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Interactions among social monitoring, anti-predator vigilance and group size in eastern grey kangaroos

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Group size is known to affect both the amount of time that prey animals spend in vigilance and the degree to which the vigilance of group members is synchronized. However, the variation in group-size effects reported in the literature is not yet understood. Prey animals exhibit vigilance both to protect themselves against predators and to monitor other group members, and both forms of vigilance presumably influence group-size effects on vigilance. However, our understanding of the patterns of individual investment underlying the time sharing between anti-predator and social vigilance is still limited. We studied patterns of variation in individual vigilance and the synchronization of vigilance with group size in a wild population of eastern grey kangaroos (*Macropus giganteus*) subject to predation, in particular focusing on peripheral females because we expected that they would exhibit both social and anti-predator vigilance. There was no global effect of group size on individual vigilance. The lack of group-size effect was the result of two compensating effects. The proportion of time individuals spent looking at other group members increased, whereas the proportion of time they spent scanning the environment decreased with group size; as a result, overall vigilance levels did not change with group size. Moreover, a degree of synchrony of vigilance occurred within groups and that degree increased with the proportion of vigilance time peripheral females spent in anti-predator vigilance. Our results highlight the crucial roles of both social and anti-predator components of vigilance in the understanding of the relationship between group size and vigilance, as well as in the synchronization of vigilance among group members.

Keywords: vigilance; anti-predator behaviour; social monitoring; synchronization; group living; eastern grey kangaroo

1. INTRODUCTION

Several adaptive functions are generally ascribed to vigilance in groups of animals subject to predation, including predator detection (Bednekoff & Lima 1998*a*) and gaining information from other group members to limit competition (Tchabovsky *et al*. 2001), acquire information about food patches, avoid aggression or look for mates (Beauchamp 2001). Indeed, numerous factors have been reported to influence vigilance activity in group-forming prey species (Treves 2000). Some of these are directly related to group dynamics (such as group size, position of the individual within the group and inter-individual distances; Fernández-Juricic *et al.* 2007), others to individuals' characteristics (such as age–sex class and reproductive status; Lung & Childress 2006) and others to the environment in which prey live (such as predation risk, distance to cover and characteristics of food resources; McNamara & Huston 1986; Roth *et al*. 2006).

Thus, social and environmental factors both influence vigilance activity and two kinds of vigilance occur: anti-predator vigilance during which individuals scan for predators and other sources of danger, and social vigilance during which individuals look at other group members. However, because of incompatibility between vigilance and investment in other activities such as foraging, reproduction or other social interactions, prey have to trade off between vigilance against predators, monitoring other group members and resource acquisition (Sirot & Touzalin 2009). Anti-predator vigilance has been most investigated because of its direct contribution to the adaptiveness of group living. The risk to individuals of predation may be reduced in large groups as a result of dilution (Bednekoff & Lima 1998*b*). In addition, an individual can benefit from an increase in group size by reducing its own rate of vigilance, thus increasing its time available for feeding, without reducing the group's probability of detecting potential danger (Ale & Brown 2007). The decrease in individuals' vigilance with increasing group size has been extensively supported by studies in both birds and mammals (Lima 1995*a*; Fairbank & Dobson 2007). However, a few studies have shown an increase in individual vigilance with group size (Robinette & Ha 2001), while others did not detect any group-size effect on vigilance (Jones 1998), in particular in primates (Rose & Fedigan 1995; Treves *et al.* 2001). This variation in group-size effects on vigilance is not understood.

Treves (1999) proposed that vigilance may sometimes not decrease with group size because of social vigilance. The time spent monitoring other group members would

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tend to increase with group size because the number of interactions among individuals is expected to increase when group size increases. However, this hypothesis remains mostly untested with empirical data quantifying both the anti-predator and social components of vigilance. Our understanding of how prey invest in each component of vigilance in the context of group living, how this investment is affected by group size and finally how the benefits of predator detection in larger groups are balanced by increasing costs of social vigilance due to increased competition still remains limited.

Competition for access to food, assessment of food quality, reproduction, territoriality and kleptoparasitism can all cause prey to spend time monitoring conspecifics (Valone & Templeton 2002). Social vigilance has been investigated in birds and mammals including primates (Robinette & Ha 2001; Kutsukake 2006). Social vigilance can also be advantageous if it allows individuals to gain information on the level of predation risk (Ellard & Byers 2005); animals might adjust their own vigilance in response to information gained from other group members' behaviours; for example through vigilance postures; flight or alarm calls (Lima 1995*a*,*b*).

Several studies on both birds and mammals have shown that individuals scan somewhat synchronously (Ebensperger *et al.* 2006; Beauchamp 2009). Ruxton & Roberts (1999) argued that, even if group members act independently of one another, we might expect synchronization of vigilant acts of group members when, for instance, a potential danger, acting as an extra-group synchronizer, has been detected by each individual at the same time. Thus, stimuli that motivate individuals to raise their heads, whether environmental or social, can trigger synchrony among group members, producing temporal clustering of scanning by group members. It has been shown that a vigilant act performed by one group member can affect the vigilance activity of other group members and the probability of an individual being vigilant can depend on other group members' activities (Fernández-Juricic *et al.* 2004*a*; Jackson & Ruxton 2006). The decision of an individual to adopt a vigilant posture seems to depend largely on what it and other group members were doing (i.e. scanning or foraging) just previously and on group size (Pays *et al.* 2009*a*). Thus vigilance in a group can be contagious, as a result of an adaptive response to the vigilance of companions, and an individual's decision to be vigilant might be partly independent of the real level of risk in the environment (Sirot & Touzalin 2009; see also Giraldeau *et al.* 2002). Therefore, we might expect that both the environmental and social components of vigilance play key roles in the mechanisms generating synchronization of vigilance within groups, but this has not yet been investigated in any species.

We studied a population of the eastern grey kangaroo (*Macropus giganteus*), a wild herbivorous marsupial subject to predation, to investigate how group size affects patterns of anti-predator and social vigilance. As the eastern grey kangaroo is one of the most social of the macropodid species, its vigilance is strongly expected to have both anti-predator and social functions. Some previous studies of this species have reported that individual vigilance decreased with group size (Jarman 1987; Pays *et al.* 2007) whereas others did not detect any significant variation (Colagross & Cockburn 1993); these studies did not distinguish environmental from social vigilance. Thus, we tested first whether overall individual vigilance in our population decreased with group size (as predicted by Pulliam's 1973 model). Second, we tested Treves's (1999) suggestion that while anti-predator vigilance should decrease with group size, social vigilance should show the opposite pattern. Third, as we know that individual kangaroos tend to synchronize their bouts of vigilance activity (Pays *et al.* 2007), we investigated whether the degree of synchrony was affected by the relative amounts of time that individuals spent in social versus anti-predator vigilance, while controlling for group size. We show that group-size effects on vigilance cannot be understood without analysis of both anti-predator and social vigilance.

2. MATERIAL AND METHODS

(a) *Study area and animals*

Fieldwork was carried out in Sundown National Park (Queensland, Australia; 28°9′ S, 151°58′ E) in January–March 2009, during summer. The study area is composed of a mosaic of eucalypt forest, woodland and open pastures of predominantly native species. We recorded behavioural sequences early in the morning (05.30–07.30) and late in the afternoon (17.00–19.00) when animals came onto the pasture to forage; kangaroos sleep during the other daylight hours. Animals were not marked for individual recognition. Groups of eastern grey kangaroos are known to split up and merge frequently and are described as open-membership groups. The study area contained over 150 kangaroos. Predators of kangaroos in the study area included red foxes (*Vulpes vulpes*), wedge-tailed eagles (*Aquila audax*) and occasional dogs, with foxes being threats mainly to juvenile kangaroos. The kangaroos may occasionally be exposed to dingos (*Canis lupus dingo*), as well.

(b) *Recording data*

We collected behavioural data by videotaping (video camera Sony DCR-HC51E, optical zoom × 40) all members of a focal group of kangaroos for a 5 min period (see the electronic supplementary material, appendix A, for details). All group members were in the camera's field of view during sampling. To characterize behaviour, we considered an animal as vigilant when it did not move its feet and raised its head above horizontal, scanning its surroundings. No ambiguities were encountered in distinguishing vigilant from non-vigilant animals. We considered a group as kangaroos who maintained social and spatial cohesion during focal sampling and whose most peripheral associate was within 15 m of another group member (Jarman 1987). No ambiguities in determining group membership were encountered in the sampled groups.

When the observer filmed a group, he recorded group size, sex of individuals, presence of young-at-foot (but see the electronic supplementary material, appendix A for more details), time of day (morning or afternoon), wind strength (none, low, medium), cloud cover (cloudy, sunny), habitat type (completely open pasture with short grass, open pasture with several trees, bushy pasture), distance to cover (0–25, 26–50, 51–100, 101–200, more than 200 m) and position of the individuals within the group (peripheral, central, mixed—'mixed' refers to individuals that moved between peripheral and central positions during the 5 min sequence). During the video sequences, group members did not exhibit apparent inter-individual interference and/or aggression, as would be expected if there was competition for access to food.

For analysis, video sequences were converted to analytic sequences. For each individual, a binary sequence (0 = foraging activity and 1 = vigilance activity) was constructed reflecting its activity state precisely at each second for 300 s. We recorded the activity (vigilance and foraging) of each group member at precisely the same time, and were therefore able to investigate individual and group patterns of vigilance using the methods described below.

We determined whether an individual exhibited an anti-predator or social act of vigilance based on articles quantifying the field of view of mammal species including macropods (Heesy 2004; Changizi & Shimojo 2008) and using head orientation (and thus the gaze direction) to determine the target of individuals' visual attention (Fernández-Juricic *et al.* 2004*a*,*b*; Quirici *et al.* 2008). We considered an individual to exhibit an anti-predator vigilant act when it scanned in a direction away from group members and a social vigilant act when it looked at group members. Using head orientation, we did not have any difficulty characterizing acts of vigilance as anti-predator or social acts. An individual could engage successively in both anti-predator and social vigilance during a bout of vigilance; in that case, the durations of each type of vigilance were recorded.

As we were interested in factors influencing the head orientation of vigilant individuals we used only a subset of individuals in the groups that we sampled to control for the effects of potential confounding factors. (i) As it has already been reported that sex affects vigilance in the eastern grey kangaroo, only females were taken into account. Pays & Jarman (2008) reported that females were individually more vigilant than males, but that their vigilance rate was unaffected by the presence of males and group vigilance did not differ between female-only and mixed-sex groups of the same size. (ii) Theory assumes that vulnerability to predation differs between central and peripheral individuals (Hamilton 1971) and thus perception of predation risk might differ between the two positions. In addition, distinguishing social from anti-predator vigilance was more accurate for peripheral animals; thus, we considered only peripheral females. (iii) We analysed only groups of at least three individuals (see the electronic supplementary material, appendix A, for more details) and considered peripheral individuals that were facing out from the group to be exhibiting anti-predator vigilance, while peripheral individuals facing into the group were assumed to be showing social vigilance. We only sampled relatively immobile groups in which individuals stayed in the same locations during the video sequences. Using these criteria, we used data from 139 females.

(c) *Data analyses*

From the analytical sequences of the 139 sampled peripheral females, times spent in all vigilance combined, anti-predator vigilance (scanning in a direction away from group members) and social vigilance (looking at group members) were recorded. We then calculated for each female the proportion of total time spent vigilant, the proportions of time spent in anti-predator and social vigilance, and the proportion of total vigilance time spent in social vigilance. For this last proportion, a value of 0.5 indicated that individuals spent similar times in social and anti-predator vigilance. We investigated the relationships between group size and these proportions using linear mixed-effects models fitted by restricted maximum likelihood, including group identity as a random effect. We included other independent variables in the models to control for the effects of time of day, wind strength, cloud cover, habitat type and distance to cover. For the assumptions of normality and homoscedasticity to be fulfilled, proportions were logit transformed (Pays *et al.* 2007).

To investigate whether the relative proportions of anti-predator and social vigilance and group size affected the patterning of collective vigilance, we used a method that we have already described in a previous study (Pays *et al.* 2009*b*). Therefore we only summarize it here. For each observed group, we calculated a Pearson's correlation coefficient between the binary sequences (0 for non-vigilant and 1 for foraging) of each possible pair of individuals within the group. We then calculated the mean of the pairwise correlation coefficients for each observed group and compared this mean with the zero value expected under the assumption that individuals scan independently of one another (value also shown by simulations; see Pays *et al.* 2007) using a Wilcoxon t-test for paired samples. If individuals tended to be vigilant independently of one another, the observed values would not be statistically different from zero. If individuals tended to coordinate their vigilance in non-overlapping bouts, the observed coefficients would be significantly lower than zero, whereas if individuals tended to synchronize their vigilant bouts, the observed coefficients would be significantly greater than zero.

The proportion of the total vigilance time that was spent in anti-predator vigilance was calculated for 139 sampled females in peripheral positions in 75 groups. We then tested for the effect of the mean proportion of vigilance time spent in anti-predator vigilance on the mean correlation coefficient values (the degree of synchrony among the members of each group) in groups that showed synchrony, controlling for group size. For the assumptions of normality and homoscedasticity to be fulfilled, we applied a Fisher's z transformation $\tanh^{-1}(x)$ (inverse hyperbolic tangent; David 1949) to the correlation coefficients (x).

Statistical analyses were computed with R software (R Development Core Team 2007).

3. RESULTS

(a) *Individual vigilance*

Controlling for the effects of time of day, wind strength, cloud cover, habitat type, distance to cover and position of individuals within groups, linear mixed effects models revealed no significant effect of group size on the proportion of total time peripheral females spent in vigilance ($F_{1,62} = 0.224$, $p = 0.638$; figure 1*a*; see the electronic supplementary material, appendix B). However, females decreased their time devoted to anti-predator vigilance (coef. ± s.e. = -0.092 ± 0.054, $F_{1,72} = 3.970$, $p = 0.051$; figure 1*b*; see the electronic supplementary material, appendix C) and increased their time exhibiting social vigilance as group size increased (coef. ± s.e. = 0.081 ± 0.040, $F_{1,73} < 0.001$, $p = 0.046$; figure 1*c*; see the electronic supplementary material, appendix D).

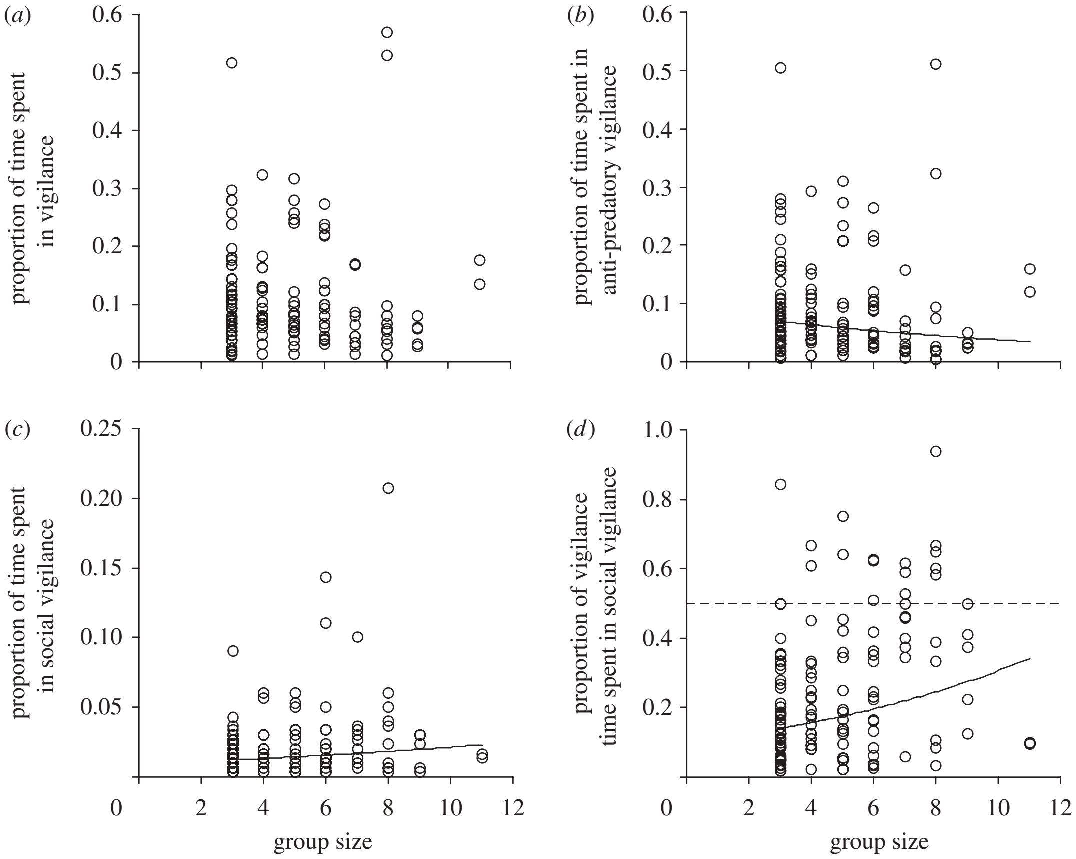

Figure 1. Effects of group size on the proportions of total time that peripheral females spent in (*a*) all vigilance, (*b*) anti-predator vigilance and (*c*) social vigilance, and (*d*) on the proportion of their total vigilance time that they spent in social vigilance. The dotted line shows where the proportion of time spent in social and anti-predatory vigilance are equal.

The mean proportion of total vigilance time spent in social vigilance was 0.25 for peripheral females, indicating that on average peripheral females spent significantly more of their vigilance time in anti-predator than social vigilance (Wilcoxon *t*-test for paired samples: $t = 9492.5$, $n = 139$, $p < 0.001$). Moreover, after controlling for the effects of time of day, wind strength, cloud cover, habitat type and distance to cover, a linear mixed effects model showed that group size significantly affected that proportion ($F_{1,73} = 8.319$, $p = 0.005$; figure 1*d*; see the electronic supplementary material, appendix E). According to the sign derived for the effect of the proportion of total vigilance time spent in social vigilance (0.163 ± 0.057), individuals tended to decrease the proportion of vigilance time that they allocated to anti-predator vigilance in favour of time spent looking at group members as group size increased.

(b) *Collective pattern of vigilance*

The means of the correlation coefficients within groups (mean ± s.e. = 0.043 ± 0.143) were significantly higher than the expected ones under the assumption that individuals scanned independently of one another (Wilcoxon *t*-test for paired samples: $t = 110\,306$, $n = 606$, $p < 0.001$), showing that bouts of vigilance were more synchronous within groups than expected. Forty-eight groups (i.e. 65%) had mean correlation coefficients more than 0. We tested for effects of the mean proportion of vigilance time that peripheral females spent in anti-predator vigilance and group size on the degree of synchrony for those 48 groups using a linear fixed effect model. Backward selection showed that the degree of synchrony increased with the proportion of total vigilance time spent in anti-predator vigilance (coef. ± s.e. = 0.18 ± 0.07, $F_{1,47} = 7.429$, $p = 0.009$) but was not affected by group size ($F_{1,46} = 0.082$, $p = 0.776$).

4. DISCUSSION

In our population the proportion of time peripheral females spent looking at other group members increased with group size whereas the proportion of time they spent scanning the environment decreased as group size increased; as a result overall vigilance levels did not change with group size. This result supports Treves's (1999) suggestion that group living allows individuals of prey species to reduce the time they spend on predator detection, as suggested by Pulliam (1973), but also causes individuals to increase time spent monitoring other group members (Hisch 2002). Such an increase in individual vigilance with group size might allow group members to gain information to limit competition for food or avoid kleptoparasitism, but also might be important for reproduction and territoriality (Smith *et al.*1999; Beauchamp 2001). Our results show that this social component of vigilance is crucial to understanding the individual investment allocated to vigilance and whether, vigilance varies with group size in a particular population (and, if so, why). If populations differ in their risk of predation (for instance the occurrence or density of dingoes), habitat structure (for instance habitat openness) or food availability, the importance of anti-predator vigilance and the cost of vigilance in terms of lost feeding time might vary (Butler *et al.* 1995; Roth *et al.* 2006), causing the intensity of the group-size effect to vary also. These kinds of differences among populations might explain why some previous studies have reported significant group-size effects on individual vigilance in eastern grey kangaroos (Jarman 1987), while other studies have not found these (Colagross & Cockburn 1993). Changes in the availability of oestrous females and other social factors would affect social vigilance. Future studies should investigate inter-population variation in the group-size effect by quantifying environmental and social factors that might contribute to the understanding of why some populations of kangaroos exhibit a group-size effect on vigilance and others do not.

We have shown that social and environmental factors both influence the individual decisions of an individual about vigilance. Although social monitoring and predator detection can sometimes be done concurrently, the time trade-offs associated with vigilance behaviour in our study seemed to be mostly driven by anti-predator scanning in peripheral kangaroos, since we found that peripheral animals faced out from the group during most of their vigilance time. This result contrasts with the finding that the vigilance behaviour of brown capuchin monkeys (*Cebus apella*) was dramatically affected by social monitoring as the number of neighbours was the main factor influencing individual vigilance (Hisch 2002). However, we focused on the vigilance of peripheral females, and peripheral animals are expected to be more exposed to predation than central animals, and thus might spend more time than central animals in anti-predator vigilance.

The time that peripheral female kangaroos devoted to social vigilance was lower than for anti-predator vigilance for all except perhaps the largest-sized groups, but the time spent monitoring other group members increased with group size, agreeing with other studies (Hisch 2002). We did not investigate vigilance activity in groups of over 11 kangaroos because of methodological constraints; such large groups were difficult to find in the study area and it was not possible to keep all members of such large groups in the camera's field of view for 5 min. However, we expect that in such large groups, social vigilance would surpass anti-predator vigilance. It would be interesting to investigate the trade-offs between the two components of vigilance in large groups and test the hypothesis that the costs of social vigilance would be very high in such groups compared with the advantages of the dilution of risk and collective detection. This hypothesis predicts that individuals might leave large groups for smaller ones in which vigilance trade-offs would be more advantageous. The vigilance trade-offs are also expected to differ for peripheral versus central individuals. Individuals in the centre of groups would be expected to show higher levels of social vigilance; we did not study such individuals because of the difficulty of distinguishing social from anti-predator vigilance in central animals.

We found that the degree of synchrony among group members in bouts of vigilance increased with the proportion of their total vigilance time that peripheral individuals spent in anti-predator vigilance. Individuals surrounded by neighbours displaying high levels of vigilance may perceive a high predation risk, through the process of social information transfer, and respond by increasing their own vigilance, even if no predator is present (Sirot 2006). Thus we suggest that the time that an individual spends scanning the environment would be perceived as a signal of potential danger by other companions (FitzGibbon 1989, 1990), who would react by showing the same behaviour through a copying phenomenon. Several authors studying bird flocks under attack have recorded that, if an individual fleeing because it has detected a predator communicates this information to its groupmates, this triggers an immediate departure of other birds in a few seconds, increasing their chance of escaping (Hilton *et al.* 1999; Cresswell *et al.* 2000; Quinn & Cresswell 2005). Thus individuals are able to use the behaviours of other group members to estimate the intensity of a threat, as well as its location (Ellard & Byers 2005). This result also suggests that individual kangaroos are often aware of whether particular groupmates are scanning the environment for danger or watching other individuals, or are at least maintaining awareness of the direction in which peripheral individuals are facing.

We used head orientation to determine whether an individual exhibited an anti-predator or a social act of vigilance. Although we based our procedures on knowledge of angles of vision in mammals, and other researchers have used head orientation (and thus the direction of gaze) in mammals and birds to determine the target of individuals' visual attention (see §2), we cannot be absolutely certain of kangaroos' perception and field of view. In any case, in certain situations individuals are surely able to be both environmentally and socially vigilant at the same time; for example, by looking at a neighbour while being attentive to the environment beyond that neighbour. Thus, the two components of vigilance (monitoring group members and scanning the environment) are not necessarily mutually exclusive. It would be interesting to conduct experimental studies manipulating social, ecological and spatial factors to determine which factors lead individuals to adjust the time they devote to anti-predator vigilance versus social monitoring.

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