IS RHINO DEHORNING SCIENTIFICALLY PRUDENT?

Joel Berger¹ and Carol Cunningham²

¹Programme in Ecology, Evolution and Conservation Biology ²Department of Environmental and Resource Sciences University of Nevada (MS-186), Reno, Nevada 89512, USA Field address (from February 1996 until July 1997): PO Box 142, Moose, Wyoming 83012, USA

ABSTRACT

We contrasted calf survivorship of horned and dehorned black rhino (Diceros bicornis) females in the Namib Desert, and have reported elsewhere that calf mortality was higher in a dehorned population sympatric with spotted hyaenas (Crocuta crocuta) than it was in a hyaena-free area or where mothers were horned. Our findings have been controversial because sample sizes are small and data on some ecological variables were not offered. Here, we clarify our research protocols and substantiate prior findings with comparative data on potentially confounding variables such as horn size similarities, hyaena abundance, patterns of precipitation, herbivore biomass, the location of domestic stock, and adult rhino mortalities. We suggest that management decisions based on empirically-derived data might be better than those based on no data at all.

INTRODUCTION

Over the last three decades, populations of black rhinos (*Diceros bicornis*) have dropped nearly 97%, so strategies aimed at preventing extinction have required emergency action (Western, 1987; Leader-Williams, 1993). One such tactic has been dehorning, a programme debated in Kenya nearly 15 years ago (Western, 1982) and first tried in Namibia in 1989 because funds for anti-poaching patrols were limited (Lindeque, 1990).

Previously, we suggested that when dehorned mothers were sympatric with spotted hyaenas (*Crocuta crocuta*) in the Namib Desert, fewer calves were recruited than in the absence of hyaenas. We also pointed out that drought was likely to have exacerbated these effects and that our sample of 10 calves was small (Berger & Cunningham, 1994a,b). Our findings have been challenged by government and non-government officials in Namibia (Loutit & Montgomery, 1994a,b; Lindeque & Erb, 1995). Here we present new data and summarise previous findings to clarify and substantiate our position. As before (Berger *et al.*, 1994), we do not take issue with the possibility that government horn harvesting might reduce poaching pressure on rhinos. What we are concerned with are biological issues concerning dehorning and data as they relate to management decisions. Lindeque and Erb (1995) raised issues ranging from statistics and data interpretation, topics critical to any scientific assessment. We address their claims in three sections: research methodology and hyaena abundance; factual errors; and evaluation of confounding variables. We close by addressing the public interest and suggesting why independent research is in the best interest of conservation.

RESEARCH METHODOLOGY AND HYAENA ABUNDANCE

Study design

Our research was aimed at assessing components of rhino social biology, including calf survival, and involved a three-way comparison of contiguouslydistributed rhinos in the northern Namib Desert with contrasts among: 1) horned rhinos in the presence of dangerous predators (lions, Panthera leo, and spotted hyaenas); 2) dehorned rhinos in the absence of dangerous predators; and 3) dehorned rhinos in the presence of spotted hyaenas. The fourth category, horned rhinos in the absence of predators, does not presently occur in the Namib Desert. Of course, having a fourth study area fulfills the requirements of a balanced study design because calf survival may vary randomly and knowledge of calf mortality under all conditions is clearly relevant. Nevertheless, it seemed reasonable to forgo information from sites where predators are absent and rhinos horned because of the presumption that without predators calf survival should not change.

Abundance of spotted hyaenas

Lindeque and Erb (1995) suggest that our study design was flawed because spotted hyaenas occur throughout the study region. Support for their claim is unbalanced. They fail to cite Skinner and van Aarde (1981) who surveyed the Namib Desert for brown *(Hyaena brunnea)* and spotted hyaenas and reported "we still have no idea what numbers occur in the area or range". Instead, they cite Skinner & Smithers (1990) although these authors provide range maps only and not data of the resolution needed to distinguish among our three respective study regions. Additionally, the use of unpublished records to bolster their argument is questionable because it is impossible to decide how credible the records are.

Lindeque and Erb (1995) reported spotted hyaenas at a rhino carcass in the Doros Crater (DC) area. They were fortunate in their observation because, on average, spotted hyaenas in the northern Kalahari spent less than six minutes on a carcass (Cooper, 1990), yet the Namib Desert rhino in question had been dead for about three weeks when discovered (Morkel, 1992). Lindeque and Erb (1995) also imply that it is difficult to distinguish between the tracks of spotted and brown hyaenas. However, both Damara herdsmen in the Namib Desert and !Xo trackers in the Kalahari can distinguish between the species because of "the relative difference in size between the front and back feet. In the brown hyaena the back feet are much smaller than the front feet, while in the spotted hyaena the difference is not nearly so marked" (Mills, pers.comm.; Liebenberg, 1990).

We evaluated hyaena abundance using standard methods employed in southern Africa, using counts of tracks crossing roads (Mills et al., 1984). We recorded every possible hyaena spoor on roads and elsewhere. If Lindeque and Erb (1995) are correct that both species of hyaenas are widespread, then our inclusion of all hyaena signs would inflate the number of hyaenas irrespective of species. We also used more direct methods to distinguish between brown and spotted hyaenas. Vocalisations of spotted hyaenas were recorded nightly as either existing or absent. This approach is conservative because it discounts the possibility that more than one animal may be present or calling. We also recorded how many brown and spotted hyaenas were seen per day spent in the field (and by accounting for km/transect; see Table 1 and below for details) but, as above, groups were recorded as single observations.

	North of the veterinary fence		Doros Crater		Springbok	
	Transect Length	Biomass	Transect Length	Biomass	Transect Length	Biomass
1991						
Wet	20±3(10)	65±20	44±5 (5)	44±8	36±10(4)	29±12
Dry	51±7 (5)	5± 3	55±5(15)	35±8	30± 3(5)	20±12
1992						
Wet	15±22(4)	64±30	48± 4(3)	56± 6	45±10(9)	57±41
Dry	57±15(5)	46±25	49±11 (4)	30±16	35± 4(4)	15± 8
1993						
wet	67±17(5)	106±78	35±5 (3)	114±80	39±13(13)	62±23
Dry	55±8(14)	25± 9	16±2(12)	16±10	26± 4(6)	12± 4

Table 1. Mean length ($km \pm SE$,) of 126 transects and herbivore biomass (kg/km 2) during wet and dry seasons in three census areas of the northern Namib Desert.

Sample size in parentheses. Area sizes are NVF: 1,858km²,' DC: 3,418km²; SR: 1,710km²

At no site were brown hyaenas seen. Spotted hyaenas were noted at only two of our three study regions (see Figure). Irrespective of species, there was not a single track, vocalisation, or sighting in the DC area although transects there totalled more than 1,675km (Table 1). Similarly, there was no evidence of lions in the DC area. We therefore designated the site as predator-free. DC differed from the other two areas (vocalisations: G-Test for Independence, Gadj=1.01, p<0.001; a test for Homogeneity of Variance reveals that neither site with hyaenas differs from each other but both differ from the DC area; p<0.001). The frequency with which tracks were detected also varied among sites (Figure 1) (Kruskal Wallis Test, H = 10.89, p<0.004) with the DC area differing from the other two area (p<0.01).

FREQUENCY OF HYAENAS

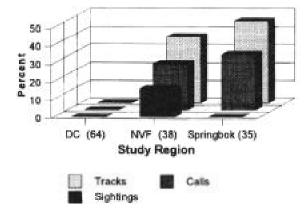


Figure. The proportion of transects (listed in Table 1) EURIHEWTHER TRANSFORMUSIEMTINGS: SAMPERING UASER ON AUNIDER WHIGH HISCHIN PARENTRASION OF A SHARE OF A SHARE SUMPLIES OF A SHARE OF SPOTED AND A SHARE AS WERE NOTED SIGNLING and calls are for spotted hyaenas.

Why spotted hyaenas were not seen at the Springbok River (SR) site although tracks and vocalisations were noted is easy to explain. We made no effort to observe them there. When hyaena-like calls emanated on multiple occasions next to our SR camps, we made no effort to verify that they were indeed made by hyaenas. We believe that we can discriminate the calls of spotted hyaenas from those of other mammals. Nevertheless, our other data, shown in the Figure, make clear that hyaena presence varied regionally and consistently during the period of our study and that one area was free of hyaenas and lions.

FACTUAL ERRORS

Drought

Lindeque and Erb (1995) suggest "the alleged rhino calf deaths coincided with the worst drought in human memory in Namibia". We evaluated their claim in two ways using data on rainfall inside the study area (Wereldsend: =72 mm/yr; Owen-Smith, unpublished; N=12 years) and to the north (Sesfontein: x=95 mm/ yr; Namibia Weather Bureau Statistics, Windhoek; N=24 years). First, we described the proportion of years in which less precipitation occurred than during the 1992-1993 wet season. Next, we asked what proportion of successive years received less rain than that recorded during the 1991-1992 and 1992-1993 period combined. Irrespective of the method used, we found no support for the claim that the drought when the calves disappeared was the worst. Data from Wereldsend and Sesfontein, respectively, indicate that on a per year basis, 33% and 21% of the years had less rainfall. On a multiple year basis, the proportions of periods with less rain were 25% and 17%. So, although conditions at our sites were drier than average, Lindeque and Erb (1995) cannot accurately state that "this" drought really was the worst in human memory.

Rhino mortalities

Lindeque and Erb (1995) purport that the SR site was drier than others. They cite a Normalised Difference Vegetation Index (unpublished data) and point to animals at that site being in poor condition. They also refer to the starvation of a sub-adult rhino. None of these is prime evidence for the SR animals being differentially affected than desert rhinos elsewhere.

If SR animals were in poorer condition, Lindeque and Erb (1995) might have a case. However, a previously published analysis shows otherwise (Berger *et a!.*, 1994). Briefly, we used a one-way analysis of variance to determine whether mean body condition scores (pelvic, spinal, and rib prominence; as suggested for rhinos by Keep [1971]) varied among desert regions. If the SR rhinos were in the worst condition, their hypothesis would be supported. However, body condition did not differ among sites (F_2 9=1 .80)(Berger *eta!.*, 1994). Furthermore, Lindeque and Erb's (1995) table incorrectly lists the site of the subadult mortality as SR. It was the DC region, correctly stated by Lindeque and Erb (1995) in the text. Two adults died during 1992-1993 north of SR, our site with horned rhinos. Similarly, an adult male and calf died in the DC region in 1990. None of the deaths were included in Lindeque and Erb's (1995) table. Except for the calf mortality which involved poaching, the other three were apparently natural as horns were recovered at the site and there were no signs of bullets. Thus, mortalities were not confined to the SR site as implied by Lindeque and Erb (1995) but occurred in all study regions.

Lindeque and Erb (1995) rely on the data of Loutit to estimate calf births and deaths. However, Loutit's reports are contradictory, sometimes claiming one calf death or two (Loutit & Montgomery, 1994a,b). Furthermore, although Loutit and Montgomery claim that their records are continually updated, there was a three year period after the 1989 dehorning operation in which half of the remaining eight dehorned rhinos were identified incorrectly (Berger et al., 1994). Thus, reliance on the unpublished records of Save the Rhino Trust (SRT) or those supplied by SRT to the Ministry appears imprudent if the goal is to understand local population structure and distribution.

Had Lindeque and Erb been aware of results of surveys carried out by their own Ministry biologists (DuPreez, unpublished), they would have confirmed our evidence of two births in the SR. Our subsequent report of two missing neonates stemmed from observations of mothers without young calves (Berger & Cunningham, 1994b). The third missing calf was surmised from further observations of a cow with an enlarged udder. In mammals as varied as cheetahs and caribou, the presence of swollen udders and absence of young has been used to gauge mortality (Laurenson, 1994; Cameron & Ver Hoef, 1994). We see no reason why rhinos should be different.

In support of this idea, we point out that the calfless female observed with a swollen udder in early 1993 gave birth in mid-1994 (Lindeque & Erb, 1995). Given a 16-month gestation period of a rhino and our observation of her, approximately 17 months before the estimated 1994 birth date, it seems likely that just after the calf was lost the mother recycled, was impregnated, and gave birth in mid-1994.

Number of dehorned rhinos

We believe Lindeque and Erb (1995) are mistaken about the number of dehorned rhinos. In 1989 there were 12, eight more in 1991, for a total of 20, not 28 as reported in their table.

Horn size, missing and maimed calves, and evolution

Lindeque and Erb (1995) argue that "horn dimensions per se are not that important for the protection of calves... (because)... these parameters would have evolved toward an optimal shape and length rather than varying to the degree seen in all populations" and suggest rhino horns show "extreme" variation under natural conditions. We have presented data elsewhere from four populations in which Lindeque was a co-author (Berger et al., 1993) showing that coefficients of variation in horn size range from 31 to 62%. However, since horn length is significantly related to age in both sexes (Berger & Cunningham, 1995), it makes little sense to argue about the functional significance and optimal design of horns without controlling for age. It is incorrect to imply that just because a trait is variable the possibility of selection is relaxed (Barnard, 1991). With respect to the size of anterior horns of mothers, the fact remains that in areas with spotted hyaenas, mothers with surviving calves had anterior horns that were significantly longer (X=40cm, N=4) than mothers with regrowing horns whose calves disappeared (X=23cm; N=3)(Wilcoxon Test; W = 22; p<0.029).

It is also important to ask what, if any, evidence from other sites may suggest that horns are associated with calf protection. Lindeque (1990) made such an attempt and suggested a null hypothesis, that negative biological effects are not expected from dehorning, a decision "taken in the absence of strong evidence of likely detrimental effects" (Lindeque, 1990). Is the a *priori* assumption that predation may not affect horned rhinos or their calves reasonable? We believe a more thorough search of the literature and discussion with other researchers would have raised the alternative possibility - that predation affects calves to a higher level of scrutiny.

The maiming of calves, defined here as ear or tail loss, was apparently not considered, nor was the possibility that calves that have died might not be detected. In support of dehorning, Lindeque (1990) claimed an association between calf recruitment and spotted hyaena density in Etosha, the implication (we presume) being that hyaenas do not affect calf survival. However, there are problems with this assertion. First, the rhino mothers are horned. If horns are a deterrent to potential predators, then one might not expect heightened calf mortality. Second, data are not offered on either hyaena densities or calf survival. If the alleged association exists, little may be concluded since calf mortality rates are unknown as is potential prey biomass. Hyaenas may simply be feeding on more abundant and less formidable prey.

Nevertheless, maimed calves are known from the Aberdares (Kenya), Umfolozi (South Africa) and Etosha and the Kaokoveld (Namibia) (Berger & Cunningham, 1994c). At Namibia's Waterberg Plateau Park, where spotted hyaenas do not occur, maimed calves were not reported as of late 1993 (Erb, pers. comm.). It is now clear that spotted hyaenas have the potential to maim calves: a regression analysis of the association between the proportion of maimed calves to spotted hyaena density explains 92% of the maiming variance (p<0.002; Berger & Cunningham, 1994c). While cause and effect cannot be distinguished, such relationships should lead to the supposition that hyaenas may affect calves when mothers are horned and therefore, that when mothers are dehorned, predation-related effects may result. However, it is still not known what proportion of calves are lost to predators. In Etosha for example, over the three-year period during which our study was conducted, one of 10 newborn calves died before reaching six months of age. These data, while not suitable as a control for our horned desert population, offer a glimpse of the natural mortality in a horned population with potential predators.

EVALUATION OF CONFOUNDING VARIABLES

Lindeque and Erb (1995) raise issues ranging from statistics and data interpretation to ecology and researcher disturbance. After addressing each point, we summarise our findings with respect to dehorning in the Namib Desert.

Ecological differences among areas

Lindeque and Erb (1995) argue that our study regions, namely DC (hyaena-free), SR (dehorned mothers with spotted hyaenas), and north of the veterinary fence (NVF; spotted hyaenas and occasional lions with horned mothers), differ, and therefore our contrasts are ill-conceived. However, if the areas differ strongly, then estimates of herbivore biomass also should differ. We evaluated ecological variation among study areas by contrasts of large herbivore biomass, data gathered during 126 driving transects that varied in mean length from 15.1 to 67.4km and covered a total of 5,106km (Table 1). Crude (as opposed to ecological) density (Eisenberg & Seidensticker, 1976) was the number seen per km² with sightings recorded to within one kilometre on each side of a vehicle. Because data were not normally distributed (means and variance were correlated), data were log transformed with Y=log(x+1) to avoid the problem of having zeros in which the log is negative infinity (Zar, 1984).

Using the biomass data presented in Table 1, neither study region nor year produced significant influences $(F_272=0.09; F_2, 7_2=1.40);$ only season did $(F_172=9.74)$ p<0.01) These data suggest similarities among areas, not the striking differences alleged by Lindeque and Erb (1995). Furthermore, in an attempt to show that the SR was overgrazed, Lindeque and Erb reported "some 500 small stock (goats and sheep) and cattle were moved into the SR rhino concentration area". They cited Loutit and Montgomery (1994b) who had misinterpreted Morkel's (1992) report of a rhino mortality in the DC region when 408 head of cattle and 85 goats had been counted. Thus, the site where a young rhino apparently starved to death was not the actual site that Lindeque and Erb (1995) claimed to be the one where domestic stock had overgrazed the area.

In sum, our measures of rhino body condition and changes in patterns of herbivore biomass across three contiguously distributed study areas lead us to believe that the regions were ecologically similar. Lindeque and Erb (1995) should demonstrate that the geographic variation they purport is responsible for differences in rhino performances.

Prudence and statistics in conservation biology

Lindeque and Erb (1995) point out that Martin (in press) used the same statistical procedures as we, but reached a different conclusion. Unable to address this issue without seeing the Martin paper (which had no record of being accepted for publication in *Conservation Biology* [E. Main, managing editor, pers. comm.]), it is worthwhile examining why we reported differences in calf survivorship among our three study regions.

We previously used the Fisher's Exact Test (FET) which, in analyses of these sorts, has been criticised because it requires that both marginal totals be fixed (Berger & Kock, 1989). However, the number of possible calf deaths is not fixed. A more appropriate analytical technique is the conditional binomial exact test (CBET; Rice, 1988), more powerful and appropriate for small samples (Jenkins, 1995). Although our prior analyses using the FET revealed

statistical differences (p<0.05), with the CRET differences are even more substantive (DC vs SR, p=0.01 17; DC vs NVF, p=0.0062; both one-tailed). Thus, given the existing data, we must initially reject the hypothesis that dehorning does not decrease calf survival.

Additional data must, of course, be gathered to address the issue more fully and, as we have pointed out elsewhere (Berger & Cunningham, 1994a,b), the results were collected under a specified set of conditions in the Namib Desert. Calf mortalities could have been exacerbated by the migration of herbivores promoted by low rainfall. Rhinos did not migrate and predator-prey ratios changed (Cunningham & Berger, in press). Where spotted hyaenas utilise both migratory and sedentary herbivores, predation is more intense on local prey during the dry season (Cooper, 1990). There is no reason to expect that hyaenas were incapable of killing the calves of mothers who had been dehorned, particularly because prey switching in carnivores is common (Hamlin et al., 1984; Karanth & Sunquist, 1995).

Despite our finding of differences in calf survival among sites, there is a broader issue. Had the differences not been significant at the p<0.05 level, should we have been complacent to accept the null hypothesis (Toft & Shea, 1983), in this case that dehorning does not decrease calf survival? The risk of wrongly accepting the null hypothesis (a Type II error) appears much greater than that of accepting the alternative - that dehorning affects calf survival. If we are wrong and dehorning does not affect calf survival, calves will still be recruited into populations. Given that sample sizes are small and, therefore, the power to detect differences low, we believe that any acceptance of the null is imprudent. Erring on the side of conservative strategies would seem to be in the better interest of rhinos, at least until greater statistical power can be gained.

Data interpretation and experimental design

While Lindeque and Erb (1995) have taken issue with our comparative analyses, they did not report calf survival of known females pre-and post horn removal. Prior to dehorning, at least two and more likely three SR cows gave birth to calves that survived until at least one year of age. After dehorning none survived (Berger & Cunningham, 1994b). Using the CBET, the differences are significant, even with the more conservative sample of only two births (p=0.026). Thus, irrespective of whether we either contrast areas or use pre- vs post-dehorning comparisons, the evidence supports our contention that calf survival of dehorned mothers was lower in areas with spotted hyaenas.

Researcher disturbance and hidden calves

Lindeque and Erb (1995) questioned whether our presence affected the period of separation between mothers and young. Because young calves often do not accompany their mothers to water, they may be preyed upon during their mother's absence. Is it possible that our presence caused calf abandonment? Yes, but we think not and offer three arguments why. First, after spending two weeks with a Ministry and SRT dehorning team in 1991 that made use of six to 15 trackers, four to eight vehicles, and a helicopter, there was massive disturbance to rhinos in the DC area. Calf abandonment did not occur but calves were more than six months of age.

Second, we adopted methods used by both Ministry biologists and SRT trackers for finding and photographing rhinos. These included following tracks, moving to within 70m of animals to photograph horns so that size could later be estimated (Berger et al., 1993), and more distant observations with spotting scopes. In five cases, we discovered mothers had been separated from young calves by finding spoor near water and following it back to sites where the two animals re-united. To our knowledge, calf abandonment has not occurred although the relationship between humans and mother-young periods of separation has not been studied systematically. Third, in no case where animals fled from us did we discover that mothers and calves separated. Thus, the only study region from which calves disappeared was that where dehorned mothers were sympatric with spotted hyaenas.

THE PUBLIC INTEREST

While the public, NGOs and many governments remain committed to the protection of rhinos, viewpoints differ with respect to the most appropriate methods. Clearly, rhinos will not survive *in situ* without substantial funding (Leader-Williams, 1990). Whether dehorning can be used effectively remains an open question and our results from the Namib Desert have been used and debated from different perspectives. Table 2 summarises our major hypotheses and possible effects of different variables on calf survival. Do our data prove that the missing calves were killed by spotted hyaenas? No, but they suggest that other factors are less likely to have played the prominent roles claimed by Lindeque and Erb (1995).

It is important to explain our decision to publish our findings despite the small sample. First, numerous claims have been made in host countries about the wisdom of dehorning. Second, despite claims of effective monitoring programmes, the fact is that calves were missing. Third, we felt that the scientific and conservation communities as well as the public had a right to know. Because inter-birth intervals of desert rhinos may average three years or longer, the time required to bolster our sample would have been several more years. We attempted to circumvent this problem by continuing to monitor and evaluate pregnancies. Meanwhile, we filed reports with the Namibian

Table 2. Summary of major hypotheses, tests and potentially confounding variables concerning calf recruitment in dehomed rhinos in the Namib Desert.

Construct	Tests and Evidence	Comment	Source	
dehorning does not affect calf survival	 between-site contrasts of horned and dehorned mothers (p<0.006) individual contrasts, pre-and post-dehorning (p<0.012) 	three sites only	1,2	
sample size	subdivided among three sites	10 calves	2	
hyaenas evenly distributed	between-site contrasts of spoor, calls, and observations	detected at two sites only	1	
areas differ ecologically	 sites contiguously distributed)contrast rhino body condition contrast herbivore biomass 	-differences not detected -differences not detected	2,3	
maternal age	age estimation by horns	primiparity unlikely	2,4	
drought	1) compare 1992-1993 with prior years 2)compare 1991 -1 992 and 1992-1993 combined with prior years	not the "worst drought in human memory in Namibia"	1	
overlap of maternal horn sizes	contrast mothers with surviving and non-surviving calves in areas with and without hyaenas	p<0.029(N=7)	1	
calf presence	small tracks of female lactating	97% accuracy	2	
human disturbance	same methods used at all sites	calf separation has not occurred	1.	

Sources: 1- this paper, 2-Berger & Cunningham (1994b), 3-Bergeret al. (1994), 4-Berger(1994).

government and met with top ranking officials over the issue of missing calves and poor records.

Our study to evaluate biological consequences of horn removal had received official approval by the Namibian government. Despite a research programme that included more than 100 individually-known rhinos, horn size data on more than 95% of these, and more than 1,030 hours of observation during 197 night watches, because of our results our research permits were not renewed.

Still, the real issue is not whether our study should have been continued but what is in the best interests of rhinos (Cunningham & Berger, in press). In the long term, the Namibian government will have to decide whether it is better to operate in a data-less vacuum than to sanction research when it is unclear whether the a *priori* outcome will support policy. This is precisely why conflicts of interest must be avoided, so that scientifically-based research is truly independent.

ACKNOWLEDGEMENTS

For providing access to unpublished data and weather records we thank numerous co-operators: Pierre Du Preez, Peter Erb, Bill Gasaway, Duncan Gilchrist, Eugene Joubert, Pauline Lindeque, Rupert Lofte, Garth Owen-Smith, SRT, and the Namibian Ministry of Environment and Tourism. We greatly appreciate the thoughts, comments, and criticisms of Phoebe Barnard, Janet Rachlow, Peter Stacey, Rob Simmons, an anonymous reviewer and Ruth Chunge. We did not always follow their suggestions and they do not necessarily endorse our views.

REFERENCES

Bamard, P. (1991) Ornament and body size variation and their measurement in natural populations. *Biol. J. Linn. Soc.* 42,379-388.

Berger, J. & Kock, M. (1989) Type I and Type II errors in the real world. *J. Wild!*. *Dis.* 25,451-454.

Berger, J., Cunningham, C. & Gawuseb, A.A. (1994) The uncertainty of data and dehorning black rhinos. *Cons. Biol.* 8,1149-1152.

Berger, J. (1994) Science, conservation, and black rhinos. *J. Mamm.* 75,298-308.

Berger, J., Cunningham, C., Gawuseb, A. & Lindeque, M. (1993) Costs and short-term survivorship of hornless black rhinos. *Cons. Biol.* 7,920-924.

Berger, J. & Cunningham, C. (1994a) Active intervention and conservation. *Science* 263,1241-1242.

Berger, J. & Cunningham, C. (1994b) Phenotypic alterations, evolutionary significant structures, and rhino conservation. *Cons. Biol.* 8,833-840.

Berger, J. & Cunningham, C. (1994c) Horns, hyaenas, and rhinos. *Research and Exploration* 10,241-244.

Berger, J. & Cunningham, C. (1995) Predation, sensitivity, and sex: why female black rhinoceroses outlive males. *Beh. Ecol.* 6,57-64.

Cameron, R.D. & Ver Hoef, J.F. (1994) Predicting parturition rate of caribou from autumn body mass. *J. Wild!. Manage.* 58,674-679.

Cooper, S.M. (1990) The hunting behaviour of spotted hyaenas (*Crocuta crocuta*) in a region containing both sedentary and migratory populations of herbivores. *Afr. J. Ecol.* 28,131-141.

Cunningham, C. & Berger, J. (In press) *Horn of* Darkness: Rhinos and Conservation Chimeras in *Africa*. Oxford University Press.

Eisenberg, J.F. & Seidensticker, J. (1976) Ungulates in southern Asia; a consideration of biomass estimates for selected habitats. *Biol. Cons.* 10,293-308.

Hamlin, K.L., Riley, S.J., Pyrah, D., Dodd, A.R., & Mackie, R.J. (1984) Relationships among mule deer fawn mortality, coyotes, and alternate prey species during summer. *J. Wild!. Manage*. 48,489-499.

Jenkins, S.H. (1995) Carfentanil, bison, and statistics: the last word? *J. Wild!. Dis.* 31,104-105.

Joubert, E. & Eloff, F.C. (1971) Notes on the ecology and behaviour of the black rhinoceros *Diceros bicornis* Linn 1758 in South West Africa. *Mado qua*, 1,5-53.

Karanth, R.U. & Sunquist, M.E. (1995) Prey selection by tiger, leopard, and dhole in tropical forests. *J. Anim. Ecol.* 64,439-450.

Keep, M.E. (1971) Observable criteria for assessing the physical condition of the white rhinoceros *Ceratotherium simum simum. Lammergeyer* 13,25-28.

Laurenson, M.K. (1994) High juvenile mortality in cheetahs (*Acinonyx jubatus*) and its consequences for maternal care. J. Zoo!. Land. 234,387-408.

Leader-Williams, N. (1990) Black rhinos and African elephants: lessons for conservation funding. *Oryx* 24,23-29.

Leader-Williams, N. (1993) Theory and pragmaticism in the conservation of rhinos. In: *Rhinoceros Biology and Conservation* (ed. 0. A. Ryder). San Diego Zoological Society, San Diego, Ca.

Liebenberg, L. (1990) A Field Guide to Animal Tracks of Southern Africa. David Phillip Publishers, Cape Town.

Lindeque, M. (1990) The case for dehorning the black rhinoceros in Namibia. S. Afr. J. Sci. 86,226-227.

Lindeque, M. & Erb, P. (1995) Research on the effects of temporary horn removal on black rhinos in Namibia. *Pachyderm* 20,27-30.

Loutit, B.L. & Montgomery, S. (1994a) Rhino conservation. *Science* 265, 1157-1158.

Loutit, B.L. & Montgomery, S. (1994b) The efficacy of rhino dehorning: too early to tell! *Cons. Biol.* 8,923-924.

Mills, M.G.L., Nel, J.A.J. & Bothma, J. Du P. (1984) Notes on some smaller carnivores from the Kalahari Gemsbok National Park. Supplement to *Koedoe* (1984), 221-227. Morkel, P.V. (1992) Report on the death of a black rhino (*Diceros bicornis bicornis*) in the Ugab River. Save the Rhino Trust, Windhoek, Namibia. Unpublished report.

Rice, W.R. (1988) A new probability model for determining exact P - values for 2 x 2 contingency tables when comparing binomial proportions. *Biometrics* 44,1-22.

Skinner, J.D. & Van Aarde, R.J. (1981) The distribution and ecology of the brown hyaena *Hyaena brunnea* and spotted hyaena *Crocuta crocuta* in the central Namib Desert. *Mado qua* 12,231-239.

Skinner, J.D. & Smithers, R.H.N. (1990) *The Mammals of the Southern African Subregion*. University of Pretoria, South Africa.

Toft, C.A. & Shea, P.J. (1983) Detecting communitywide patterns: estimating power strengthens statistical inference. *Am. Nat.* 122,618-625.

Western, D. (1982) To dehorn or not to dehorn. *Swara* 5,22-23.

Western, D. (1987) Africa's elephants and rhinos: flagships in crisis. *Tree* 2,343-346.

Zar, J.H. (1984) *Biostatistical Analyses*. Prentice Hall, Engelwood Cliffs, New Jersey.