Population Constraints Associated with the Use of Black Rhinos as an Umbrella Species for Desert Herbivores

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Abstract: *The numerous tactics used to conserve biodiversity include the designation of protected areas, political change, and research and education, the latter involving paradigms such as insular biogeography and the "umbrella species concept." In Namibia lands removed from national park status in 1970 and currently under the jurisdiction of indigenous people now contain one of the few unfenced populations of black rhinos (*Diceros bicornis*) remaining in Africa. Theory predicts that the protection of umbrella species will ensure the survival of other biota that require(s) less space. To gauge how well biodiversity might be retained by examining the spatial needs of a small population of black rhinos, I used data gathered under various ecological conditions to estimate mean and minimum population sizes of six large herbivores of the Namib Desert ranging in size from giraffe (*Giraffa camelopardalis*) to springbok (*Antidorcas marsupialis*) and ostrich (*Struthio camelus*). My results indicate that annual differences in rainfall, both within and between seasons, resulted in wide fluctuations in herbivore population sizes for all species except rhino. Although other herbivores switched to areas of higher rainfall, rhinos did not. The data suggest that under conditions of extreme environmental variance the space used by rhinos alone was unlikely to assure the existence of populations of other species in excess of 250 individuals. Fifty percent of the species failed to exceed 150 individuals 50% of the time and one third of the species never attained populations in excess of 50 individuals. However, by employing assumptions about the spatial needs of rhino populations numbering up to 100 individuals, the mean minimum population sizes attained by any of four desert herbivores is 535. A future challenge in using rhinos and other large-bodied species as umbrellas for organisms of either similar or dissimilar trophic levels will be the refinement of estimates of population viability.*

Restricción de Poblaciones Asociadas con el Uso de Rinocerontes Negros como "Sombrilla de Especies" para Herbivoros del Desierto

Resumen: *Las diversas tácticas utilizadas para la conservación de la biodiversidad incluyen la designación de áreas protegidas, cámbios politicos, y investigación y educación. Esta última incluye paradigmas como la biogeografia insular y el concepto de "sombrilla de especies." En 1970 los parques nacionales en Namibia fueron donados a poblaciones indigenas. Actualmente, estas areas contienen una de las pocas poblaciones de rinocerontes negros (*Diceros bicornis*) salvajes existentes en África. Teoricamente se predice que la protección de especies asegurará la supervivencia de otras biotas que requieran menor espacio. Para determinar que tan bien la biodiversidad podria ser restinizada por medio del estudio de los espacios necesarios para pequeños poblaciones de rinocerontes negros, datos obtenidos bajo diferentes condiciones ecológicos fueron utilizados para estimar la media y los tamaños mínimos de población de seis tipos de herbivoros grandes del Desierto de Namib. Estas especies varian en tamaño desde jirafas (*Giraffa camelopardalis*) a springbok (*Antidorcas marsupialis*) y avestuces (*Struthio camelus*). Los resultados indican que las diferencias anuales en pre-*

*cipitación durante y entre temperados, han resultado en una fluctuación ámplia en el tamaño de pobla-
ciones de herbívoros de todas las especies con excepción de los rinocerontes. Aún cuando otros herbivoros
migraron hacia áreas de mayor precipitación, los rinocerontes no lo hicieron. Los datos sugieren que en
condiciones de extrema variación ambiental, el espacio utilizados solamente por los rinocerontes no aseg-
uraba la existencia de otras poblaciones que excediaran 250 individuales. Cincuenta porciento de especies
no alcanzaron los 150 individuos 50% de los veces y un tercio de los especies munca logró exceder pobla-
ciones de 50 individuos. Sin embargo empleando suposiciones sobre los espacios necesarios de las pobla-
ciones de rinocerontes enumerándolas hasta de 100 individuos, la media en los tamaños de población min-
ima que alcanzaron las cuatro especies de herbívoros del desierto fue de 535. Un futuro desafio utilizando
rinocernotes y otros especies de grandes proporaciones como sombrilla para organismos tanto de niveles tró-
ficos similares o diferentes, seria el refinamiento en los cálculos de viabilidad de la población.*

Introduction

For regions where detailed data are lacking, an increasingly popular idea about how to best conserve biodiversity is the concept of "umbrella species." The rationale is simple: by protecting the minimum areas needed for a viable population of a single, large-bodied species, sufficient space should also be maintained for the viability of smaller and more numerically abundant species in that area (Wilcox 1984). The idea is a logical outcome of life-history analyses in which relationships among body size, density, and population size have empirical bases (Robinson & Redford 1986; Belovsky 1987; Kinnaird & Eisenberg 1989). Among the more recognized, yet untested, examples of the umbrella species concept is that involving grizzly bears (*Ursus arctos*) in the Greater Yellowstone Ecosystem (Glick et al. 1991). Other umbrella species that might be useful in protecting biodiversity include tigers (*Panthera tigris*; Tilson & Seal 1987), cougars (*Felis concolor*; Beier 1993), and wildebeest (*Connochaetes* sp.; McNaughton & Banyikwa 1995), species that vary both in body size and local population abundance. In addition to large-bodied candidates, specialized species such as Red-Cockaded Woodpeckers (*Picoides borealis*) (Walters 1991) and Bay checkerspot butterflies (*Euphydryas editha bayensis*; Launer & Murphy 1995) have also been suggested. The above possibilities are mainly from developed countries with well-protected reserves and detailed inventories (Newmark 1987, 1995).

Without the well-funded institutions of temperate North America and Europe, the situation differs in many developing countries. Sub-Saharan Africa, for example, contains 29 of the world's 36 poorest countries (Bonner 1992), biological knowledge is poor, and access to both money and technology for conservation planning is extremely limited (Barnard 1995). Although large tracts of land are either available or have already been set aside for conservation (Adams & McShane 1992), it is there that land reform and redistribution have the potential for broad ecosystem alterations. In the absence of detailed inventories, the umbrella species concept might be useful in determining whether such lands are adequate to maintain current levels of biodiversity.

Among the largest species receiving explicit mention as umbrellas are rhinos, "because the habitat required to sustain their viable populations is sufficiently large to encompass appreciable parts of natural ecosystems" (Foose 1993:39). Rhinos also possess traits typically associated with the umbrella species concept—large size, low reproductive rates, and big home ranges (Wilcox 1984; Landres et al. 1988; Mills et al. 1993).

Here, I ask whether black rhinos (*Diceros bicornis*) are useful as an umbrella species. "Useful" in this context means that areas used by rhinos are sufficiently large to maintain populations of other species. Specifically, I examine the concept empirically by using rhinos and six other large herbivores in the Namib Desert, and I determine the probability that each attains a designated population size. Ideally, the umbrella species concept should apply to guilds at multiple trophic levels, but in this case the only available data are for ungulates and ostrich (*Struthio camelus*).

As a construct in conservation planning the umbrella species concept may be important where human power, funding, or expertise are limited. If, for instance, rhinos or other species prove to be good umbrellas, then it may be possible not only to garner support for biodiversity issues from a largely sympathetic lay public, but ecosystem managers might more effectively protect viable populations of other species simply by concentrating on those with large spatial requirements. Thus, some sort of empirical test seems worthwhile. Another reason for learning how broadly the concept may be applied is that areas within the Namib Desert have been proposed as possible reserves and deproclaimed from national park status; therefore, an assessment of what might actually be conserved by protecting areas used by rhinos is more than an academic venture. If the concept loses validity because exceptions are frequent or assumptions unrealistic, then it seems prudent to know where shortcomings occur and under what, if any, conditions the concept may be useful.

Background and Methods

Rhinos and Land Reform in the Namib Desert

Black rhino populations throughout Africa have been reduced by more than 97% since the 1960s (Western 1987; Leader-Williams 1993). Presently, the continent's only unfenced population with more than 100 animals is in the Namib Desert (Berger et al. 1993). A portion of this area was once included in Etosha National Park, whose area in 1907 when under German colonial rule was 99,000 km^2 (Owen-Smith 1986). Due to the lack of surface water and remoteness, much of the area remains largely unpopulated by humans, but the park's size was progressively reduced until about 1970, when a redistribution plan was adopted by the (then) managing authority, the Republic of South Africa. Under this plan desert areas of the park were deproclaimed, although under Namibian rule these nonpark areas are now managed jointly by Namibia's Ministry of Environment and Tourism and by a council of the indigenous people, Damaras and Hereros. Etosha's present size is about 22,700 km^2, and the park is entirely fenced. Its rhinos are disjunct from the free-ranging desert population to the west.

Although none of the deproclaimed desert areas is fully protected as a formal reserve, they maintain high herbivore diversity (Holmes 1992); beginning in late 1993, local harvest of large mammals (but not rhinos) has been permitted. During the last 25 years proposals have surfaced at least three times suggesting that portions of the northern or central Namib Desert should be set aside as reserves that include local people (Owen-Smith 1972; Carter 1989; Damaraland Kings Council 1992).

Study Areas and Home Range Size

My 7000-km^2 study area includes a portion of the Kaokoveld (19°70′–20°80′ S, 13°80′–14°20′ E), an area of the Namib Desert contained within the Kunene Province of Namibia. The region is rugged and mountainous, with open gravel plains bisected by dry riverbeds (Joubert & Eloff 1971; Simmons et al. 1991). It contains both rhinos and elephants (*Loxodonta africana*) at the edge of their natural range (Viljoen 1989), where the latter have the largest home ranges recorded anywhere in Africa (5800–8700 km^2; Lindeque & Lindeque 1991). The study region is the same as that used to examine the responses of desert rhinos to possible predation (Cunningham & Berger 1997).

Annual precipitation averages 75 mm (the mean of 30 years' data from Sesfontein to the north and 9 years' data from Wereldsend in the study area). Rainfall increases along a west-east gradient. It is as low as 19 mm/year along the Skeleton Coast, increasing to 200 mm along escarpments 50–70 km inland (Viljoen & Bothma 1990).

To calculate the home range size of individual rhinos, I relied on software used in the analysis of animal location data (Kenward 1990). Briefly, templates were constructed to match the scales of maps upon which spot locations of known animals were recorded. Locations were estimated to within the nearest 500 m. The sizes of home ranges represent minimum convex polygons with harmonic means (Kenward 1990) and are based on 276 data points for 22 rhinos (males: $\overline{X} = 12.0 + 1.87$ [SE] locations per individual; females: $12.9 + 1.71$). Six additional animals were excluded because none had more than five reliable resightings. Although problems of independence and autocorrelation exist in analyses such as these (White & Garrott 1990), telemetry-acquired data for rhinos in desert areas, where home ranges may exceed 2000 km^2, were not feasible because (1) the detection of rhinos from the ground is generally less than 3 km and (2) aerial tracking was too costly. Nevertheless, the small number of repeat sightings per individual up to a 10-year time span (1984–1993, unpublished data) should underestimate home-range size among Namib Desert rhinos and result in a conservative estimate relative to that reported for black rhinos elsewhere (Fig. 1).

Herbivore Numbers and Biomass

I divided the study area into three subsections prior to estimating the density of large herbivores, each a geo-
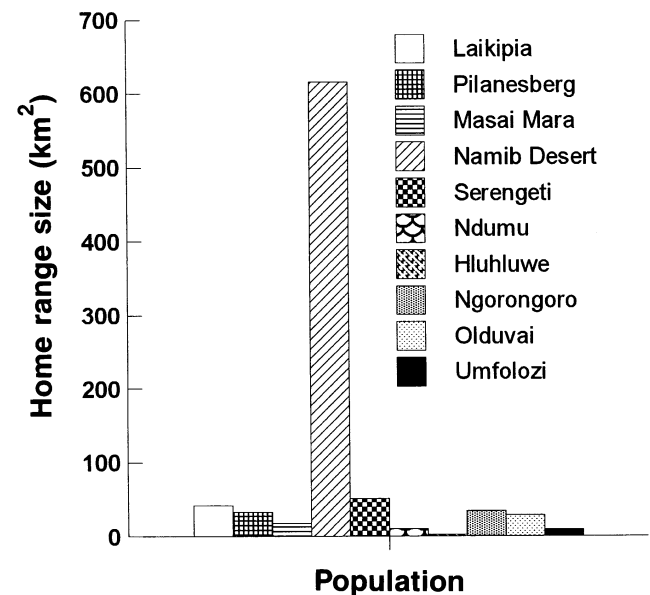

Figure 1. Mean home range size of black rhinos (sexes combined) from 10 African populations: Umfolozi (Owen-Smith 1988); Olduvai (Goddard 1967); Ngorongoro (Kiwia 1989); Hluhluwe (Hitchins 1969); Ndumu (Conway & Goodman 1989); Serengeti (Frame 1980); Namib Desert (this study); Masai Mara (Mukinya 1973); Pilanesberg (averaged from high and low estimates in Adcock 1994); Laikipia (averaged from high and low estimates of males only from Brett, in Adcock 1994).

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

Season	Uniab		Ugab		Springbok	
	Transect length	Biomass	Transect length	Biomass	Transect length	Biomass
1991						
Wet	20.3 ± 3.2 (10)	65 ± 20.1	43.7 ± 5.2 (5)	44 ± 7.9	36.2 ± 9.6 (4)	29 ± 11.8
Dry	50.7 ± 6.9 (5)	5 ± 2.7	55.3 ± 5.0 (15)	35 ± 8.2	30.3 ± 3.3 (5)	20 ± 12.0
1992						
Wet	15.1 ± 2.15 (4)	64 ± 30.3	48.4 ± 3.6 (3)	56 ± 5.7	45.1 ± 10.3 (9)	57 ± 40.5
Dry	57.4 ± 15.0 (5)	46 ± 25.2	48.7 ± 11.3 (4)	30 ± 15.8	35.2 ± 4.4 (4)	15 ± 8.2
1993						
Wet	67.4 ± 16.8 (5)	106 ± 78.0	34.5 ± 5.2 (3)	114 ± 80.4	39.0 ± 12.9 (13)	62 ± 23.4
Dry	55.4 ± 7.5 (14)	25 ± 9.2	16.3 ± 1.5 (12)	16 ± 9.8	25.5 ± 4.3 (6)	12 ± 4.0

Sample size in parentheses; areas (km^2) are Uniab, 1858; Ugab, 3418; and Springbok, 1710.

graphical unit in which rhino subpopulations occurred (Berger et al. 1994). I drove 5106 km in these areas during 126 transects that varied in mean length from 15.1 to 67.4 km (Table 1). Transects followed both river courses and bisected them. A professional tracker (A. Gawuseb) sat on top of our vehicle; he, C. Cunningham, and I recorded the number of animals of each species seen within 1 km on both sides of the vehicle. Crude (as opposed to ecological) density (Eisenberg & Seidensticker 1976) was the number of animals seen per square kilometer driven. To minimize the effects of samples of less than 30, adjusted coefficients of variations were calculated (Sokal & Rohlf 1995).

The species and their respective (female) biomass (kg) (Stuart & Stuart 1988; Skinner & Smithers 1990; Bertram 1992) were as follows: springbok (*Antidorcas marsupialis*), 37; ostrich, 111; kudu (*Tragelaphus strepsiceros*), 157; gemsbok (*Oryx gazella*), 210; mountain zebra (*Equus zebra*), 230; giraffe (*Giraffa camelopardalis*), 850; rhino, 1000. Seasons were categorized as wet or dry, the former when precipitation fell between December and March, except in 1993 when rain occurred primarily in February.

In estimating herbivore densities, which tend to be low in xeric environments (Coe et al. 1976), it is not surprising that a large number of transects produced no animals and resulted in data that were not normally distributed. Because the means and variance were correlated ($r = 0.88$, $p < 0.01$), data were log transformed with $Y = \log(x + 1)$, which avoids the problem of having zeros in which the log is negative infinity (Zar 1984). There was no relationship between transect length and number of animals for any species nor were sample size and variance in biomass correlated in either dry ($r = 0.02$) or wet ($r = 0.12$) seasons.

The method of census was not ideal. For instance, because distance estimates to the subjects were not recorded, it was impossible to derive a probability of sighting index as recommended by Caughley (1977). And because of the wide transects, it was sometimes uncer-

tain whether the animals encountered fell precisely within the 1-km limit. There are other sampling issues. First, because of the high variance inherent in many population estimates (Buckland et al. 1993), parametric standard deviations are unknown. It was not realistic to increase sample size in this case. Therefore, I calculated confidence limits using the t distribution, which is more sensitive to small sample sizes than the normal distribution (Sokal & Rohlf 1995). The lower 90% confidence limit was approximated by $t_{0.10(df)} = X - [(t) \text{var}/n]$. Second, my data matrix contained 126 cells (7 species [rhinos included], 2 seasons, 3 years, 3 study regions). Of these, 79% were filled because species were encountered. So, to enable density estimation for unfilled cells, I assumed that an animal would have been sighted during the next kilometer driven. This method results in a higher number of animals than would occur otherwise. For instance, if five 50-km^2 transects produced no gemsbok (density = 0.0 km^2), an adjusted estimate would be derived by adding a single animal to one of the transects, resulting in this case in a density of 0.004/ km^2. This procedure suffers from discounting the possibility of encountering large herds. And, as in any study of gregarious mammals, there are issues concerning statistical independence. The associations of individuals or groups may be influenced by the presence or absence of others, and the inevitable pooling of unidentified individuals sighted on different days increases the possibility that the same individuals may enter the data set more than once.

Fortunately, these problems may not be insurmountable. During xeric periods, whether in deserts or more mesic regions, group sizes tend to be lower (Berger 1988; Mills 1990; Bailey 1993), so it is realistic to assume that fewer individuals would be encountered. Also, as in other assessments of large-herbivore abundance (Scheel 1993), my study regions were censused similarly and any resulting errors are probably systematic among sites. Most important, it was possible to check on the validity of my Namib Desert herbivore estimates. I examined the extent to which my values fit the slopes of regressions of

Table 2. The amount of variation in log herbivore biomass explained by mean annual precipitation on arid African savannas when each of the designated locations is omitted from the overall data set.*

Location omitted	a	b ($\times 10^{-3}$)	r^2	t	p
Akagera	1.378	3.695	0.976	4.79	<0.001
Tsavo East	1.574	2.906	0.922	3.84	<0.002
Hwange	1.562	3.035	0.897	0.26	ns
Kruger	1.563	2.999	0.900	2.00	ns
Okavango	1.555	3.031	0.903	0.60	ns
Mkomazi	1.541	3.039	0.912	10.90	<0.001
Etosha	1.571	3.039	0.903	0.22	ns
Kalahari - Gemsbok	1.601	2.981	0.892	1.68	ns
Namib - Naukluft	1.602	2.968	0.870	0.94	ns
Namib - Kaokoveld	1.311	3.501	0.848	2.20	<0.05
With all sites included	1.561	3.044	0.902	—	—

*The t and p values are for comparisons of two slopes with the designated location included and omitted. (All data except Namib-Kaokoveld from East 1984.)

large herbivore biomass on mean annual precipitation using data from nine other African arid savannas (Table 2). This test is crucial. If my data do not fit expectations based on analyses from other arid savannas, the differences might arise because my sampling techniques were inadequate or for other reasons, perhaps because human influences (e.g., illegal wildlife utilization) skew population densities. If, on the other hand, my estimates of large herbivores of the Namib Desert are in accord with relationships reported from other arid environments, it should be possible to examine rhinos as umbrella species.

The Probability of Achieving Viable Populations

Although real data on the minimum population size necessary to resist extinction have typically proved elusive for most mammals, a generally acceptable level of risk has been that in which a population has a 99% probability of survival for 1000 years (Shaffer 1981). Given that 97% of Africa's black rhinos have been lost in the last three decades (Western 1987; Ryder 1993), black rhinos would clearly make for poor umbrella species. From a biodiversity viewpoint, however, it is useful to explore the spatial needs of rhinos in relation to the population sizes of other species. There are two issues, black rhino abundance and estimates of population size of the other herbivores at the Namib Desert study areas.

The 28 Kaokoveld rhinos that inhabited my study region from 1991 to 1993 were known individually but the population size was lower than it would have been had not 15 other rhinos been removed through poaching (Owen-Smith 1986) and relocation to other sites (Cunningham & Berger 1997). Although it is important to note the reduction in population size, the area I report as being used by rhinos may not have been appreciably larger because many of the 15 animals that were removed came from sites also used by the existing 28 individuals. Nevertheless, 43—or even more—rhinos is

unlikely to represent a viable population. To evaluate possible persistence of the other large herbivores within the study area, I address the question of the probability that each species maintains a specified population size. Because it is generally unclear what actually constitutes viable populations or how they vary among species, I used a range of designated population sizes (50, 100, to 250) and calculated the frequency with which mean population size for each species maintained the designated levels seasonally over 3 years. I also repeated the same procedure using the lower (90%) confidence limits. As a construct for biologists interested in population persistence, lower limits are more useful than upper ones because small populations are more susceptible to extinction than larger ones (Pimm et al. 1988; Berger 1990).

Results

Rhino Ranges and Herbivore Biomass

Mean home-range sizes did not differ between rhino males (730 ± 209 km^2 [SE]; $n = 9$; range 60–2185 km^2) and females (538 ± 161 km^2; $n = 13$; range 101–2067 km^2) (variances were equal: $F_{max} = 1.17$, NS; $t_{8,12} = 0.16$; NS). Although home range is often sensitive to the number of data points, in this case neither male nor female home ranges were correlated with the frequency of resightings (males, $r = -0.10$; females, $r = 0.38$). So, to compare how the area used by Namib Desert rhinos contrasts with that of black rhinos elsewhere in Africa, I combined the sexes (Fig. 1).

In arid regions animal biomass is reduced (Coe et al. 1976) and home ranges are generally larger than those in more mesic areas (Owen-Smith 1988; Caro 1994). Namib Desert rhinos fit the expected pattern, although mean home-range size at my study area exceeds that of Africa's other populations by tenfold or more (Fig. 1).
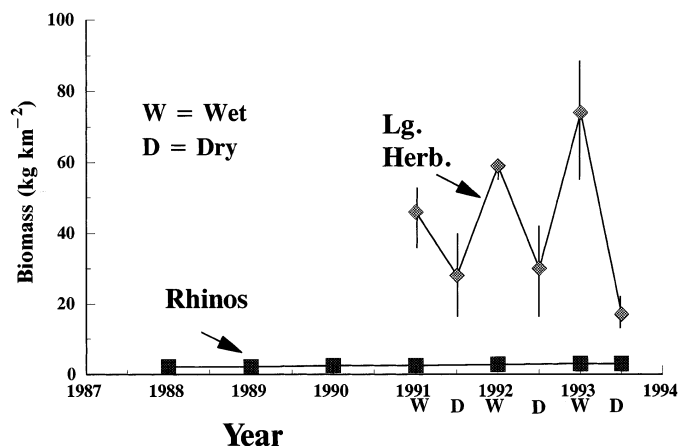
Figure 2. Mean biomass (± SE) for black rhinos and six other large herbivores. Sample sizes and other descriptive statistics are given in Table 1. Data from 1988–1990 unpublished files of Namibian Ministry of Tourism and Environment and G. Owen-Smith.

The wide disparity could arise because the Namib is much drier than other regions and because values from other areas were generally based on only 1 or 2 years of monitoring, or both.

For desert rhinos, fluctuations in biomass were trivial relative to those of other herbivores (Fig. 2). On a seasonal per-species basis, the adjusted coefficient of variation in biomass was lowest for rhinos (3.5%) and was exceeded by more than 30 times by that of ostrich (101.1%) and springbok (113.3%). For the other species, the adjusted coefficients of variation were as follows: zebra (55.2%), giraffe (64.3%), gemsbok (67.4%), and kudu (87.1%). Of factors that affected the biomass fluctuations among subregions (Table 1), only seasonal influences were detectable (ANOVA; $F_{2,72yr} = 0.086$, NS; $F_{site} = 1.399$, NS; $F_{season} = 9.742$; $p < 0.01$), a finding that reinforces the intuitive expectation that precipitation drives arid systems (Coe et al. 1976; Caughley 1987) and promotes large fluctuations in population sizes (Prins & Douglas-Hamilton 1990).

Probabilities of Population Persistence

To what extent do the six herbivores attain population sizes varying from 50 to 250? Differences are illustrated in Fig. 3. At one extreme were springbok whose population size always exceeded 250 individuals. At the other end were giraffes which—based on average values—achieved a target population of 50 only 33% of the time; with the lower 90% confidence limits, they never reached any of the five designated (50–250) population levels. No species other than springbok had a 100% probability of achieving population sizes of 250 or more (Fig. 3).

The probability of maintaining populations at designated population sizes is strikingly reduced when the lower (90%) confidence limits are used. Four species (mountain zebra, ostrich, kudu, and giraffe) never had a 100% probability of reaching even the smallest population size (50); only gemsbok and springbok did. With

the 90% lower confidence limits, the change in probability of having 250 individuals dropped: 70% for mountain zebra, 34% for gemsbok and ostrich, and 16% for kudu (Fig. 3). Whereas using data on the 90% confidence limits obviously represents a conservative attempt to minimize errors in deriving population estimates that produce low population sizes, even by using mean values, only springbok would be conserved at designated target levels if the areas used by rhinos were the only ones protected. In other words, the probability is high that size-
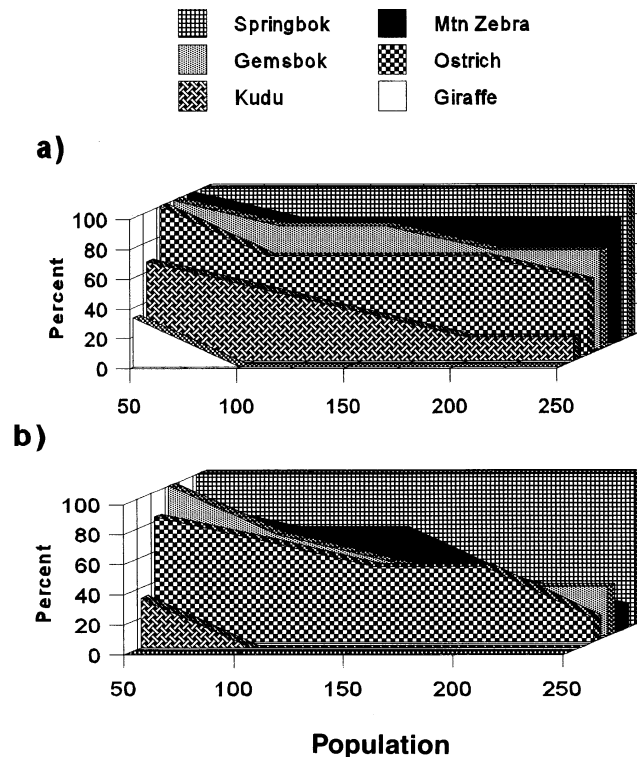

Figure 3. Probability of achieving designated population sizes with mean (a) and lower (90%) confidence limits (b) by six Namib Desert herbivores.

able populations of five of the six herbivores would be lost without a larger protected region.

Assessment of the Data

Although the above analyses are based on population sizes of the different species within the study area, my estimates of animal abundance may have been biased by census methodology. Prior information on the biomass of large African herbivores is available to enable a check of how well my estimates fit those from elsewhere in Africa (Fig. 4). Using data from areas of similar soil status (East 1984) with mean annual precipitation of less than 800 mm, I confirmed the predicted relationship between rainfall and herbivore biomass. Precipitation explained 85% of the variance (Table 2).

Then, I included my Namib (Kaokoveld) data on biomass (Fig. 4). Although the amount of variance in biomass explained improves to 90.2%, slopes with and without Namib-Kaokoveld data also change (Table 2). When my data are included there is no statistical change in the correlation itself ($z = 0.437$; $p = 0.66$). By excluding data on biomass from other locations one at a time, the variance in biomass accounted for by precipitation varies from 87% to 97.6% (Table 2). Exclusion of other data points (Akagera, Tsavo East, and Mkomazi) singly changes the slopes of the regression more than the Namib-Kaokoveld data did (Table 2). It appears that my census techniques were unlikely to produce estimates of biomass that deviated substantially more from a line of best fit than did those reported for a third of the locations in arid African savannas. These results suggest that it is reasonable to use Namib Desert (Kaokoveld) data to evaluate whether the area used by rhinos was likely to protect populations of other large herbivores.

Although my Namib data are in accordance with those expected for African savannas (Fig. 4), they differ in two important ways. First, an obvious nonmammal was included, the ostrich, whereas ostriches were excluded from prior assessments. The inclusion inflates my biomass esti-

mates relative to those of other studies. Second, my use of female body mass taken from the literature underestimates biomass because all species are sexually dimorphic, with males outweighing females. Males were present, but their sex ratios were unknown. The extent to which these over- and underestimates affect each other is unknown.

Discussion

During the past 30 years portions of the northern Namib Desert have been both deproclaimed from protected status and suggested as reserves (Owen-Smith 1972; Carter 1989; Damaraland Kings Council 1992). Although proposals regularly surface that emphasize the special status of rhinos, rarely has it been possible to derive empirical estimates of what else may be conserved by focusing on spatial areas used by rhinos. My analysis offers a first approximation by concentrating on a restricted subset of biodiversity—organisms of a similar trophic level. There are two general issues, what may be achieved under ideal conditions by reliance on the umbrella species concept and limitations imposed by real world situations.

Much use of the umbrella species concept has been geared toward gaining public support. For example, by protecting areas of well-known and charismatic species such as grizzly bears or maned wolves (*Chrysocyon brachyurus*), the Greater Yellowstone Ecosystem and South American grasslands, respectively, might be more able to maintain viable populations of other plants and animals (Glick et al. 1991; Hunter 1995). Biologically, however, concepts such as "umbrella," "indicator," and "keystone" species have been thorny because they have different meanings for different people (Landres et al. 1988; Mills et al. 1993; Estes & Duggin 1995). For the umbrella species concept to be useful, numerous assumptions are required. Most critically, the umbrella species must in itself have a high probability of persistence. Despite the use of spatially large areas by species such as rhinos, tigers, or grizzly bears, if the population has a low probability of avoiding local extinction, then
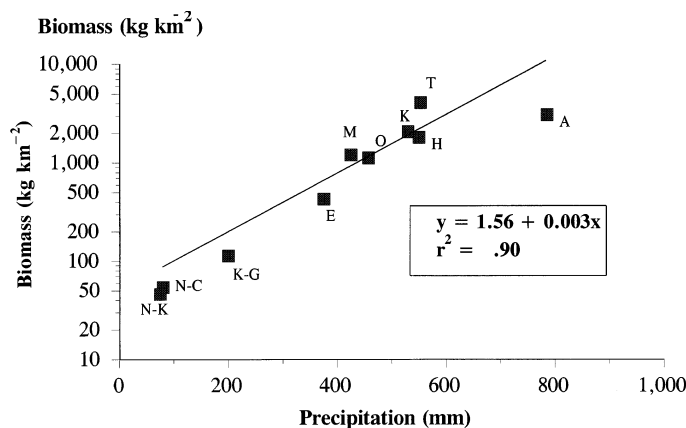

Figure 4. Relationship between mean annual precipitation and large mammal biomass from nine arid African savannas (East 1984). The Namib-Kaokoveld (N-K) point includes ostrich (this study). Locations as follows: A, Akagera; T, Tsavo-East; H, Hwange; K, Kruger; O, Okavango; M, Mkomazi; E, Etosha; K-G, Kalahari-Gemsbok; and N-C, Namib Central.

inevitably appropriate umbrellas will be more-common species simply because of their higher probability of long-term persistence.

Not only is an umbrella species' persistence important, but for the taxa falling below it so are concerns about the areas conserved and the status of adjacent lands. If immigration into the area is possible, then the probability of population persistence for all taxa should increase (Newmark 1987, 1995; Stacey & Taper 1992). But where lands outside protected areas are no longer suitable, migration by large herbivores can create insurmountable problems (Western 1989).

For practical purposes, there may be good reasons for using black rhinos to garner conservation support but, as an umbrella for biodiversity, these may be limited. About 75% of the world's populations already number less than 50 individuals (Ryder 1993). Africa's only unfenced population with more than 100 animals is in the Namib Desert. Thus, most black rhinos already exist on conservation lands; as an umbrella for taxa of a similar trophic level, black rhinos are mostly a fait accompli.

With respect to the Namib Desert, my data allow an assessment of the idea that umbrella species protect areas used by other species. Although black rhinos were unlikely to use sufficient space to assure that all herbivores except springbok regularly attained population sizes of 250 (Fig. 3), the results are based on 28 animals, not the 100 or more that occupy a much broader region of the Kaokoveld. Therefore, it seems appropriate to assess how the probability of achieving different designated population sizes for the other five herbivores might have changed if I had included a greater number of rhinos in the sample.

I first assume that the population estimates that I report can be expanded across broader and heterogeneous desert regions. The extent to which this is true is unknown. To be conservative—that is, to decrease the region of study—I also assume that the area contained the entire ranges of 15 additional animals—ones that were poached or removed for translocation. I then multiplied the size of that region by 1.16, the factor needed to achieve the area required for 50 rhinos (excluding calves). Data from the dry season when population sizes are lowest (Table 3), indicate that gemsbok, zebra, and ostrich all attain mean population sizes between 230–275. Only giraffe fail to achieve 50 animals. However, if

areas used by 100 rhinos were to be preserved, then the mean population sizes for the large herbivores (Table 3) should be multiplied 2.33; on average, therefore, for even the species with the fewest number of individuals (kudus and giraffes), populations would be at 189 and 98 respectively. Whether these would be sufficient to avoid extinction in the long run is unknown.

A more prudent estimate of what might be conserved in areas used by 50 rhinos may be gauged by considering the lower 90% confidence interval (Table 3). Dry-season estimates of gemsbok, zebra, and ostrich population sizes vary from 109 to 163; neither kudu nor giraffe attain populations in excess of 43 individuals. Clearly, the larger the protected area is for rhinos, the greater the population size(s) will be for other species.

But real-world constraints may compromise the maintenance of designated population sizes. No reserve has been proposed that would incorporate the entire range of Namib Desert rhinos. Also, lands to the east of my rhino study region are still relatively uninhabited by local people and stock, so space is currently available for the native herbivores to move. But if outlying regions were to become unavailable (e.g., because of additional fencing, loss of migration routes, the development of boreholes), then the non-rhinoceratid herbivores would be precluded from areas beyond the boundaries of contemporary rhino range and population sizes would diminish. If, the rhinos areas alone were established as a reserve with adjacent lands ignored, however, adequate protection for the nomadic herbivores would still not be assured. Herbivore assemblages elsewhere show similar patterns. For instance, protected regions of the Kalahari Desert and northern Tanzania also have ungulate populations that decline with decreasing precipitation (Mills & Retief 1984; Prins & Douglas-Hamilton 1990). So, where environmental variance is high (as is typical of most xeric environments; Caughley 1987), the prudent conservation tactic will always be to minimize risks of extinction by protecting large regions.

To enhance prospects for longer persistence, areas larger than those used by Namib Desert rhinos alone may have to include more-mesic regions, sites that nomadic herbivores use when drought intensifies. In the absence of data on spatial requirements during both average and extreme conditions, it may not be possible to reduce the risk of population collapse due to unusual cli-

Table 3.   Adjusted estimates of population size ($\pm$ SE) 1991–1993 for large herbivores within areas predicted for a population of 50 black rhinos in the northern Namib Desert.

Season	Gemsbok		Zebra		Kudu		Giraffe		Ostrich	
	Dry	*Wet*	*Dry*	*Wet*	*Dry*	*Wet*	*Dry*	*Wet*	*Dry*	*Wet*
Average	275	684	252	451	81	184	42	43	230	582
	(89)	(107)	(60)	(75)	(17)	(60)	(11)	(12)	(46)	(216)
Confidence limits,	109	341	124	293	43	54	29	24	163	247
lower 90%	(38)	(129)	(67)	(94)	(11)	(28)	(11)	(10)	(81)	(115)

matic events (Weatherhead 1986). Problems involving congruent biotic and legal boundaries are a continual conservation dilemma (Newmark 1985), although community-based programs may ameliorate some of the concerns (Owen-Smith 1986; Bonner 1992).

Boundary issues aside, the assessment of biodiversity obviously requires more than consideration of large herbivores. My results simply represent a first empirical derivation of population sizes of species falling within the range of a putative umbrella species. They serve to highlight some real world problems that confront conservationists interested in using the umbrella species concept as a biological tool rather than as a heuristic construct.

For umbrella species to be useful, they ought to be represented by populations whose population size has a high certainty of persistence. This means that, to assure long-term viability, populations will have to be large and environments substantially protected from rapid ecological change. For instance, wildebeest in the Serengeti have been suggested as an umbrella species (McNaughton & Banyikwa 1995), and they may well be an excellent example because they have large population sizes and they migrate over large areas.

Although I have equivocated about the usefulness of black rhinos as an umbrella species, this is not because they fail to conform with expectations based on life histories. Desert black rhinos possess huge home ranges (Fig. 1), and the area needed to sustain a viable population would contain sufficiently large populations of most other herbivores of a similar trophic level. Rather, like tigers and other species sought for their economic value, their long-term viability is questionable. This doesn't mean that rhinos cannot be a meaningful umbrella species, but it may be difficult for them to attain the population size necessary to assure their long-term viability. More should be done to investigate the concept of umbrella species, especially demographic assessments of biodiversity at trophic levels different from those of the putative umbrella species.

Acknowledgments

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