

Behavioural ecology in managed reserves: gender-based asymmetries in interspecific dominance in African elephants and rhinos

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Abstract

As large-bodied mammals become restricted to progressively smaller fragments of former habitat, competitive interactions and interspecies aggression are likely to intensify. Data on the outcomes of 159 encounters between endangered African pachyderms revealed that: (1) female elephants (*Loxodonta africana*) dominated both sexes of black rhinos (*Diceros bicornis*); and (2) rhino males but not females displaced elephant bulls. The results of an additional 127 interactions involving pachyderms and 12 additional mammals ranging in size from cheetahs (*Acinonyx jubatus*) to giraffe (*Giraffa camelopardalis*) indicates that females of either pachyderm deny immediate access to limited resources. Although the evolution of gender-specific asymmetries in interspecific dominance has received little formal study, it may best be explained by understanding patterns of parental investment; however, from a conservation perspective, one consequence of size-related dominance is that with continued containment of elephants and rhinos in managed reserves, the most handicapped species are likely to be the smaller ones.

INTRODUCTION

While the study of sex differences in behaviour has contributed much to fields as disparate as medicine, agriculture, and evolution (Ralls, Brownell & Ballou, 1980; Endler, 1986; Nesse & Williams, 1995), its link to issues concerning the maintenance of global biodiversity has been tenuous. The omission is understandable because conservation biology has traditionally dealt with genes, species, and ecosystems, not behaviour (Soulé, 1986). Nevertheless, as wild populations are increasingly restricted to insular reserves, conflicts will arise which, for large-bodied species, may include the raiding of crops, spread of disease, and habitat alterations (Owen-Smith, 1988; Sukumar & Gadgil, 1988; Berger & Cunningham, 1994a). Despite knowledge of intraspecific consequences of spatial and demographic restrictions (Boyce, 1989; Sutherland, 1996), among mammals other than a few primates (Ihobe, 1990; Wrangham & Peterson, 1996), neither interspecies aggression nor the extent to which it varies by gender has received formal attention. Such knowledge is important because: (1) factors influencing the behaviour of females and males will remain incomplete if we fail to account for interactions between species; and (2) where gender-based asymmetries in interspecific aggression exist, community-level processes may be compromised by the

differing effects of some species on others. For instance, where interspecific dominance is related to body size, as suggested when feral and native species co-exist (Berger, 1986), the management and conservation of biological communities will require more sophisticated information on causes and consequences of interspecific aggression.

Despite their current status as flagship species (Western, 1987; Ryder, 1993), neither gender nor dominance in interactions between rhinos and elephants is well understood, partly because of their nocturnal nature and the lack of repeatedly observable interactions. Descriptions of encounters between these pachyderms have been anecdotal or rooted in folklore. In *The Travels of Babar* interspecific animosity was described some 60+ years ago: 'The rhinoceroses have fled and are still running. . . . What a glorious day for the [victorious] elephants.' (De Brunhoff, 1934). As early as the 1830s, naturalists varied as to which species was dominant: 'When the elephant and the rhinoceros come together and are mutually enraged, the rhinoceros avoiding the blow of the trunk and the thrust of the tusks, dashes at the elephant's belly and rips it up' (Alexander, 1838), and, 20 years later, 'strength in the elephant is infinitely superior to the rhinoceros but the latter . . . having encountered an elephant, made a furious dash at him, striking his long sharp horn into the belly of his antagonist with such force as to be unable to extricate himself; and, in his fall, the elephant

crushed his assailant to death' (Andersson, 1856). Whether these accounts were embellished is unknown.

Here, we explore the general hypothesis that body size and interspecies dominance are related, and examine it with data from 286 natural encounters involving African elephants, black rhinos, and 12 other mammals. More specifically, we show that this relationship is not so straightforward because asymmetries in dominance are also gender-based. Such information is valuable for two principal reasons. First, in devising realistic strategies to maximize the viability of local populations of Africa's two endangered pachyderms, re-introduction, translocation, or containment will continue to play increasingly important roles in conservation. If, however, reserves become overcrowded, then interspecific impacts may be heightened. Despite our lack of understanding of this topic in reserves of any size, without knowing the extent to which both gender and interspecies aggression and dominance modify access to limited resources, it will be impossible to more accurately predict effects at either the species or community level. Hence, our aim is simple – to offer empirical information on potential competitive interactions. Second, the data help to reinforce the advantage of including behavioural ecology as a field in developing interdisciplinary links to conservation biology.

BACKGROUND AND METHODS

The data on interspecific interactions stem from 1044 h of observation during 201 nights spent between 1991 and 1994 within the 22 700 km² Etosha National Park, Namibia. We focused on three discrete sites, designated here simply as 'A', 'B', and 'C', because of the possibility of continued poaching. The areas are separated by about 70 and 200 km (Cunningham & Berger, 1997). More than 98% of 52 individually known adult rhinos were philopatric to respective study sites; thus, we considered our areas as independent. For each interaction we recorded the following: gender, the number of individuals of each species present, distances of separation when displacements occurred (estimated in rhino body lengths), reproductive status (calf present or absent), and associated behaviour patterns. We calculated the probability that two events differ using Fisher's Exact Probability Test and accounted for the frequency that each gender was present. Although general linear models are appropriately applied to a series of variables, in analyzes such as the ones we employed a more direct estimation of statistical power is possible when using exact probability tests.

In Etosha, rhinos and elephants are most active at night. To enhance observations, we relied on natural moonlight or artificial lighting, and often illuminated areas with 750 000 candlewatts from a spotlight shielded by an infrared filter. We also modified a Litton Electron Device (M911a) attached to a 500 mm Nikon f/4 lens which magnifies the size of images about 13 times. Rhino–elephant encounters (Fig. 1) involved 159 displacements;

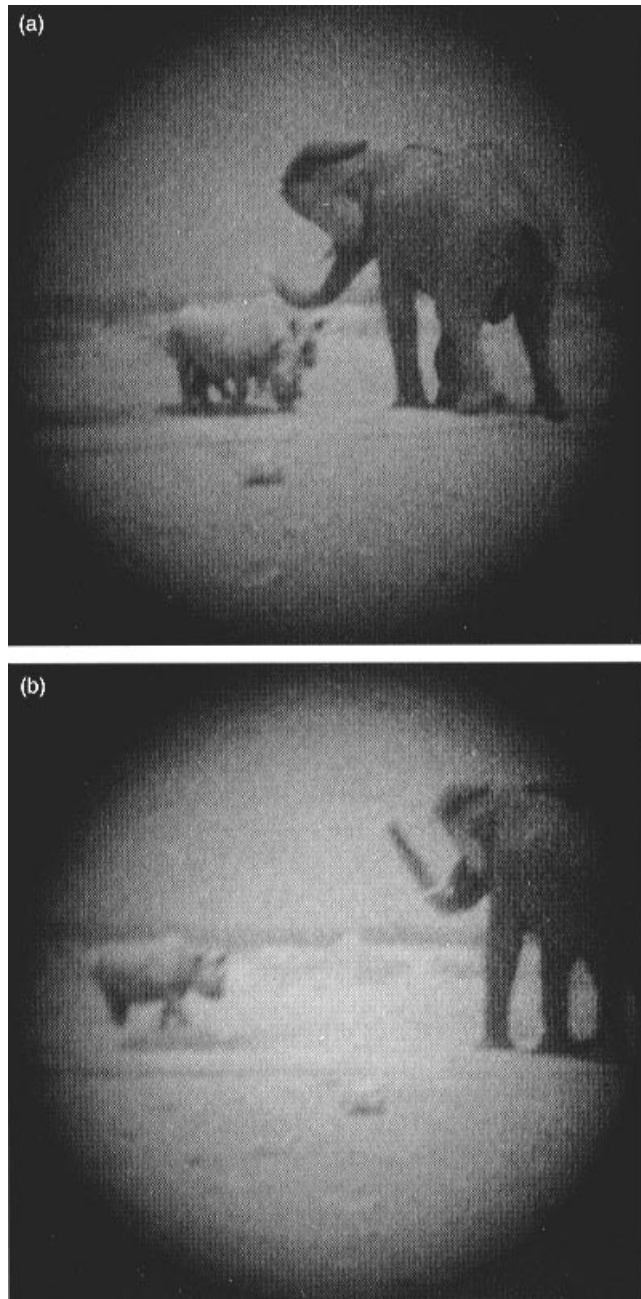


Fig. 1. Typical aggressive interaction between rhinos and elephants. (a), elephant male swings trunk and flaps ears at mother and calf; (b), trunk swiping at a male rhino.

the remaining 127 involved pachyderms with 12 other mammals (listed in Fig. 4). We considered a displacement as an event in which an individual or group moved from a site owing to the presence of others. If the encounter involved a behavioural action other than mere presence, we recorded it as an aggressive displacement. When individuals were clearly aware of the presence of others but failed to depart, by definition, displacements did not occur. Thus, displacements were not associated with every potential encounter.

Elephants live in two basic social groupings, clans which consist of family units (mothers, juveniles and

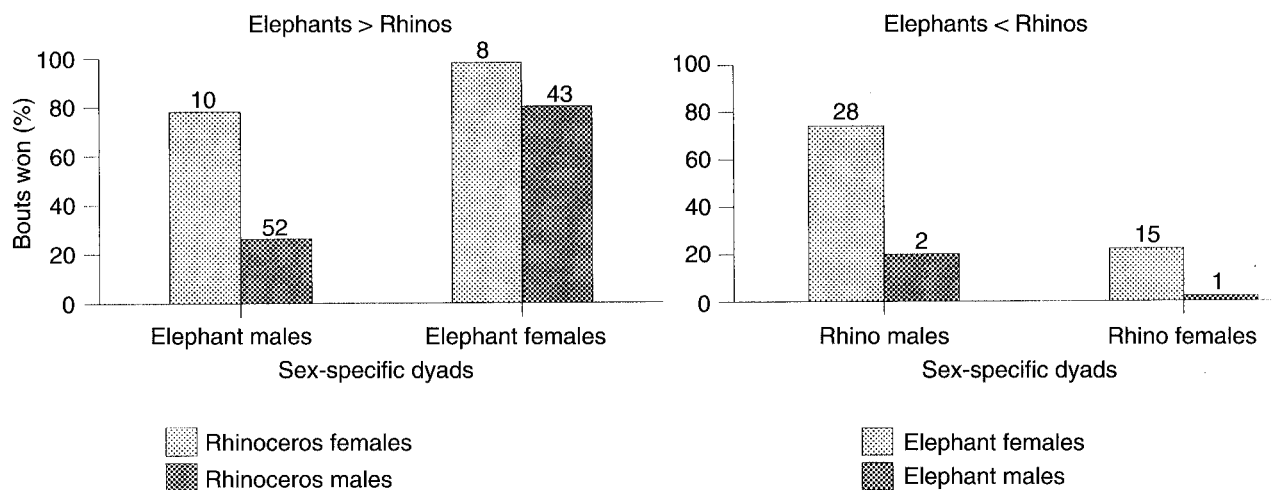


Fig. 2. Effects of species and gender on dyadic outcomes (percentage of bouts won) during sex-specific interspecies encounters in which elephants dominated (>) rhinos or vice versa. Sample sizes as indicated. The two-tailed binomial probability that actual outcomes differ from equality ($P = Q = 0.5$) for each of the four dyadic combinations are (from left to right): $n = 38$, $Z = -2.76$, $P < 0.006$; $n = 67$, $Z = -4.40$, $P < 0.00001$; $n = 9$, $P < 0.062$; $n = 45$, $Z = -5.96$, $P < 0.00001$.

young) and male groups (Moss, 1983; Moss & Poole, 1983); in Etosha, these contained from 7–47 and 1–8 individuals, respectively. For rhinos, both sexes tend to be solitary but nocturnal aggregations of up to 12 individuals occur in and around waterholes (Cunningham & Berger, 1997). In the interspecies interactions we witnessed, only solitary male rhinos or mother–calf units were involved. Although we also observed interspecific interactions between the pachyderms with other species, those involving the displacement of carnivores by rhinos were recorded but those with elephants were not.

RESULTS AND DISCUSSION

If body size alone affects the outcome of encounters, then elephants should invariably displace rhinos. This was not the case. While elephants supplanted rhinos 71% ($n = 113$; $P < 0.00001$, binomial test) of the time, gender played a prominent role (Fig. 2). Elephant females were dominant in 94% of 54 interactions. Conversely, rhino females displaced elephants in only 14% of interactions ($n = 111$), whereas male rhinos were victorious in 63%.

The gender-based asymmetries in interspecific outcomes were not the result of one study site contributing disproportionately to the overall data set. Rhino males displaced elephants more than 50% of the time and females never more than 15% at any study area (Fig. 3). These findings are also not an artifact of a single individual contributing disproportionately to the data sets. With the frequency of displacements by the most successful male from each study area removed, the asymmetry in proportion of male:female victories remains unchanged (study area A, $P = 0.477$; area B, $P = 0.682$; area C, $P = 0.727$). Similarly, no single female contributed disproportionately to losses (A, $P = 0.556$; B, $P = 0.525$; C, $P = 0.455$). Although power is decreased as samples are subdivided, the probability of a Type II

error is not especially troublesome because of inter-site consistencies in asymmetries among the study areas (Fig. 3). These data indicate that, although elephants displaced rhinos more often than the converse (71% versus 29%), the difference occurs because elephant females rather than males won a higher proportion of interspecies encounters (Fig. 2). Whether interspecies differences in outcome were due to elephant gender *per se* or group size cannot be disentangled since females occur in larger groups than males, and females were always in family groups.

Among rhinos, clear gender-related differences existed. Compared to females, males charged elephants more (11 events to one; binomial probability, $P = 0.0001$), interacted at closer distances (males, $\bar{X} = 12.7 \pm 2.9$ body lengths \pm SEM; females, $\bar{X} = 19.5 \pm 1.7$ body lengths; $n = 54$; Mann–Whitney, $Z = 4.0$; $P < 0.0001$), and were involved in more interactions where outcomes were uncertain (50 to 12; binomial probability, $P = 0.00001$). These results suggest that female rhinos are more timid and less likely to escalate encounters with elephants than are males. The difference is not related to horn or body size differences since the sexes of black rhinos are monomorphic (Berger & Cunningham, 1995).

If maternal investment influences the direction of interspecific encounters, then females of different reproductive status should vary behaviourally. This prediction is unsupported. Parous and non-parous rhinos were supplanted at similar levels (86%, $n = 95$; 83% $n = 24$; $P = 0.47$). To show that such a difference is statistically significant ($P < 0.05$) and, hence, avoid the possibility of a Type II error would require a sample of more than 1500 interactions, assuming half involve each female category at the observed proportions. Our 201 nights of observation yielded data on 286 interspecies encounters of which 119 involved rhinos of differing reproductive status. So, assuming that our sampling from 1991 to 1994 would be representative of other

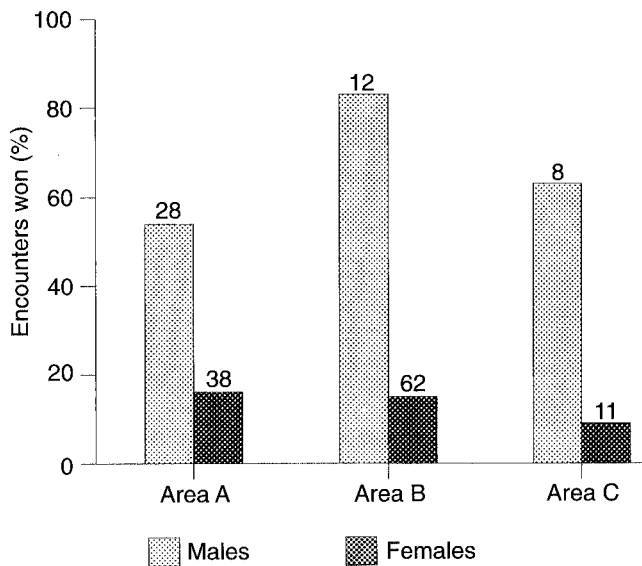


Fig. 3. Effects of study area and rhino gender on dyadic outcomes (percentage of bouts won) during encounters with elephants. Sample sizes as indicated. Replicated goodness-of-fit tests as follows: G_H (females) = 0.36, $P < 0.95$; G_H (males) = 3.43, $0.10 < P < 0.20$.

years, to achieve the recommended sample of 1500 interactions necessary for statistical significance would require an unrealistic additional 27 years of study.

Although a total of 221 interspecies dyads occurred between pachyderms, 72% ($n = 159$) involved displacements (Fig. 2). Of those, the intensity of aggression varied and included the following behaviours (% of encounters): *by elephants* – trumpeting (9%), ear flapping (14%), trunk swipes (3%), and running charges (0.6%); *by rhinos* – horn threats (6%) and charges (7%). Only once did contact occur when a male elephant failed to avoid a charging male rhino. We could not determine whether injuries resulted.

To what extent does gender-based interspecific aggression exist when pachyderms interact with mammalian carnivores and herbivores? Of 115 encounters between rhinos and other species, females supplanted carnivores 62 times and herbivores 37 times (Fig. 4); more often than did males ($P = 0.0001$; Fig. 4). So, unlike their timorous behaviour when with elephants (Figs 1–3), female rhinos were interspecifically more aggressive. For elephants, a similar pattern existed: herbivores at waterholes were supplanted more frequently by females than by males (11 events to one; binomial probability, $P = 0.0193$). Thus, while female pachyderms were interspecifically more dominant than males, female rhinos adjusted their behaviour according to the size of opponent. They aggressively displaced smaller species but rarely did so to elephants.

Why the sexes behave differently has been a topic of much interest (Clutton-Brock, 1991), but interspecific dominance by females and males has received scant attention. Three non-exclusive explanations may help to clarify the evolution of gender-specific asymmetries in such behaviour. First, since neither male rhinos nor

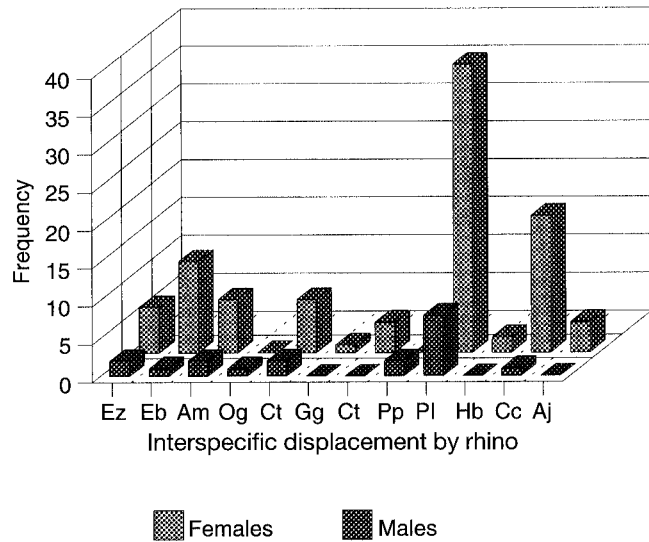


Fig. 4. Frequency that 12 species of mammals were displaced from waterholes by female and male black rhinos. Species as follows: Ez, mountain zebra; Eb, plains zebra; Am, springbok; Og, gemsbok; Ct, wildebeest; Gg, giraffe; Pa, warthog; Pp, leopard; Pl, lion; Hb, brown hyena; Cc, spotted hyena; Aj, cheetah. Frequency of displacements (in parentheses) by elephant as follows: *females* – Ez (1), Eb (1), Am (1), Og (4), Ct (2), Pa (1); *males* – Eb (1).

elephants appear to experience much predation by non-human predators (Sukumar, 1989; Berger & Cunningham, 1995), the incentive to drive away carnivores appears minimal. Similarly, except for interactions between the pachyderms, males of either species infrequently supplanted herbivores. Second, although female rhinos and elephants are not prey, their young are subjected to predation (Goddard, 1967; Berger & Cunningham, 1994b; Poole, 1996; Cunningham & Berger, 1997). Therefore, by chasing away predators themselves or prey that may attract carnivores, interspecific aggression may be a type of maternal defense. That non-parous mothers behave similarly is not inconsistent with this yet untested hypothesis because, by displacing potential prey or predators, those individuals might be less likely to risk close proximity in the future (Berger, 1979; Caro, 1994). Thus, interspecific aggression by non-parous females could be a low-cost form of future parental investment. Third, pachyderms may simply be protecting access to limited resources. If, however, this was the case, the occurrence of gender-specific asymmetries is puzzling since both sexes require water although lactating females more so.

While evolutionary explanation is fundamental in behavioural ecology, from a conservation perspective knowledge of the consequences of interspecific aggression and dominance is important for three principal reasons. First, when the translocation of endangered species occurs into small protected areas (Kleiman, 1989; Miller, Reading & Forrest, 1996), mortality risks can be minimized by understanding patterns of interspecific interaction. For example, in South Africa's

Pilanesberg National Park, which is less than 0.5% the size of Etosha, between 10 and 17 adult white male rhinos were killed most probably by young male elephants relocated there as orphans (Daley, 1996; Joubert, 1996). Insular reserves are increasingly likely to serve not only as repositories for endangered species translocations but also for errant individuals, as often happens in Yellowstone National Park where 'problem' grizzly bears or wandering wolves are regularly returned (Blanchard & Knight, 1995; Phillips & Smith, 1996). Second, species-specific consequences of displacement must be accounted for during conservation planning. For example, because of their generally subordinate status (Fig. 2), black rhinos will inevitably have reduced access to water when elephants are present. But when rhinos and not elephants are the largest herbivore in small protected areas, other species are likely to be displaced. Finally, numerous reserves contain boreholes (wells) which increase their capacity to support large numbers of elephants (Hancock, 1990; Hall-Martin, 1992; Chafota & Owen-Smith, 1996). Because pachyderms are inter-specifically dominant (Fig. 4) and elephants may congregate for hours at waterholes, or destroy them after depletion (Hancock, 1990; Joubert, 1996), other species could be precluded from access (Fig. 4), thus exacerbating the potential for widescale alterations in community structure.

Among future challenges will be to determine the extent to which gender-based asymmetries in inter-specific aggression and dominance exist in other species, communities, and trophic levels. If investigators are purist in nature and focus solely on native organisms, then valuable opportunities to evaluate potentially serious effects of feral and other alien species will be lost (Berger, 1986). For behavioural ecology to play a stronger role in conservation biology, it will be necessary to move beyond evolutionary explanation and to apply data more directly to human-induced changes in biological systems (Caro, in press).

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