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Reviewed work(s):
Source: *Oikos*, Vol. 77, No. 2 (Nov., 1996), pp. 207-216
Published by: Blackwell Publishing on behalf of Nordic Society Oikos
Stable URL: http://www.jstor.org/stable/3546059
Accessed: 09/11/2011 11:53

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OIKOS 77: 207–216. Copenhagen 1996

# Animal behaviour and plundered mammals: is the study of mating systems a scientific luxury or a conservation necessity?

**Joel Berger**

Berger, J. 1996. Animal behaviour and plundered mammals: is the study of mating systems a scientific luxury or a conservation necessity? – Oikos 77: 207–216.

Darwin claimed "the practice of polygamy leads to the same results as would follow from an actual inequality in the number of the sexes". Biologists interested in conservation have focused on offshoots of this deceptively simple theme including reproductive competition, sexual selection, and copulatory dynamics. Few would dispute that an understanding of mating relationships is important. Here, I ask – important for what? Using two species of large mammals that have suffered 97% reductions in population size, I make two points. First, in attempts to restore populations some individuals or even lineages may be competitively inferior, leaving behind few or no progeny, a scenario depicted empirically using two lineages of North American bison (*Bison bison*). Second, where human utilization of economically valuable morphological structures has been proposed (as for rhino horns), knowledge of current utility is required to predict possible biological effects. Preliminary data on black rhinos (*Diceros bicornis*) suggest that dehorned mothers are less able to defend their calves from spotted hyenas (*Crocuta crocuta*) than intact mothers. For conservation, some issues in animal behaviour will always hold greater relevance than others. The study of mating systems, unless defined very broadly, is likely to have more relevance in captive propagation and population restoration than other issues involving the conservation of biodiversity.

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Although behavioural ecologists and conservation biologists both attempt to enhance the understanding of systems through scientific study, disciplinary similarities are few. "Behavioural ecology" is a concept-oriented field driven by evolutionary theory, and practitioners focus on questions about individuals and populations. "Conservation biology," on the other hand, while including populations, is applied and has as its goal reducing the loss of biodiversity. For behavioural ecologists, the study of mating systems has played a decisive role in developing and understanding theory. Might the same be claimed by conservation biologists? In this paper I consider a broad component of animal behaviour, mating systems, and ask whether such study is a conservation necessity or, simply, a scientific luxury.

Judging from an eclectic assortment of books on the biology of conservation published during the last decade (Table 1), the answer would be almost an unequivocal *no!* Less than 50% of the books gave behavioural issues much play, and discussion never constituted more than 25% of the material. While the books represent general treatments of conservation and not case studies of single species, it is evident that current students are being trained to appreciate issues in conservation without exposure to much more than cursory ideas in animal behaviour.

A topic regularly implicated for its importance in the area of conservation biology is the study of mating systems. Contributions to conservation genetics have come about by using data on sex ratio skew and

Accepted 25 January 1996

ISSN 0030-1299

Table 1. An annotated list of recent (1986–1996) general conservation books that vary in emphases on the prominence of behavioural paradigms. Determinations are subjective with asterisks ranging from none to five (highest). MS – mating systems; OB – other behaviours.

| Title | Prominence | | Reference |
|---|---|---|---|
| | MS | OB | |
| Fundamentals of conservation biology | * | | Hunter 1996 |
| Conservation biology in theory and practice | | | Caughley and Gunn 1996 |
| Population management for survival and recovery | | | Ballou et al. 1995 |
| Conserving wildlife | | | Jacobson 1995 |
| Serengeti II | * | * | Sinclair and Arcese 1995 |
| Endangered species recovery | | | Clark et al. 1994 |
| Principles of conservation biology | | | Meffe and Carroll 1994 |
| Creative conservation | * | | Mace and Feistner 1994 |
| Living within limits | | | Hardin 1993 |
| Essentials of conservation biology | * | * | Primack 1993 |
| Beyond captive breeding | | * | Gibbs 1992 |
| Last animals at the zoo | * | * | Tudge 1992 |
| Ghost bears | | | Grumbine 1992 |
| Ecological principles of nature conservation | | | Hansson 1992 |
| Neotropical wildlife use and conservation | | * | Robinson and Redford 1991 |
| Management and conservation of small populations | | * | Clark and Seebeck 1990 |
| Conservation for the twenty-first century | | * | Western and Pearl 1989 |
| Biodiversity | | | Wilson 1988 |
| Viable populations for conservation | | | Soulé 1987 |
| Restoration ecology | | | Jordan et al. 1987 |
| Conservation biology | * | | Soule 1986 |
| The ecology and management of biological invasions in southern Africa | | | Macdonald et al. 1986 |

reproductive success to estimate effective population size ($N_e$) (Barrowclough and Rockwell 1993). Other areas of behaviour, some peripherally tied to mating systems such as infanticide (Caro and Durant 1995), dispersal (Chepko-Sade and Halpin 1987), and conspecific attraction (Smith and Peacock 1990), have also been applied fruitfully to issues in conservation. Yet, in many circumstances it remains unclear how, where, or even *if*, the study of many aspects of contemporary behaviour relate to conservation.

Darwin, of course, established the foundation for the study of evolution and pointed out that "the practice of polygamy leads to the same results as would ... inequality in the number of the sexes; ... many males cannot pair and the latter will assuredly be the weaker or less attractive individuals" (Darwin 1871: 232). This deceptively simple statement can be linked to the current study of such issues as dominance, sex ratios, parental investment, and both sexual dimorphism and sexual selection. Where, however, study of such phenomena can contribute to conservation is less obvious. Here I consider several possible ways that the study of mating systems may contribute to the conservation of plundered populations.

Specifically, I use black rhinos (*Diceros bicornis*) and North American bison (*Bison bison*), the former being decimated by 97% in the last three decades and the other reduced by more than 99% last century, to illustrate both the potential and limitations of approaches steeped in behavioural ecology. I use two constructs tied to the study of sexual selection – 1) intrasexual competition and 2) horns – and conclude by arguing that, despite my enthusiasm for some "behavioural" approaches to conservation issues, I remain equivocal in believing that behavioural ecology has a major role to play in conservation biology.

## The study of mating systems within the context of conservation challenges

The greatest threat to Earth's biodiversity is the unmitigated growth of humans (Ehrenfeld 1981, Ehrlich and Ehrlich 1981). Because less than 5% of the planet's terrestrial surfaces have been set aside for conservation purposes, the maintenance of biotic processes will be governed more by what occurs outside reserves rather than within them (Janzen 1983, Western and Pearl 1989). Also, because most reserves are small, other problems may be expected. For instance, North America's largest grassland national park is the Badlands in South Dakota (40°50′N, 102°20′W), about 1000 km$^2$. In size, relative to all USA state and federal reserves, the Badlands falls within the top 85–90%. Since the rate at which areas are protected is declining and very few spacious reserves are now being created, species that require large tracts to attain sizeable populations may increasingly require some form of management. The distinction between wild and captive will become even more hazy, especially for larger species, as time progresses.

Blue wildebeest (*Connochaetes taurinus*) offer a good example. In Etosha National Park, Namibia they are totally fenced within the 23 000 km$^2$ size reserve where they no longer migrate to feeding areas beyond park boundaries. Populations within the 25 000 km$^2$ Serengeti ecosystem are not fenced and migration occurs although populations at the extreme western edge are bordered by some two million Tanzanians and poaching impacts wildebeest demography (Campbell and Hofer 1995). Functionally, these systems share similarities. Both are inevitably confined by human actions, each population roams freely despite de facto outer limitations, and predation by lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*) occurs in each environment. But there are also large differences. Etosha wildebeest are declining perhaps because of the long term effects of fencing (Gasaway et al. in press) whereas Serengeti's population remains stable (Sinclair 1995).

Not all species or populations enjoy a high probability of survival and, where populations are small, supplementation of individuals or entire genetic lineages may be desirable (Stanley-Price 1989). However, the consequences of such actions are often questionable (Ryman et al. 1995). Indeed, hatchery-reared and wild salmon (*Oncorhynchus kisutch*) differ behaviourally with the former being poor competitors and leaving behind fewer offspring than wild-reared conspecifics (Fleming and Gross 1992, 1993). It is here – the recovery, restoration, and supplementation of populations – that the study of mating systems holds promise, particularly where the aim is to understand both the fate(s) and cause(s) of individual differences in reproduction and how these might subsequently affect population structure. But whether such study, even in small reserves, is as critical to conservation as is the conservation of landscapes is a matter of perspective (Soule and Mills 1992).

## Bison and restoration: the Badlands

### *Background*

Bison are the largest terrestrial mammal of the New World. The species is sexually dimorphic and polygynous with some males more than twice the size of females. Populations were reduced from an estimated 40–60 million individuals to less than 1000 last century (Roe 1970). Restoration efforts begun at the turn of the century resulted in the establishment of multiple isolated groups between 1888 and 1919, a Montana (National Bison Range) population had 40 animals, others on prairie environments in Nebraska, South Dakota, and Oklahoma contained less than 15 (Berger and Cunningham 1994a). Because today's prairie environments are highly fragmented, migration can no longer occur without human assistance.

To restore the population at Badlands National Park that became extinct prior to 1870, bison were reintroduced during two episodes. The first was in 1963 with the release of 28 animals. Founders came from North Dakota and Nebraska, but all were descendants from an initial 1907 population of six animals at the Fort Niobrara National Wildlife Refuge in north-central Nebraska. The Nebraska lineage (NL) had been supplemented with 11 males over nearly a 50-year period although it is unknown whether any of the introduced 11 males mated. The second re-introduction at Badlands was in 1984 when bison from Colorado National Monument in western Colorado were released. The Colorado lineage (CL) stemmed from 3 individuals traced back to 1925; their founders came from a park in Denver in 1906. Thus, both lineages derive from a half dozen founders or less and were separated for at least 77 yr until becoming sympatric in South Dakota in 1984.

### *Methods*

Analyses of allozymes at 24 presumptive loci showed no lineage differences in unique alleles and, for one polymorphic locus (MDH-1), allele frequencies did not vary between lineages (McClenaghan et al. 1990). Additionally, while unsampled in the Badlands population, mitochondrial DNA fragment sizes from bison populations elsewhere showed no regional differences (Cronin 1986), although it is possible that the use of other genetic techniques might produce interpopulation variation. For instance, in Pere David deer (*Elaphurus davidianus*) which have been bred in captivity for perhaps 3000 yr and with a captive population derived from fewer than 20 individuals there is an apparent lack of genetic variability, yet inbred young still experience greater mortality than outbred ones (Foose and Foose 1983, Ballou 1989). So, the issue of whether the two Badlands lineages differ remains unresolved.

Field data on mating, ecological, and other within- and between-lineage relationships were gathered from 1985 to 1989 by Carol Cunningham, an annual field crew of 4–6 assistants, and myself. Briefly, during the study period more than 200 individuals were known and the population expanded from 300 to 775. Individuals were identified by ear tags, brands, and hair and horn anomalies. Information on body mass and growth was obtained by weighing animals on cattle scales or estimated from equations based on relationships between morphological variables and mass (Berger and Peacock 1988). A photogrammetric that estimates with greater than 95% accuracy was used to estimate calf weight (Jacobsen 1986). Additional details are found in Berger and Cunningham (1994a).

Reproductive data were based on evidence from 261 copulations. Both focal animal and instantaneous sampling techniques were used during more than 8750 h of observation. At Badlands, females generally give birth to a calf per year in April, and reproductive success (RS) was determined by assessing offspring production and survival, the latter which averages greater than 95% annually (Berger and Cunningham 1994a). For males, RS was estimated by counting the number of times an individual copulated with different females. In the two cases (0.8%) in which more than a single male copulated with the same female, males were assigned a proportional representation of the putative offspring.

## Consequences of reproductive asymmetries among individuals and between lineages

The sexes varied in their abilities to produce offspring (Fig. 1). The most successful male putatively fathered 28 calves; the most successful female only 5. Irrespective of sex, the least successful individuals left behind none. Although age had marked effects on calf production, when analyses were restricted to the most fecund cohorts, 5–13 yr olds for females and 7–12 yr olds for males, the differences between the sexes remained striking. Over the four-yr period 1985–1988, mean RS for prime-aged males and females was 4.9 and 2.5 respectively, whereas the variance among males and females was 33.5 and 1.9, respectively.

These values are likely to underestimate the true differences between the sexes because: 1) mortality of non-breeding animals has not been included, an exclusion which results in heightened values of selection intensities (Howard 1988); and 2) although annual juvenile mortality at Badlands averages less than 5% (Berger and Cunningham 1994a), for many mammals males generally experience greater mortality than females (Ralls et al. 1980, Clutton-Brock et al. 1982). Thus, the sex differences in variation in RS reported here are likely to be even greater under more 'natural' conditions.

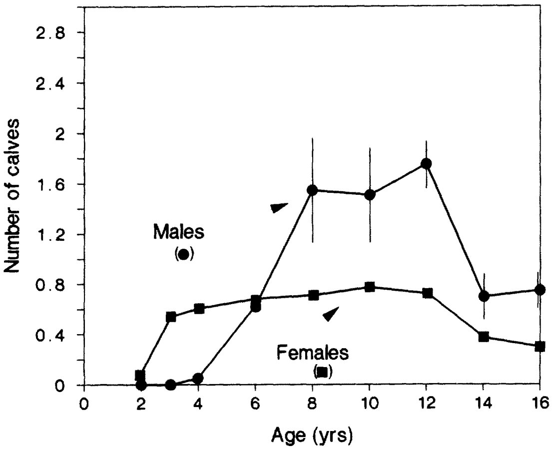

Fig. 1. Mean age specific fecundity (per yr) (±se) in female (1985–1989) and male (1985–1988) bison at Badlands National Park. Sample sizes, in parentheses as follows: males; 4-5 yr (40), 6 (28), 7-8 (34), 9-10 (24), 11-12 (19), 13-14 (24), 15+ (22); females; 2 yr (24), 3 (26), 4-5 (48), 6-7 (41), 8-9 (44), 10-11 (48), 12-13 (30), 14-15 (23), 16+ (24).

Reproductive competition can be gauged in numerous ways including the use of behavioural and reproductive data (Clutton-Brock 1988). Among the topics that have relevance for conservation are effective population size ($N_e$) (Allendorf 1986) and lineages asymmetries (Thompson 1986), each because they contain information about the amount of genetic material potentially available for future evolutionary change.

### *Effective population size*

This construct is useful in conservation genetics because it offers an estimate of the rate of change of selectively neutral heterozygosity (Frankel and Soule 1981). $N_e$ also has limitations because it offers a single value under ideal conditions only and at a given point in time. And, it does not account for population fluctuations or other historical factors (Lande and Barrowclough 1987, Pimm et al. 1989). Still, it is among the best conceptual measures available for assessing potential changes in genetic diversity (Allendorf 1986).

With respect to restoration efforts at Badlands, both CL and NL bison were allopatric for up to 77 yr and the NL varied widely in population size (from 6 to more than 200). Any measure failing to incorporate these temporal and demographic properties would be misleading but the inclusion of such parameters does not, of course, guarantee a reflection of reality.

To estimate $N_e$ for bison, a generation interval of bison of 6.75 yr has been assumed (Shull and Tipton 1987). At Badlands, then, the 2 lineages are represented by about 9 and $12\frac{1}{2}$ generations. Although demographic data for most of these generations are crude, it is still possible to estimate $N_e$ over the period of allopatry by making the following additional assumptions: 1) the birth sex ratio is 50:50 (after Green and Rothstein 1991); 2) calf survival approaches 100%; 3) adult males are removed from the population at twice the frequency of females (the adult male:female ratio of CL bison was 1:2; and 4) the reproductive skew in the past was similar to that documented during this study (past data unavailable).

$N_e$ may be approximated by employing the geometric mean to account for fluctuating population sizes (in my case for each lineage during periods of allopatry) employing Lande and Barrowclough's (1987) equation

$$1/2\left[1-\left\{\prod_{i=1}^{t}[1-1/2N_e(i)]\right\}^{1/t}\right],$$

where $t$ is the number of generations. The calculations reveal that despite attaining a high $N_e$ of 82, the average value for NL animals is only 9.5; that of the CL bison is about 2.5 (Fig. 2). Clearly, both lines have been inbred for a long time.

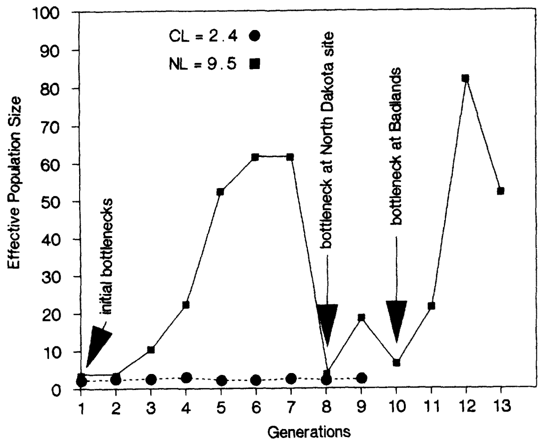

Fig. 2. Changes in estimated $N_e$ for fluctuating Nebraska and Colorado lineage (NL and CL, respectively) bison prior to sympatry at Badlands National Park, South Dakota. Bottlenecks refer to reductions in population size when animals from the source population were transplanted to a new site prior to arrival at Badlands. (Modified from Berger and Cunningham 1994a)

### *Asymmetries between lineages*

Although both lines are characterized by small effective population sizes, one way to maximize genetic representation in subsequent generations is for all animals to breed equally, a frequent goal of captive breeding programs (Thompson 1986). If, however, certain individuals are more reproductively successful than others, the potential for genetic loss increases because certain genomes may be less represented. For the Badlands population, do interlineage differences in RS occur? If so, do asymmetries exist for males only, females only, and which lineage may be favored?

First, I review the findings for males. Of 37 total males (32 NL and 5 CL) matched by age to remove age-related effects on reproduction, no CL males copulated. The result of "no mating" is unlikely to result from sampling bias because CL males were deliberately observed nearly 50% more than NL males and the binomial probability that the 5 CL males would be selected at random from the total population of non-breeding males is 0.01. In fact, on average not only did CL males spend less time in defense of females, but they were more than $2\frac{1}{2}$ times as likely to be displaced by NL males of similar size than the converse (Berger and Cunningham 1994a). CL males were unsuccessful breeders. If the same patterns occurs over their lifetimes, only sex-linked traits from such males will be found in future generations.

For females, lineage differences in fecundity and calf survivorship were not evident (Berger and Cunningham 1994a). However, the failure of CL males to mate resulted in a $F_1$ generation of neonates comprised of either NL (male) × NL (female) or NL (male) × CL (female) crosses, offspring designated as either inbred or outbred.

Interlineage differences in the growth rates of calves occurred (Table 2). Calves of outbred descent attained only 70% of the body mass of inbred ones, differences that carried over to the ages at which primiparous cows produced calves (Table 2). Whether these differences in growth were of genetic origin is unclear but they did not arise as a consequence of variation in maternal body condition or size, dominance, home range location, or year or date of birth (Berger and Cunningham 1994a).

The lineage differences in offspring growth have two potential life history consequences with relevance to conservation. First, among numerous vertebrates, body mass buffers against environmental extremes, especially cold, and during unusually harsh winters heavier individuals may experience reduced mortality (Murie and Boag 1984). Second, because the NL juvenile females grew faster and reproduced earlier than those of CL mothers, over time the CL mothers should become less abundant in future generations since early maturing bison have more offspring (Green and Rothstein 1991). Thus, it appears as if the CL bison are not being incorporated genetically into the population at the desired level.

Both sexual and natural selection appear to be playing prominent roles in the restoration of this population. For instance, sexual selection, operating through the effects of male-male competition is resulting in the exclusion of CL males from mating. Among females, however, the source of lineage differences can be traced to natural selection where $F_1$ juveniles of outbred descent experienced slower growth. With other factors equal, delayed puberty should result in fewer lifetime offspring.

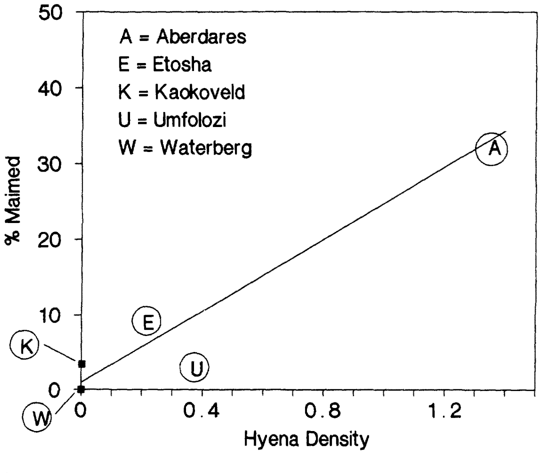

Fig. 3. Relationships between spotted hyena densities and the proportion of maimed calves at different sites, as follows: Aberdares, Kenya (Sillero-Zubri and Gottelli 1991); Etosha, Namibia (Gasaway et al. 1989, Berger unpubl.); Umfolozi-Hluhluwe, South Africa (Hitchins 1986, 1990; Whateley 1981); Kaokoveld, Namibia (Berger unpubl.); Waterberg Plateau, Namibia (Erb unpubl.).

## Horns within the context of rhino conservation

Many conservation programs champion the idea of demographic and genetic management, especially when the population sizes of rare or endangered species reach precarious levels (Meffe and Carroll 1994, Ballou et al. 1995). For black rhinos there are plans for captive propagation, ex situ management, and intercontinental transfers (Ryder 1993). The far sighted look ahead 50+ generations and outline ways to maximize genetic diversity. However, genetics has little to do with the in situ conservation of black rhinos because in just 3 generations more than 95% have been lost (Leader-Williams 1993). The reduction is due to poaching for horns and not due to diminishing habitats. So, how might behavioural ecology bear on rhino conservation?

Three African countries, Zimbabwe, Namibia, and Swaziland, have resorted to dehorning their white (*Ceratotherium simum*) and black rhinos. The logic is simple; without horns, the incentive to poach should vanish. Although dehorning is a controversial measure, conventional protectionist tacts and the worldwide ban against horn trade have failed to protect rhinos. In Namibia, dehorning was performed initially in remote areas where populations occurred at low densities, and with the hope that anti-poaching rangers could redirect their activities to other areas (Lindeque 1990).

## Adaptive paradigms

Among large mammals including primates, ungulates, and pinnipeds sexual dimorphism and apparent degrees of polygyny are associated (Harvey et al. 1978, Alexander et al. 1979, Clutton-Brock et al. 1980). Not only are males generally larger than females in these groups, but they are more ornamented, often with tusks, capes, antlers, manes, and/or horns. While females may select males on the basis of traits that might advertise condition, most evidence suggests an intrasexual role for such secondary sexual characteristics (Clutton-Brock 1982, Andersson 1994).

### *Possible functions for horns and consequences of dehorning*

Horns evolved independently several times in numerous ungulate lineages of the Oligocene and Miocene (Geist 1966) but the major proliferation occurred in the African bovid radiations of the Pliocene (Janis 1982). Rhinos are the only extant horned perrisodactyls, the first, *Diceratherium*, appearing with paired nasal appendages during the Miocene. Another ornamented lineage of perrisodactyls, the Chalicotheres, went extinct during the Pleistocene (Munthe and Coombs 1979). Numerous functions of horns have been proposed, most having been applied to sexually dimorphic species where the sexes differ in ornamentation (Packer 1983, Kiltie 1985). Since most perrisodactyls (equids, tapirids, rhinoceratids) are monomorphic in body size, the evolution and function(s) of such adornment may differ between them and dimorphic taxa.

The major hypotheses for conspicuous ornaments (Geist 1966, Clutton-Brock 1982) as they may apply to rhinos are, they: 1) function in intraspecific combat; 2) deter predators; and 3) serve in mate choice.

With respect to rhinos, conservationists are interested in immediate issues, not the causes of horns per se. The most critical is whether dehorned rhinos will be safe from poachers. If not, there is no need to continue the dehorning exercise (Berger and Cunningham 1994b). If dehorned rhinos are not poached, it will be necessary to know how quickly horns re-grow because rhinos with regrown horns will inevitably become increasingly vulnerable to poachers. Additionally, there are issues associated with the study of mating systems. Is the dehorned species monomorphic or sexually dimorphic? Depending on the answer, different roles for the horn may be posited. Are dehorned individuals or their offspring more susceptible to non-human predation? Are hornless individuals and, males in particular, at a mating disadvantage?

### *Background and study design*

To investigate possible consequences of dehorning, Carol Cunningham and I studied black rhinos from 1991–1993 in two areas of Namibia: 1) Etosha National Park (19°S, 14°40′–17°E), a fenced 23 000 km$^2$ area where horned rhinos live sympatrically with potentially dangerous predators, spotted hyenas and lions; and 2) the northern Namib Desert (ca 19°S70′–20°80′S, 13°80′–14°20′E),. In the latter we focused on a 7000-km$^2$ region where dehorning operations occurred in 1989 and 1991. Area "A" contained horned rhinos that were left intact and were sympatric with hyenas and occasional lions. Area "B" had dehorned rhinos (1991) but lacked hyenas and lions while Area "C" had dehorned rhinos (1989) that overlapped with spotted hyenas.

The study areas were essentially contiguous with one another, with "A" and "C" being separated by a country-length veterinary cordon fence. Occasional movements of animals between these areas occur (Loutit and Montgomery 1994a, b) although we did not observe animals moving back and forth (Berger et al. 1994). The density of predators at respective sites is imprecisely known but transects that involved more than 5100 km of driving in open habitats produced evidence of hyenas or lions in Areas "A" and "C" but not in "B" (Berger et al. 1994). Horn size was calculated using the same equipment as described for bison. Additional details are given in Berger and Cunningham (1994c, 1995).

Table 2. Summary of relationships in growth, body mass, and age at which the first calf was produced in bison descended from either Colorado (CL) or Nebraska (NL) lineage mothers mated with NL fathers only. Sample sizes in parentheses. For the simple regression, $Y$ = mass (kg) and $X$ is age (d). Inbred: NL × NL crosses; Outbred: NL × CL crosses. Within lineage sex differences in growth were not detectable at 180 d.

| | Regression | $r^2$ | $P$ | Mass (kg) at 180 d (65) | Age (yr) of first calf (30) |
|---|---|---|---|---|---|
| Inbred | $176.33 \log X - 225.68$ | 0.75 | $<0.001$ | 172 | $3.2 \pm 0.01$ (se) |
| Outbred | $132.95 \log X - 179.12$ | 0.66 | $<0.001$ | 121 | $3.9 + 0.02$ |

Statistical probabilities of between-lineage differences in regression coefficients and age at first calf are ($t = 3.88$) $P < 0.001$ and ($t = 2.10$) $P < 0.05$, respectively.

## Horns and possible predation

### *Hyenas, calf maiming, and survival*

To address some of the conservation issues, data are required on 1) calf production and survivorship, 2) maternal horn size, and 3) predation. Unfortunately, rhinos are nocturnal and, in the Namib Desert, individuals may have home ranges up to 2000 km$^2$ and, due to low densities, samples sizes are small. Little is known about the frequency of predation on young rhinos by lions and hyenas although adults are generally immune by virtue of their large size (Goddard 1967, Ellliot 1987, Berger and Cunningham 1995).

Some information is available on potential effects of predators. Calf maiming (Hitchins 1986, Sillero-Zubri and Gottelli 1991), that is the loss of ears or tails, has been reported from at least four African populations, and 92% ($P < 0.002$) of the variance of maimed calves is explained by the density of spotted hyenas (Fig. 3). Several possibilities may account for this association. It may simply be spurious, re-enforced by a small sample. Or, where clan sizes are larger, such as at sites where the frequency of maiming was higher, clan size is typically associated with prey biomass (Henschel and Tilson 1988, Mills 1990) and hyenas may be bolder. Or, perhaps at sites where rhino prey constitutes a relatively higher proportion of biomass, calves may be attacked more often. Whatever the true cause(s) of the association between maiming and hyena density, it is clear that horned mothers have not always prevented the maiming of their offspring.

If horn size affects the outcome of maternal defence, then short(er) horned mothers should be characterized by either 1) a higher incidence of maimed calves, or 2) experience poorer calf survival, or both. Each idea can be examined.

With respect to the first prediction, maternal anterior horn size (MAHS) was contrasted between mothers with calves of different status. MAHS [$\bar{x} = 43.0 \pm 1.1$ (se) cm ($N = 30$)] for mothers of intact calves and those with maimed calves ($\bar{x} = 37.6 \pm 5.0$ $N = 5$) did not differ ($t = 1.56$; NS, df = 33), although given the small sample the possibility of committing a Type II error (Cohen 1988) and falsely accepting the null hypothesis of no effect may be high, 0.72. For example, to show that MAHS has a significant effect ($P < 0.05$) by retaining the actual means reported above and assuming a 90% probability that the 95% confidence interval in horn size is less than or equal to 5 cm, the required sample would have to be 173 mothers. Given the impracticality of acquiring such data, all that can reasonably be concluded is that the idea that horns are important in calf defense cannot be rejected, nor can it be accepted.

However, because rhinos have been dehorned, the second prediction may be subjected to a test, albeit crude. Recall that, in the Namib Desert, calves were born at three types of sites, where mothers were intact and sympatric with hyenas and occasional lions ("A"), where animals were dehorned and without potential predators ("B"), or where animals were dehorned and with spotted hyenas only ("C"). Using a total of 10 calves in the three regions, all 4 and 3 calves from "A" and "B", respectively, survived to at least one year of age, whereas none of the remaining calves from "C" survived. Despite the admittedly restrictive sample, the differences in calf recruitment are significant [$P = 0.017$; Fisher's (3 × 2) Exact Test; "B" vs "C", $P = 0.05$; "A" vs "C", $P = 0.029$]. A conditional binomial probability exact test may be more appropriate for data in which the frequency of marginal totals are not fixed (Rice 1988). Using this more powerful technique, the 1-tailed probability of calf differences in recruitment rate are: "A" vs "C", $P = 0.0062$; "B" vs "C" $P = 0.017$. These preliminary findings suggest that horns may have current utility and that mothers cannot safely protect neonates for at least 3 yr after horn removal, a period when the mean size of *regrown* anterior horns is about 47% the length of the anterior horns of mothers never dehorned (Berger and Cunningham 1994c).

### *Interpretations based on small samples and unusual environmental events*

These results have not been without controversy, and questions about small samples, calf survival, and the lack of witnessed interactions with predators at desert sites have been raised (Loutit and Montgomery 1994a, b). Thus, a short elaboration seems worthwhile. Only two calves were known to have been born in Area "C"; a third was assumed because a putative mother was observed calfless but with a protruding udder, the latter indicating a presumed third calf (Berger and Cunningham 1994c, Berger et al. 1994). However, to be deliberately conservative and underestimate neonate mortality, the differences in neonate survivorship between sites "C" and either "A" or "B" can be estimated by assuming that only two calves were born and died. In either scenario, the probability of differences is 0.10 or lower (or with Rice's test, the $P = 0.026$ or less). Adherence to conventional statistical wisdom (e.g. $P < 0.05$) would, in the case of Fisher's Exact Probability Test, result in rejecting the hypothesis that dehorning affects neonate survival. However, because the possibility of a Type II error exists, the broader conservation issue is whether to reject the hypothesis that dehorning has negative effects and accept the idea that calf recruitment remains unaffected. Prudence appears to be the wiser tact in endangered species when a Type II error carries greater liability than a Type I error (Connor and Simberloff 1986, Jenkins 1995).

A different issue is the examination of alternate hypotheses. Few comparative field studies can be truly experimental because precise controls are not always possible with respect to such variables as habitat variation, differing densities, even differing ages of animals in subpopulations. Although potential predator pressure varied among Namib Desert study areas, other factors might have resulted in calf mortality in one area but not others. Food maternal age, and year of dehorning are all possibilities examined elsewhere (Berger and Cunningham 1994c, Berger et al. 1994). Unfortunately, rare ecological events which might have produced the mortalities are difficult, if not impossible, to replicate. For instance, during 1993 drought caused the migration of most large herbivores, possibly forcing the hyenas which remained to switch to another prey source – calves of dehorned rhinos. Only continued study would allow evaluation of this possibility.

## Is the study of mating systems a scientific luxury or a conservation necessity?

There is no easy answer. Using the above examples from plundered populations of two large mammals, I could easily claim that the study of mating systems is, or is not, important for conservation. The answer depends on how broadly or restricted, mating systems are defined. If interpreted broadly, then areas tangential to mating systems such as sexual dimorphism and sexual selection, dispersal dynamics and spatial distribution, even sex ratio adjustment and inter- and intrasexual competition can be included. If defined narrowly to topics dealing solely with skew in reproductive success, then the application of the study of mating systems to conservation will deal primarily with social structure, effective population size, restoration, and captive propagation.

As can be gauged from Table 1, few texts on conservation have allocated much space to behaviour probably because, when compared to the magnitude of habitat loss and coincident decreases in biodiversity, behaviour plays only a small role in conservation. Still, Table 1 offers an unnecessarily restrictive view of the contribution that behaviour and mating systems may play in understanding population and conservation phenomena (Caro and Durant 1995). Plundered populations of mammals are widespread and a great deal of information on animal behaviour and mating systems is available to enhance population restoration [e.g. black-footed ferrets (*Musetla nigripes*) Seal et al. 1989; cheetahs (*Acinonyx jubatus*) Caro 1994; Przewalski horses (*Equus przewalski*) Boyd and Houpt 1994); prairie dogs (*Cynomys ludovicianus*) Hoogland 1995)].

With respect to restored populations, is the potential loss of a bison lineage worthy of concern? After all, selection must be operating as differential reproduction causes the less competitive line to fail. The answer may lie not so much in determining that one lineage is less competitive as genetic assessments could reveal similar information. Rather, an understanding of mating systems via behavioural pursuits has allowed the acquisition of detailed life history data and uncovered mechanisms leading to differential reproduction. Where the goal of future re-introductions is to assimilate lineages and, perhaps, balance founder effects, it will be important to understand characteristics of individuals. It is here that the study of mating systems can yield insights about demographic processes that bear on the genetic structure of populations. On the other hand, if the study of mating systems produces data that bear primarily on population recovery, then, as a study discipline, mating systems represent the tail end of conservation efforts, those which examine the symptoms of a problem rather than the problem itself (Caughley 1994).

With respect to populations plundered for economically valuable parts, knowledge about the evolutionary impetus of exaggerated morphological structures appears somewhat esoteric in comparison to that bearing on current utility. In the case of rhino dehorning, despite the limited evidence, studies steeped in principles of behavioural ecology leads to the suggestion that female horns may serve an interspecific function, neonate defence. Additional data are also necessary to avoid further controversy on the role of horns (Brussard 1994, Macilwain 1994).

What is clear is that the study of mating systems, broadly defined, can shed light on real world problems in conservation. At a different level, we, as behavioural ecologists, may be remiss. The de facto omission of material on behavioural contributions to general conservation issues sends an important *negative* message to a new generation of students – the conservation practitioners of the future – that research on behaviour is of limited value.

*Acknowledgements* – For support I thank the American Philosophical Society, Frankfurt Zoological Society, the Hassleblad Foundation, the Conservation and Research Center (Smithsonian Inst.), the National Science Foundation, the U. S. Agency for International Development, Rhino Rescue, Ltd., The Wildlife Conservation Society, World Wildlife Fund, the Univ. of Nevada's Agricultural Experiment Station and Graduate School, the National Geographic Society, the Wildlife Preservation Trust, and the U. S. National Park Service. Namibia's Ministry of Environment and Tourism permitted the first three years of rhino research. Staffan Ulfstrand encouraged the development of this paper and comments from Carol Cunningham and Tim Clutton-Brock improved it. Aron Rothstein helped with the conditional binomial exact test.

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