Zambia and Tanzania. Leader-Williams (1988) indicated that the number of adult males and females before poaching in his Luangwa Valley population changed from 37 and 29 to 17 and 15 (respectively) after poaching occurred. The shift, though also against adult males, failed to differ ($p < .18$). However, when combined with the Etosha sample to minimize the possibility of a Type II error, males were harvested disproportionately ($p < .04$). And, during 15 years of poaching the ratio of adult males to females in Ngorongoro Crater was halved (Table 2).

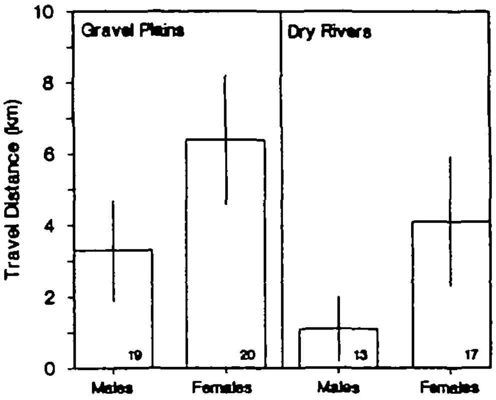

Figure 3
Effects of sex and habitat on mean travel distance from initial disturbance to a resting site by black rhinos. The dry river sample includes 7 cases in which unhabituated Etosha animals were followed from disturbance to resting site in mopane or acacia woodland. Total number of encounters indicated at base of columns and bars are ±1 standard deviation.

The conclusion that males are more susceptible to human predation is reinforced with two additional analyses. First, coupling the prior information with data from Kenya, Zimbabwe, and South Africa (Table 2) we contrasted sex ratios in unprotected and protected populations (or areas with data prior to widespread poaching) using each site independently; adult males exceeded females in nine of ten "safe" regions but not in four (Ngorongoro, Luangwa Valley, Etosha, Khorixas-Seisfontein) of five areas with poaching ($p = .017$). To be conservative, we used only a single value for each of the Tsavo and Hluhluwe/Umfolozi populations because gene flow is (or was, in the case of Tsavo) possible rather than using single values for respective subpopulations. Mkuzi and Ndumu were omitted; both are small, recently introduced populations. The data from Etosh and Luangwa, both before and after the periods of exceptional mortality, were used separately in analyses. Second, to check whether the secondary sex ratios might result from differences at birth rather than extrinsic factors, we evaluated birth sex ratios using data of the American Association Zoological Parks and Aquaria (1950–1989) and the International Studbook for African Rhinos (1969–1986); the respective primary sex ratios (47:53, $n = 101$; 49:51; $n = 127$) failed to differ from parity or adult sex ratios at unharvested sites.

Sex ratio alterations and behavior

Why sex ratio shifts occur in populations with human predation is now apparent. Adult males are relatively stolid, females being more sensitive to potential predators. Although both sexes fled irrespective of habitat (Figure 3), males moved less than females, covering a distance that is likely to be inadequate to avoid armed humans.

The sex differences are likely to arise in two unrelated ways. First, females may be more responsive to dangerous predators as a form of future investment. If harassment of predators is consistently directed by potentially dangerous animals like rhinoceroses toward lions and hyenas, then future predation attempts on their own offspring may be diminished (Berger, 1979). Second, because the asymmetries in behavioral responses to predators

Table 2

Adult sex ratios (male:female) of black rhino populations or subpopulations during periods in which human predation was high (H) or low (L) (e.g., well protected)

Location	Sex ratio (*n*)	Human predation High	Human predation Low	References
Southern Africa				
Khorixas-Sesfontein, Namibia	1:1.27 (25)	+		1
—Kaokoveld,[a] Namibia	1.0.93 (23)		+	2
—Etosha, Namibia	1:0.83 (66)		+	3
—Kariba Basin, Zimbabwe	1:0.87 (43)		+	4
Luangwa Valley, Zambia	1:0.78 (66)		+	5
—Hlulhuwe, South Africa	1:0.91 (82)		+	6
—Corridor, South Africa	1:0.90 (74)		+	6
—Umfolozi, South Africa	1:0.71 (72)		+	6
Mkuzui, South Africa	1:0.78 (41)		+	6
Ndumu, South Africa	1:1.20 (33)		+	6
East Africa				
Ngorongoro, Tanzania	1:0.78 (66)		+	7
Ngorongoro,[b] Tanzania	1:1.63 (21)	+		8
Serengeti, Tanzania	1:1.20 (44)		+	9
Oldavai, Kenya	1:0.86 (41)		+	7
Amboseli, Kenya	1:0.75 (21)	+		10
—Masai-Mara, Kenya	1:0.82 (71)		+	11
—Tsavo,[c] Kenya (low density)	1:1.09 (46)		+	12
—Tsavo, Kenya (medium density)	1:1.06 (35)		+	12
—Tsavo, Kenya (high density)	1:1.28 (73)		+	12
—Tsavo, Kenya (high density)	1:0.83 (55)		+	12
—Tsavo, Kenya (high density)	1:0.90 (78)		+	12
—Tsavo, Kenya (high density)	1:1.04 (51)		+	12

Cases where only a subpopulation was censured are indented with a dash.

References: 1, Hofmeyr et al. (1975); 2, this study; 3, Cilliers (unpublished); 4, Roth and Child (1968); 5, Leader-Williams (1988); 6, Hitchins and Anderson (1983); 7, Goddard (1967); 8, Kiwia (1989); 9, Frame (1980); 10, Western and Sindiyo (1972); 11, Mukinya (1973); 12, Goddard (1970).

[a] Doros Crater to Upper Uniab River.

[b] Poaching and naturality mortality.

[c] Tsavo data gathered from ground censuses in different areas of the 23,000 km^2 reserve from 1967–1969.

by males and females cannot be a consequence of sex differences in body or horn size (recall that the sexes are similar in horns and mass; see Methods), they must result from "maleness" per se. That is, with no effective predators until recently and no direct paternal investment, it appears that little incentive exists for males not to be stolid. For instance, the largest black rhinoceros suspected of being killed by predators was only about 2 years old (Elliot, 1987) although wild rhinos may live to be about 40. By their sheer size alone, most weaned individuals are immune from today's predators although that is unlikely to have been the case in the past when effective non-human mammalian predators were larger.

An additional (and intriguing) possibility for understanding why the sexes differ in their responses to humans is that males may have more to lose by abandoning resource-based mating territories than females. If this was the case, then we might not expect females to differ from males in their tendency to flee when drinking from common watering points. However, the consistent sex differences in flight [females were about 240% times as likely as males to run from us; 31% to 13%, respectively; from Table 1; (FEPT; $p = .03$)] suggests the robustness of sexual asymmetries independent of locations within their home ranges.

Conclusions and uncertainties

Our findings have relevance to both theory and conservation. First, if secondary sexual characteristics or large body size contribute to the male-biased mortality found in dimorphic mammals (Clutton-Brock et al., 1982; Owen-Smith, 1993; Ralls et al., 1980), then the sexes of monomorphic species should experience equal mortality rates. That rhinos do not conform to the expected pattern seems a contradiction, but the apparent discrepancy may be reconciled by noting that human predation has intensified only greatly during the last 30 years (Leader-Williams, 1988; Western, 1987). In populations protected from poaching, the number of adult males and females remains at parity or slightly favors males. However, among the Equidae (horses, zebras, and asses), another monomorphic polygynous family (Ginsberg and Huck, 1989; Rubenstein, 1986) of perissodactyl, secondary sex ratios favor adult females, an effect explained ultimately by more males dying because of intrasexual competition (Berger, 1983). Why black rhinoceroses depart from this pattern awaits explanation. Perhaps, in the absence of human predation, females incur high mortality relative to males that results in a more balanced adult sex ratio. Alternatively, males may survive better into adulthood because they are less costly to produce. It is also possible that males may not be as polygynous as is generally assumed (Owen-Smith, 1988), although this scenario appears unlikely given that males in wild populations may remain dominant for at least 10 years (Owen-Smith, G unpublished). Whatever the causes, it is evident that in the absence of human predation most black rhinoceros populations are at parity (Table 2) and therefore differ from the typical mammalian pattern of biased adult sex ratios.

Second, our behavioral results suggest a possible limitation to ecotourism as a conservation tactic. The Kaokoveld animals represent the last viable unfenced population of black rhinoceroses remaining in Africa. Because they also occur at the edge of their natural range and encounter people infrequently, human disturbance is likely to have subtle but significant effects due to local site abandonment. Although black rhinoceroses in other areas of Africa habituate to humans, they do not live at low densities in spartan habitats. Tourism is usually viewed as one potential way to contribute to the conservation of endangered species and the maintenance of biodiversity and, thus, it is often encouraged by financially-strapped countries. A critical challenge for the future will be to determine the point at which humans intrusions into an area will have minimal biological impacts.

Our research has been sponsored by the American Philosophical Society, Frankfurt Zoological Scoiety, Hasselblad Foundation, National Geographic Society, National Zoological Park (Smithsonian Institution), Rhino Rescue Ltd., Save the Rhino Trust, University of Nevada, Wildlife Conservation Society (New York Zoological Society), National Science Foundation, Office of Forestry, Environment, and Natural Resources Bureau of Science and Technology of the U.S. Agency for International Development (under NSF Grant BSR-9025018), and World Wildlife Fund–US. A. Cilliers most kindly provided the poaching data from Etosha; Drs. M. Lindeque, E. Joubert, P. Morkel, G. Owen-Smith, and B. Fox facilitated our research, and A. A. Gawuseb was splendid in finding Kaokoveld rhinoceroses. For insights, discussions, manuscript reviews, and unusually high levels of encouragement, we thank Drs. B. Gasaway, M. Lindeque, E. Joubert, D. Kramer, and two anonymous reviewers.

REFERENCES

Berger J, 1979. Predator harassment as a defensive strategy in ungulates. Am Midl Nat 102:197–199.

Berger J, 1983. Predation, sex ratios, and intermale competition in equids. J Zool Lond 201:205–216.

Berger J, 1986. Wild horses of the Great Basin: social competition and population size. Chicago: University of Chicago Press.

Berger J, 1991. Pregnancy incentives, predation constraints and habitat shifts: experimental and field evidence for wild bighorn sheep. Anim Behav 41:61–77.

Berger J, 1993. Rhino conservation tactics. Nature 361: 121.

Berger J, Cunningham C, 1988. Size-related effects on search times in North American ungulate females. Ecology 69:177–183.

Carbyn LN, Oosenbrug SM, Anions DW, 1993. Wolves, bison, and the dynamics related to the Peace-Athabasca Delta in Canada's Wood Buffalo National Park. Edmonton: Canadian Circumpolar Institute.

Clutton-Brock TH, 1989. Mammalian mating systems. Proc R Soc Lond B 235:339–372.

Clutton-Brock TH, 1991. The evolution of parental care. Princeton, New Jersey: Princeton University Press.

Clutton-Brock TH, Guinness FE, Albon SD, 1982. Red deer: ecology and behavior of two sexes. Chicago: University of Chicago Press.

Conway AJ, Goodman PS, 1989. Population characteristics and management of black rhinoceros *Diceros bicornis minor* and white rhinoceros *Ceratotherium simum simum* in Ndumu Game Reserve, South Africa. Biol Conserv 47:109–122.

Darwin C, 1871. Descent of man and selection in relation to sex. London: Murray.

Dickman CR, Braithwaite RW, 1992. Postmating mortality of males in the Dasyurid marsupial, *Dasyurus* and *parantechinus*. J Mammal 73:143–147.

Dinerstein E, 1991. Sexual dimorphism in the greater one-horned rhinoceros (*Rhinoceros unicornis*). J Mammal 72:450–457.

Dinerstein E, Price L, 1991. Demography and habitat use by greater one-horned rhinoceros in Nepal. J Wildl Manage 55:401–411.

Eisenberg JF, 1981. The mammalian radiations. Chicago: University of Chicago Press.

Elliot FW, 1987. Possible predation of black rhinoceros calf by a lion. Lammergeyer 38:68.

Frame GW, 1980. Black rhinoceros [*Diceros bicornis* (L.)] sub-population on the Serengeti plains, Tanzania. Afr J Ecol 18:155–166.

Freeman GH, King JM, 1969. Relations amongst various linear measurements and weight for black rhinoceros in Kenya. East Afr Wildl J 7:67–72.

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

Ginsberg JR, Huck UW, 1989. Sperm competition in mammals. Trends Ecol Evol 4:74–79.

Goddard J, 1967. Home range, behaviour and recruitment rates of two black rhinoceros populations. East Afr Wildl J 5:133–150.

Goddard J, 1970. Age criteria and vital statistics of a black rhinoceros population. East Afr Wildl J 8:105–122.

Hitchins PM, 1968. Live weights of some mammals from Hluhluwe Game Reserve, Zululand. Lammergeyer 9:26–28.

Hitchins PM, 1978. Age determination of the black rhinoceros (*Diceros bicornis* Linn.) in Zululand. South Afr J Wildl Res 8:71–80.

Hitchins PM, Anderson JL, 1983. Reproduction, population characteristics and management of the black rhinoceros *Diceros bicornis minor* in the Hluhluwe/Corridor/Umfolozi Game Reserve Complex. South Afr J Wildl Res 13:78–85.

Hofmeyr JM, Ebedes H, Fryer REM, de Bruine JR, 1975. The capture and translocation of the black rhinoceros *Diceros bicornis* Linn in South West Africa. Madoqua 9:35–44.

Joubert E, Eloff FG, 1971. Notes on the ecology and behaviour of the black rhinoceros *Diceros bicornis* Linn 1758 in South West Africa. Madoqua 1:5–53.

Kiwia HD, 1989. Black rhinoceros [*Diceros bicornis* (L.)]: population size and structure in Ngorogoro Crater, Tanzania. Afr J Ecol 27:1–6.

Leader-Williams N, 1988. Patterns of depletion in a black rhinoceros population in Luangwa Valley, Zambia. Afr J Ecol 26:181–187.

Leader-Williams N, Albon SD, Berry PSM, 1990. Illegal exploitation of black rhinoceros and elephant populations: patterns of decline, law enforcement and patrol effort in Luangwa Valley, Zambia. J Appl Ecol 27:1055–1087.

Lindeque M, 1990. The case for dehorning the black rhinoceros in Namibia. South Afr J Sci 86:226–227.

Lindeque M, Lindeque PM, 1991. Satellite tracking of elephants in northwestern Namibia. Afr J Ecol 29:196–206.

Mukinya JG, 1973. Density, distribution, population structure and social organization of the black rhinoceros in Masai Mara Game Reserve. East Afr Wildl J 11: 385–400.

Owen-Smith N, 1988. Megaherbivores. Cambridge: Cambridge University Press.

Owen-Smith N, 1993. Comparative mortality rates of male and female kudus: the costs of sexual size dimorphism. J Anim Ecol 62:428–440.

Packer C, 1983. Sexual dimorphism: the horns of African antelope. Science 221:1191–1193.

Pienaar DJ, Hall-Martin AJ, Hitchins PM, 1991. Horn growth rates of free-ranging white and black rhinoceros. Koedoe 34:97–105.

Prins HHT, Iason GR, 1989. Dangerous lions and nonchalant buffalo. Behaviour 108:262–296.

Rajpurohit LS, Sommer V, 1991. Sex differences in mortality among langurs (*Presbytis entellus*) of Jodhpur, Rajasthan. Folia Primatol 56:17–27.

Ralls K, 1976. Mammals in which females are larger than males. Q Rev Biol 51:245–276.

Ralls K, Brownell R, Ballou J, 1980. Differential mortality by sex and age in mammals with specific reference to the sperm whale. Rep Int Whaling Comm Spec Issue 2:223–243.

Roth HH, Child G, 1968. Distribution and population structure of black rhinoceros (*Diceros bicornis* L.) in the Lake Kariba Basin. Z fur Saeugetierkd 33:214–226.

Rubenstein DI, 1986. Ecology and sociality in horses and zebras. In: Ecological aspects of social evolution (Rubenstein DI, Wrangham RW, eds). Princeton, New Jersey: Princeton University Press; 282–302.

Stander PE, 1991. Demography of lions in Etosha National Park, Namibia. Madoqua 18:1–9.

Sukumar R, Gadgil M, 1988. Male–female differences in foraging on crops by Asian elephants. Anim Behav 36: 1233–1235.

Viljoen PJ, 1989. Spatial distribution and movements of elephants (*Loxodonta africana*) in the northern Namib Desert region of the Kaokoveld, Southwest Africa/Namibia. J Zool Lond 219:1–9.

Western D, 1982. Patterns of depletion in a Kenyan rhino population and the conservation implications. Biol Cons 24:47–56.

Western D, 1987. Africa's elephants and rhinos: flagships in crisis. Trends Ecol Evol 2:343–346.

Western D, Sindiyo DM, 1972. The status of the Amboseli rhino population. East Afr Wildl J 10:43–57.