Is a reduction in the individual vigilance of mothers a key evolutionary driver of group formation in white rhinos?

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A key benefit and evolutionary driver of group living is reduced predation risk. In white rhinos, groups comprise adult females, their calves and one to six unrelated subadults. Subadults benefit from group living through exposure to novel areas, and protection from territorial males (i.e. 'buddy system'). In contrast, it is unclear whether mothers benefit from group living. To determine if they benefit, or if there is simply no cost, we recorded the vigilance of white rhino mothers in different-sized groups. We predicted that as group size increased, calves would have lower predation risk and mothers would reduce their vigilance. In contrast, we found that vigilance did not decrease as group size increased. Our findings thus indicate that decreased vigilance is not a benefit that white rhino mothers gain from living in groups. Also, costs of group formation are minimal for mothers as their large body size and ability to feed on a wide range of grasses reduces competition with other group members. As a result, we suggest that the benefits obtained by subadults, coupled with the lack of costs to adult females, are the main drivers of group formation in white rhinos.

Key words: buddy system, *Ceratotherium simum*, group formation, vigilance, white rhinoceros.

INTRODUCTION

Many mammalian herbivores live in groups (Laundré *et al.* 2001; Brashares & Arcese 2002; Georgiadis *et al.* 2003). For group living to evolve in these species, there needs to be a net benefit for all individuals in the group (Krause & Ruxton 2002), or at least no costs. One of the main benefits and key drivers of the evolution of group living (Gosling 1986; Krause & Ruxton 2002) is increased predator protection via higher cumulative vigilance (termed the 'many-eyes' effect or collective detection) (Pulliam 1973; Stensland *et al.* 2003; Fairbanks & Dobson 2007), greater dilution of predation risk (Hamilton 1971; Vine 1971) and increased predator defence (e.g. bunching; Jarman 1974; Caro *et al.* 2004). Ultimately, this can lead to greater breeding success or increased survival probability of group members (Vehrencamp 1983; Turner & Pitcher 1986).

For white rhinos (*Ceratotherium simum*), groups are structured around adult females (> 7 years of age; Owen-Smith 1988). These females can be mothers or females whose calf had died (Owen-Smith 1988). Over the course of their adult lives, these females allow groups of 1–6 unrelated sub-

adults of both sexes, who have left their own mothers, to join up and move with them (Owen-Smith 1988; Shrader & Owen-Smith 2002). These associations can last anywhere from a few days to a few years (Owen-Smith 1973; Shrader & Owen-Smith 2002). Variability in association period is partly due to the adult female chasing away these subadults, and their own calf, just before she is about to give birth to her next calf (Owen-Smith 1988). In contrast, adult males (>10 years of age) are generally solitary (Owen-Smith 1988).

Shrader & Owen-Smith (2002) suggested that subadult white rhinos benefit from forming groups with adult females. These benefits include 1) reduced aggression from territorial males, 2) familiarization with novel areas, and 3) reduced predation risk. Shrader & Owen-Smith (2002) termed this the 'buddy system' and while it provides possible advantages for subadults, the question that arises is: what do adult females gain from being in these groups? If adult females tolerate the presence of subadults, it is intuitive to expect there to be some benefit from their presence or at least no cost. A potential explanation is that while in a group these females are able to reduce their vigilance and thus spend more time performing

other activities such as feeding (Pulliam 1973; Lima 1995; Ale & Brown 2007).

Generally, there is an inverse relationship between group size and individual vigilance (i.e. the group size effect; Lima 1995; Roberts 1996; Burger *et al.* 2000). This relationship can be attributed to two causes. First, if predators randomly select the individuals they attack, then predation risk is reduced by dilution as group size increases (Foster & Treherne 1981). Second, if group members do not scan for danger simultaneously, individuals can reduce their vigilance without reducing the overall group vigilance (Lima & Dill 1990; Roberts 1996).

Adult megaherbivores (i.e. herbivores >1000 kg), including white rhinos, generally do not have many predators (Owen-Smith 1988). However, lions (*Panthera leo*) and spotted hyaenas (*Crocuta crocuta*) may prey upon young megaherbivores (Owen-Smith 1973; Brain *et al.* 1999; Salnicki *et al.* 2001; Loveridge *et al.* 2006). Within the Hluhluwe-iMfolozi Park, South Africa, predation on white rhinos is low (Owen-Smith 1973). While lions can kill a 3–4-year old black rhino (*Diceros bicornis*) (~800–1000 kg; Brain *et al.* 1999), they are not typically able to kill healthy, adult white rhinos (~1600–2300 kg; Owen-Smith 1973). Likewise, spotted hyaenas are usually only successful in bringing down young or weak white rhinos (Owen-Smith 1973).

As predation risk is then higher for young megaherbivores, it may not be beneficial for a white rhino mother to reduce her vigilance as group size increases. If a mother maintained high vigilance levels, she may be better able to detect potential predators and thus better defend her calf. Furthermore, in situations when white rhinos flee from predators, calves run in front of their mothers (Owen-Smith 1973). Early detection would allow the mother to direct the calf away from danger and quickly position herself between the predator and her calf.

The aim of our study was to determine whether forming groups with subadult 'buddies' decreased the vigilance levels of white rhino mothers. If so, this would indicate a benefit of group formation for adult females. However, if mothers remain vigilant despite changes in group size, this would indicate that they rely more heavily on their own vigilance to detect potential predators. This would then exclude reduced individual vigilance as an evolutionary driver of group formation in white rhinos.

METHODS

Study site

We collected data in December 2009 and 2010 in the ~600 km^2 iMfolozi portion of the Hluhluwe-iMfolozi Park (HIP), in KwaZulu-Natal, South Africa (28°20′S, 31°51′E). During the study, the white rhino population in HIP comprised approximately 1900 individuals (Ezemvelo KZN Wildlife, unpubl. data). Potential predators of white rhino calves in the park included lions and spotted hyaenas (Owen-Smith 1973), of which there were approximately 70 and 350, respectively (Ezemvelo KZN Wildlife, unpubl. data).

Data collection

We observed white rhinos in the early morning and late afternoon when they were most active (Owen-Smith 1973). We did not collect data on rainy or windy days, as these conditions likely make it more difficult for the rhinos to detect predators and thus result in them increasing their vigilance levels. To locate white rhino groups, we drove along the network of roads within the park but did not follow a set route. All the observations were made in savanna grasslands where grass was >30 cm in height to reduce the influence of habitat. As we were focusing on the benefits of group living to mothers, we restricted our observations to groups that included a mother and her calf. These groups could be limited to two members (i.e. only a mother and her calf), or the group could comprise a mother and her calf and any number of subadult buddies (i.e. 1–5 subabults). We limited our observations to one per female, which allowed us to avoid pseudo-replication. To prevent multiple measurements being taken from the same individual, we identified all adult females by horn shape and size and any notches or tears in their ears.

In an attempt to limit disturbance of the groups, we observed them from a vehicle at a distance of approximately 100–500 m using binoculars (8 × 48) or a spotting scope (×20–60 magnification). For each group we recorded group size and the age (e.g. adult, subadult, calf; Hillman-Smith *et al.* 1986) and sex of all individuals. In addition, we categorized calves into different age classes (i.e. 0–3 months, 4 months to 1 year, 1–2 years, 2–3.5 years) based on their body size in relation to their mother (Hillman-Smith *et al.* 1986). To determine vigilance levels, we recorded the amount of time the mother was vigilant over a 300-second sampling period while she fed.
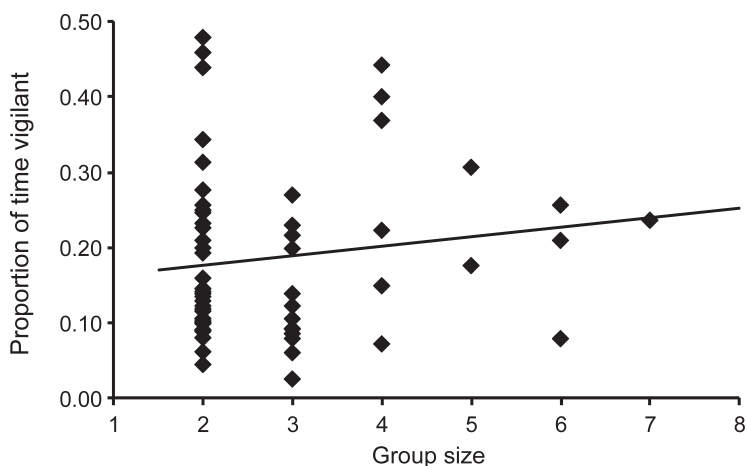
Fig. 1. Proportion of time white rhino mothers in the Hluhluwe-iMfolozi Park were vigilant with regard increasing group size (*n* = 65 groups). We calculated the proportion of time vigilant for each mother during separate observations lasting 300 seconds.

White rhinos have poor vision and rely heavily on their hearing and sense of smell (Owen-Smith 1973). Therefore, we did not define vigilance solely as head raised above shoulder level, as is typical in other studies (e.g. Frid 1997; Burger *et al.* 2000; Childress & Lung 2003; Fortin *et al.* 2004). Our definition of vigilance included 1) head fully raised and scanning, 2) head raised slightly and feeding stopped (i.e. biting and chewing), and 3) feeding, but with both ears focused forward. We considered this last category as vigilance as when a white rhino is startled, attentive or scanning (i.e. as in the other two vigilance categories), they focus their ears forward (Owen-Smith 1973). As mothers did not demonstrate all three forms of vigilance in each 300-second observation, we combined the times spent performing any of these vigilance behaviours into a single measure of vigilance.

Data analysis

We used linear regression to determine how group size affected the time white rhino mothers were vigilant (measured as a proportion of seconds vigilant during the 300-second sample). To explore the wide variance in vigilance levels we then limited our focus to mother–calf groups (*n* = 39) and ran a two-way ANOVA to determine whether the age (0–3 months, 4 months to 1 year, 1–2 years, 2–3.5 years) or sex (male, female) of a calf explained the mothers' vigilance levels. We did this as the small sample size of groups greater than or equal to four (*n* = 13) did not allow us to statistically assess the effect of age and sex across all the differ-

ent group sizes. The small sample sizes for these larger groups are not surprising, as despite the propensity for white rhinos to form groups, they generally do not form large ones (Owen-Smith 1988; Shrader & Owen-Smith 2002). Prior to analysis, we arcsine-transformed the proportions. We used Systat 13 for all analyses.

RESULTS

We sampled 65 different white rhino groups that comprised 181 individuals. These groups ranged from two to seven members. However, 60% of the groups (*n* = 39) consisted of only a mother and her calf (Fig. 1). When we tested the effect of group size on the mothers' vigilance we found that, contrary to the group size hypothesis, mothers did not decrease their vigilance levels as group size increased (slope = 0.085, intercept = 2.147, $F_{1,63}$ = 1.45, *P* = 0.233, R^2 = 0.007; Fig. 1).

Throughout our study, white rhino mothers were vigilant on average for 19% of the time they spent feeding. However, vigilance levels varied within the different group size categories with two members ranging from 5–48% (*n* = 39), three members 3–27% (*n* = 13), four members 7–44% (*n* = 6), five members 18–31% (*n* = 3), and six members 8–26% (*n* = 3) (Fig. 1). To try and explain the wide variance of vigilance levels within groups, we focused our analysis on the larger sample of mother-calf groups (*n* = 39). We found that neither the age ($F_{3,26}$ = 1.014, *P* = 0.402) or sex ($F_{1,26}$ = 0.020, *P* = 0.888) of the calf, nor the interaction of age and sex ($F_{3,26}$ = 0.766, *P* = 0.523) explained the range of vigilance levels shown by white rhino mothers.

DISCUSSION

Results of our study indicate that, in contrast to the group size hypothesis (Lima 1995; Roberts 1996), vigilance of white rhino mothers was not affected by the subadult 'buddies' increasing group size. This seems somewhat surprising based on the large number of studies on other species that have recorded a reduction in individual vigilance as groups get larger (see Elgar 1989; Roberts 1996; Fairbanks & Dobson 2007; Rieucau & Martin 2008 for examples). However, our findings are similar to other studies where mothers were found not to adjust their vigilance levels with regard to changes in group size. For example, elk (*Cervus elaphus*) mothers in Yellowstone National Park, U.S.A., did not lower their vigilance as group size increased (Childress & Lung 2003). Laundré *et al.* (2001) found that after the reintroduction of wolves (*Canis lupus*) to Yellowstone National Park, elk mothers had higher vigilance levels than non-mothers and adult males. For several species of African herbivores covering a wide range of body sizes, the largest being the African elephant (*Loxodonta africana*), Burger & Gochfeld (1994) found that mothers were more vigilant than non-mothers.

It is likely, therefore, that mothers living in groups do not reduce their vigilance as they are trying to increase the survival of their naïve offspring (Rieucau & Martin 2008). Individuals that are the first to detect danger generally have a higher chance of survival (Lima & Zollner 1996). As a result, mothers that remain vigilant are more likely to detect threats and thus be able to warn and protect their offspring. This in turn would increase their overall fitness.

The large variation in the mothers' vigilance levels within the different groups, however, is intriguing. We felt that the most likely explanation would be differences in calf age and/or sex. The reason being is that one might expect that younger, naïve calves would be at greater risk and thus require greater levels of vigilance from their mothers compared to older calves. In addition, as has been recorded for elephants (Moss 1988), male calves may be more inquisitive and move further away from their mothers than female calves. As a result, they would likely experience greater predation risk. We, however, did not find support for either of these hypotheses and thus they did not explain the variability in vigilance levels.

Variability of within-group vigilance levels might have been the result of a variable that we did not record. For example, it may be due to the age of the mothers rather than the calves. This would be interesting to explore, but accurate aging of adult white rhinos cannot be done visually (Hillman-Smith *et al.* 1986). In addition, it could also be due to individual differences in detection ability. These differences may be linked to age, but the ability to determine this is beyond the experimental design. The influence of habitat variation was avoided by the rhinos foraging primarily in savanna grasslands with grass <30 cm in height, and thus the observations were limited to this one habitat. Finally, variability in vigilance levels within the different group sizes may have been due to olfactory cues picked up by the rhinos while we were observing them. We are unable, however, to determine whether this was the case. Ultimately, the key finding is that we recorded a high variability in the mothers' vigilance levels in each of the different group sizes irrespective of sample size. As a result, we feel confident that the lack of change in vigilance levels with regard to group size reflects the variability in the mothers' vigilance levels and is not purely an artefact of the different sample sizes.

A second possible explanation of why white rhino mothers did not reduce their vigilance levels with increasing group size is that white rhino groups tend to be temporary (Owen-Smith 1988; Shrader & Owen-Smith 2002). Ultimately, this can result in daily changes in group numbers of between two to seven members. As a result, white rhino mothers may not have a consistent number of group members throughout the day and therefore it is adaptive to maintain similar vigilance levels irrespective of the size of the group that has formed around them.

If, therefore, a reduction in individual vigilance is not a benefit of group formation for white rhino mothers, then why should they live in groups? One possibility is lower predation risk via an increased dilution effect. Generally, as group size increases, dilution of predation risk becomes more effective (Dehn 1990; Beauchamp & Ruxton 2007; 2008). However, with megaherbivores, the young are the ones primarily attacked by predators (Owen-Smith 1973; Brain *et al.* 1999; Salnicki *et al.* 2001; Loveridge *et al.* 2006). As a result, mothers would benefit the most from forming groups as they would be able to dilute predation risk for their calves. However, white rhino mothers do not form groups with other mothers (Owen-Smith 1988; Shrader & Owen-Smith 2002) so there is

unlikely to be more than one calf in any group. Thus, with increasing group size, the dilution effect of the single calf would not change. In addition, mothers probably rely more heavily on predator detection, rather than dilution of risk (Pulliam 1973) to protect their offspring. This would be adaptive, as allowing a naïve calf to form part of the dilution effect could increase its predation risk (Rieucau & Martin 2008). As a result, it is unlikely that dilution reduces predation risk for calves or ultimately increases fitness for white rhino mothers.

Increased dilution, however, is not the only potential benefit of group formation. A more likely factor that would increase calf survival in white rhinos is increased predator defence (Caro *et al*. 2004). Rhinos are large animals with formidable horns. To maximize group defence, they form a rump-to-rump defensive posture when threatened (Owen-Smith 1973), the effectiveness of which is likely to increase with increasing group size. Although it seems intuitive this could then lead to higher calf survival through harassment of potential predators. However, white rhino mothers generally do not form groups when their calves are less than 3 months old and at their most vulnerable to predation (Owen-Smith 1988). This is not to say that older calves (e.g. ≥4 months) would not benefit from increased predator defence, but as groups are not permanent these benefits would be sporadic.

Alternatively, there may simply be no costs to adult females living in groups and hence no selection for mothers to avoid group formation. Female white rhinos do not hold exclusive home ranges or try to defend food resources in these large ranges (~20 km^2; Owen-Smith 1988). A key reason for this is that white rhinos are large grazers that can tolerate a wide range of food qualities (Shrader *et al*. 2006). Thus, there will generally be more food available in a female's home range than can be eaten by her and her calf. This, linked with their ability to tolerate a wide range of food types, makes it unlikely that increased group size will significantly reduce food intake via interference competition.

In conclusion, our findings suggest that reduced vigilance is not a benefit that white rhino mothers gain from living in groups, and thus is not the key evolutionary driver of group formation in the species. Furthermore, the periodic benefit of increased predator protection for their calves is also unlikely to be a key factor. Moreover, as only 40% of the mothers were in found in groups of >2

individuals, this further suggests a potential lack of benefit to group living for mothers. Yet, for mothers living in groups, there seems to be no cost in being a part of these groups. Shrader & Owen-Smith (2002) showed that white rhino subadults greatly benefit from group living through exposure to novel areas, increased protection from territorial males and potentially reduced predation risk. These benefits, coupled with the lack of costs to mothers, suggest that the benefits accrued by subadults are the most likely drivers behind the evolution of group formation in white rhinos. Thus, we suggest that when exploring group formation and maintenance in different taxa, it is important to consider not only differing adaptive benefits of all group members but also the lack of costs to some of these individuals.

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