

Does sex affect both individual and collective vigilance in social mammalian herbivores: the case of the eastern grey kangaroo?

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Abstract In several vertebrate taxa, males and females differ in the proportions of time they individually devote to vigilance, commonly attributed to sex differences in intra-specific competition or in absolute energy requirements. However, an effect of sex on collective vigilance is less often studied (and therefore rarely predicted), despite being relevant to any consideration of the adaptiveness of mixed- vs single-sex grouping. Controlling for group size, we studied the effect of sex on vigilance in the sexually dimorphic eastern grey kangaroo *Macropus giganteus*, analysing vigilance at two structural levels: individual vigilance and the group's collective vigilance. Knowing that group members in this species tend to synchronise their bouts of vigilance, we tested (for the first time) whether sex affects the degree of synchrony between group members.

We found that females were individually more vigilant than males and that their vigilance rate was unaffected by the presence of males. Collective vigilance did not differ between female-only and mixed-sex groups of the same size. Vigilance in mixed-sex groups was neither more nor less synchronous than in single-sex groups of females, and the presence of males seemed not to affect the degree of synchrony between females. Sixty-six percent of vigilant acts were unique (performed when no other kangaroo was alert), and only about one unique vigilant act in every three induced a collective wave of vigilance. The proportions of vigilant acts that were unique were 60% for females but only 46% for males. However, the sexes differed little in the rates at which their unique vigilant acts were copied. This limited study shows that the differences in vigilance between male and female kangaroos had no discernible effect upon collective vigilance.

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Introduction

In prey species, vigilance activity within an aggregation is classically viewed as conferring protection against predators (Elgar 1989; Lima 1987; Roberts 1996), and this property has been demonstrated in numerous theoretical and empirical studies (see Bednekoff and Lima 1998; Treves 2000). Although vigilance against predators has been extensively investigated (Beauchamp 2001), a range of additional factors can also influence individual proportion of time spent scanning. A general difference in vigilance between males and females has been described in several mammal taxa.

Males have been reported to be more vigilant than females in a wide range of primate species (Cheney and Seyfarth 1981; Boinski 1988; van Schaik and van Noordwijk 1989; Fragaszy 1990; Koenig 1998; Buchanan-Smith 1999; Steenbeek et al. 1999), and in ungulate species such as African buffalo *Syncerus caffer* (Prins and Iason 1989), Burchell's zebra *Equus burchelli*, blue wildebeest *Connochaetes taurinus*, waterbuck *Kobus defassa* (Burger and Gochfeld 1994) and springbok *Antidorcas marsupialis* (Burger et al. 2000). This general apparent tendency is not, however, shown consistently by all studied mammal species. In giraffe *Giraffa camelopardalis*, males were more vigilant than females during the wet season in all occupied habitats, but females were the more vigilant sex during the dry season (Ginnett and Demment 1997). Burger and Gochfeld (1994) did not observe sex differences in the amount of time spent in vigilance in African elephant *Loxodonta africana*, kob *Kobus kob* and impala *Aepyceros melampus*, nor did Ebensperger et al. (2006) in degu (*Octodon degus*), nor Smith et al. (2004) in wild mixed-species troops of primates. Similarly, although male birds usually have higher proportions of time spent scanning (Bertram 1980; Burger and Gochfeld 1988; Dalhgren 1990), females can also have the higher proportions of time in some species or circumstances (Beveridge and Deang 1987; Waite 1987).

The two hypotheses currently proposed to explain differences in the amount of time spent in vigilance between males and females predict opposite outcomes. The first hypothesis, related to intra-specific competition, suggests that, in gregarious species, direct competition between males (e.g. for territoriality or for access to females) requires them to spend time scanning to assess rivals' presence and activities (Hart et al. 1992; Reboreda and Fernández 1997). Under this assumption, the presence of several adult males in a group would (in addition to anti-predator vigilance) oblige the males to continuously monitor each other (Baldellou and Henry 1992; Rose and Fedigan 1995), in particular if an oestrous female is present. The second hypothesis suggests that the body size difference between the sexes in sexually dimorphic species (as are most medium and large herbivorous mammal species) predicts different absolute energy requirements. All else being equal, larger males would need more time to forage (Clutton-Brock et al. 1982; Illius and Gordon 1992) than smaller females. Furthermore, sex differences in diet selectivity could cause sex differences in foraging bout length (Clutton-Brock et al. 1982). If males spend more time in feeding than females, we would expect in consequence that the proportion of time that males spend in vigilance would be less than that spent by females. However, another possible hypothesis would predict a sex-related difference in the proportion of time an individual spent in scanning the environment as a consequence of

body-size dimorphism and also of responsibility for the safety of dependent young. If females are smaller than males, females might be more vulnerable to predators or disturbance than males. Indeed, larger males might be able to defend themselves actively against attack by predators. Similarly, dependent and vulnerable young might also induce females to be more vigilant than males without such responsibility. Thus, differential vulnerability, either of themselves or their young, might predict that females should be more vigilant than males.

However, predictions concerning a possible sex effect on collective vigilance, i.e. the proportion of time during which at least one individual in the group scans the environment, are less certain because fewer studies have investigated this phenomenon. Collective vigilance is affected by the proportion of time that each group member spends in this activity. So, if individual vigilance is affected by the sex of individuals, as many studies report, we would expect collective vigilance to be affected by the group composition. If males tend to be more vigilant than females, we would expect, for a given group size, to observe a higher rate of collective vigilance in a single-sex group of males than in a mixed-sex group, with a lower rate in a single-sex group of females. However, to predict the vigilance behaviour that a group of individuals should adopt in response to the risk of being preyed upon, most studies of gregarious species have currently adopted two main assumptions, without considering the sex of group members. The first assumption, adopted in most theoretical models of vigilance (e.g. Pulliam 1973; Pulliam et al. 1982; Bednekoff and Lima 1998; Scannell et al. 2001), is that group members scan their environment independently of one another. The second assumption is that, to benefit as much as possible from their respective vigilance activities, group members should coordinate their scans in non-overlapping bouts to avoid being vigilant when another group member is already vigilant (Rodríguez-Gironés and Vásquez 2002, but see Rasa 1989; Bednekoff 1997, 2001; Clutton-Brock et al. 1999 for sentinel behaviour). However, several studies have revealed, contrary to this assumption, a significant degree of synchronisation between group members in their individual vigilance bouts (Lazarus 1979; Bertram 1980; Fernández et al. 2003; Ebensperger et al. 2006). In a functional context, scanning that is independent among group members is considered an optimal solution to the high cost required to organise vigilance through coordination (Bednekoff and Lima 1998). In each collective pattern of vigilance, i.e. independence, coordination or synchronisation of vigilant bouts, it appears necessary to consider the influence of the mix of sexes of group members. Some previous studies have demonstrated that individual vigilance is significantly and positively affected by the presence of neighbours (Blumstein et al. 2001;

Treves et al. 2001; Cameron and du Toit 2005). In contexts where individuals must take account of their neighbours (in coordination or synchronisation of vigilance), we might expect the observed collective pattern of vigilance in groups to be affected by the sex of group members. If direct competition between males requires them to be vigilant to assess rivals' presence and activities (Reboreda and Fernández 1997), social vigilance (in addition to anti-predator vigilance) should increase with the presence of several adult males in a group. Thus, synchronisation of vigilance might be expected in such a context (Rose and Fedigan 1995). However, under a high predation risk, independence of scanning between group members is usually predicted, in particular for animals living in non-persistent groups (Bednekoff and Lima 1998), to achieve a better anti-predator vigilance (with a higher level of collective predator detection) than synchronisation could offer.

We studied vigilance activity in a population of eastern grey kangaroos, *Macropus giganteus*, that still experiences occasional predation. This study was limited in scope and preliminary in nature. It explored whether there is a phenomenon of sex influencing individual and collective vigilance in eastern grey kangaroos, to be explained rather than attempting to provide a full causal investigation of an established phenomenon. First, allowing for a group-size effect, we investigated the effect of an individual's sex on its vigilance, i.e. the time spent by an individual in this activity. Eastern grey kangaroos exhibit pronounced sexual body-size dimorphism (Jarman 1989), males eventually achieving body weights more than double those achieved by adults females, so the sexes might differ in energy requirements or selected dietary items and, thus, given a constrained activity budget, in the time available for vigilance and feeding. So, the energy-requirement hypothesis would predict that males would spend less time scanning their environment than adult females, but the opposite outcome would be predicted by the assumption of male–male competition within groups. Secondly, we tested the effect of group composition on collective vigilance (i.e. the time during which at least one individual in the group scans the environment). We investigated whether the sexes of individuals within a group affect the quantity and pattern of collective vigilance. Regardless of sex effect, we demonstrated in an earlier study of eastern grey kangaroos that group members tended neither to scan their environment independently of one another nor to coordinate their scans in an asynchronous way (Pays et al. 2007a). On the contrary, individuals tended to synchronise both their vigilant and non-vigilant activities. Therefore, we investigated sex effect on the degree of synchrony and how group members react to a vigilant act exhibited by a female or a male.

Materials and methods

Study area and animals

The fieldwork was conducted in July 2005 at Newholme (151° 38'E, 30° 25'S) near Armidale (New South Wales) in Australia. The study area comprises eucalypt forest, woodland and open pastures of predominantly native species. In 2004, the population on Newholme was estimated to be 300 kangaroos living on 2,000 ha, i.e. at a density of 0.15 kangaroos per hectare. The population is continuous with those on neighbouring properties (farms). The animals were not marked for individual recognition. Predators of kangaroos that occur at Newholme include red foxes *Vulpes vulpes*, wedge-tail eagles *Aquila audax* and occasional dogs, the first two species being threats mainly to juvenile kangaroos. The local dogs to which the kangaroos are exposed are farm dogs, stray domestic dogs and feral dogs *Canis lupus familiaris*. However, the kangaroo population is within dispersal range of extant dingoes *Canis lupus dingo*, and they may occasionally be exposed to them as well.

Eastern grey kangaroos form open-membership groups (Jarman and Southwell 1986) and exhibit high rates of group flux (Jarman and Coulson 1989). Neither sex is territorial, and males, which grow indeterminately throughout adulthood, compete to mate polygynously in a roving-male strategy, which gives priority access to the most dominant (usually the largest) male that detects a female during her oestrus. Males were less abundant than females in the study population (as in most wild kangaroo populations). We were unable to estimate male body size consistently from group to group, so we did not attempt to relate male vigilance to absolute or relative size. Our aim was to quantify and compare the vigilance of adults of the two sexes and to consider how that related to group size and adult composition. Thus, we wanted to minimise any variability that might be introduced by the presence or absence of juveniles. The study was conducted at a season when the population contained very few young-at-foot (unweaned juveniles excluded from the pouch but still dependent on the mother) and large pouch young (juveniles still spending much of their mother's foraging time in the pouch but able to leave it occasionally). This timing minimised the risk that female vigilance would be much affected by attention to dependent out-of-pouch young.

Recording data

Group sampling Defining whether an individual does or does not belong to a group has been extensively discussed in methodologies of behavioural studies. Ambiguities arise when animals are not tightly clumped (Frid 1997), in

particular if individuals join and leave the cluster of group members during short periods of time (Martin and Bateson 1993). In eastern grey kangaroos, Jarman (1987) considered a group as those kangaroos whose most extreme associate was within 15 m of another group member. However, in a more recent review of all macropod species, Jarman and Coulson (1989) chose 30 m as the maximal separation between two neighbours. In this study, we identified a group on the spatial basis of 30 m maximal separation between adjacent members and on the maintenance of social and spatial cohesion of the group members during all focal sampling. No ambiguities were encountered in the sampled groups.

Data were collected on foot, respecting a minimal distance of 200 m between the focal group and the hidden observer to minimise disturbance of the animals' behaviour. Most observations were made at a distance of 200–300 m. Each group was filmed with a video camera (Canon XM-1, 20× optical zoom) for a 10-min sequence during which all group members were in the camera's field of view and all were active. Frequent departures and/or arrivals of one or several individuals have been reported in the eastern grey kangaroo (Southwell 1984). Only groups whose size and composition did not change during recording were retained in the sample, and these formed the great majority of groups that we tried to sample. We avoided filming the few groups containing out-of-pouch juveniles. Because of the kangaroo's typical daily schedule of activity (Clarke et al. 1989, 1995), we recorded the sequences early in the morning and late in the afternoon when animals came onto the pasture to forage. Although animals were not marked, we avoided individual re-sampling by studying groups from a track that crossed three open paddocks over a distance of 2.5 km, allowing us to ensure spatial independence between groups sampled in the same morning or evening session. On the rare occasions when two groups were filmed in the same paddock one after another, the observer paid special attention that no group flux occurred between these two studied groups during or between the video recordings. The observer changed the direction in which he walked along the sampling track every day. At the end of the day, the observer had usually filmed only four or five groups and was confident that no group was filmed more than once during the day, and that sampled groups were independent of each other. Using these methods, 40 groups and a range of group sizes from two to six individuals were sampled, corresponding to a total of 121 individuals (i.e. sub-adults and adults, but disregarding young-at-foot or pouch-young) representing a total amount of time of 400 min. We analysed data for those groups whose composition was unambiguously determined. Although age of individuals was not directly estimated, males were easily recognised particularly because they were bigger than females in our

sampled groups but also because of differences in forelimb size and in fur colour on the throat and chest. The absolute or even the relative sizes of males could not be consistently recorded in the field, so tests of inter-male differences in vigilance were neither intended nor attempted. Two classes of groups were observed: mixed groups composed of adult males and females ($N=10$) and single-sex groups composed of females only ($N=30$). Eighty five females in female-only groups 24 females and 12 males in mixed-sex groups were sampled. No male-only groups were observed during our sampling. We paid special attention to studying mixed-sex groups and single-sex groups of females at all group sizes (from two to six individuals). No large groups were sampled because confidently identifying the sex of each individual in large groups on video was difficult because such groups were usually filmed at relatively wide angle, and hence reduced image size, to include all individuals [whose inter-individual distances were within the typical 5–8-m range reported by Jarman and Coulson (1989)].

Behaviour recording Characterising when a kangaroo was vigilant, Jarman (1987) reported two different postures, upright or crouched, in which a kangaroo might scan its environment. We considered an animal as vigilant when it raised its head above horizontal, while either crouched or standing upright (but not while crawling or hopping), and scanned its surroundings (thus, we included both of Jarman's two vigilant postures). No ambiguities were encountered in distinguishing a vigilant from a non-vigilant animal.

For analysis, the field-recorded 10-min video sequences were converted to analytic sequences. For each individual within each group, a binary sequence (0, non-vigilant activity, and 1, vigilant activity) was constructed reflecting its activity state precisely at each second for 600 s. We recorded at precisely the same time the activity of each member of the group, and that allowed us to quantify the individual and collective levels of vigilance with the methods described in the data analyses. For each focal group, we recorded the group size and the group composition.

For analyses, we adopted the following definitions:

Vigilant act	The raising by an individual kangaroo of its head to adopt the vigilant posture
Unique vigilant act	A vigilant act occurring when no other kangaroo was currently vigilant
Vigilance bout, for an individual	Unbroken time spent in the vigilant posture, having a duration greater than 1 s
Vigilance bout, for a group	Unbroken time (>1 s) when at least one group member showed

Copied act vigilance, from the initiating unique vigilant act to resumption of non-vigilance by the last kangaroo in the group to show vigilance
 An individual's vigilant act initiating an individual vigilance bout during which at least one other kangaroo displayed a vigilant act (i.e. wave-inducing act)

Data Analyses

Individual vigilance From the analytic sequences, we calculated for each individual within each group the means of the length of its scan duration and of its inter-scan duration (i.e. the time between the end of one and the beginning of the next vigilant events) in seconds, as well as the numbers of vigilant acts it performed during the 10-min sequence. The three variables, scan duration, inter-scan duration and the frequency of vigilant acts per minute, were Ln-transformed. For each individual in each group, individual vigilance was also characterised by the proportion of time that each individual within each group spent vigilant. This proportion of time was a good summary and combination of the three previous variables of individual vigilance. For the assumptions of normality and homoscedasticity to be fulfilled, we applied to this proportion a Logit-transformation: $\text{Logit}(P_{\text{ind}}) = \ln(P_{\text{ind}}/(1 - P_{\text{ind}}))$. We tested for a sex effect and a group-size effect, on each transformed variable, using linear mixed-effects models fitted by restricted maximum likelihood including a random effect due to the presence of groups. Backward selections from complete models including both variables and their interaction were performed removing the less significant factor at the threshold $\alpha=0.05$.

Collective vigilance At each second, the video-recorded sequences of all group members were aligned, allowing us to identify when at least one member of the group was vigilant, i.e. when a collective vigilance bout was occurring. We could then calculate the duration and frequency of bouts of collective vigilance and the duration of intervals between two successive bouts of collective vigilance, and these were Ln-transformed. We also calculated the proportion of time (P_{obs}) for which the group showed collective vigilance, and we applied to this proportion a Logit transformation (see the previous paragraph for details). We tested for the effect of group composition (i.e. mixed-sex group vs single-sex group of females) and of group size on the four transformed variables of collective vigilance, using linear model procedures. From a complete model

including both variables and their interaction, backward selections were performed.

Collective pattern of vigilance We tested whether the mixed-sex groups were more synchronous than single-sex groups of females. To analyse sex effect on the degree of synchrony, we used only groups containing at least two individuals. From each observed group, we calculated a Pearson's correlation coefficient between two binary sequences (0 for non-vigilant and 1 for vigilant activity) of two different individuals within the group. This coefficient was calculated for all of the possible female–female pairs ($N=113$) and female–male pairs ($N=99$). Then, we compared the correlation coefficients between these two pair combinations using a Mann–Whitney U test regardless of group size, as group size effect on the degree of synchrony has not been detected in this species (Pays et al. 2007a). We applied the same analysis comparing between female–female pairs in single-sex groups ($N=99$) and female–female pairs in mixed-sex groups ($N=14$) to test if the presence of males affected the degree of synchrony of females.

Finally, considering the mixed-sex groups, we sought an association between sex and the frequency of performing unique or non-unique acts (i.e. whether the tendency to perform a vigilant act when no other kangaroo was vigilant differed between the sexes), and we then considered whether the sexes differed in the probability that their unique acts did or did not induce a wave of vigilance among other group members (i.e. whether the sexes differed in their ability to induce waves of collective vigilance). Lack of independence among animals sampled within each group precluded the use of standard statistical tests, so the data are presented merely for discussion.

Results

Effect of group composition and group size on individual vigilance

We tested whether the individual vigilance of females was affected by the presence of males, controlling for group size, using linear mixed-effects models and differentiating between males, females in single-sex groups and females in mixed-sex groups. Firstly, analyses revealed no effect of the interaction group-size \times composition on the duration of bouts of vigilance, the duration of inter-scan bouts (i.e. non-vigilance time), the frequency of vigilant acts, and the proportion of time that an individual spent in vigilance ($\chi^2=0.86$, $\text{df}=1$, $P=0.43$). In our sampled range of group size (from two to six individuals), an effect of group size pertained only on the frequency of vigilant acts (Table 1),

with no effect on the other individual variables ($\chi^2 < 1.92$, $df=1$, $P > 0.17$). Secondly, although analyses revealed an effect of group composition on three variables ($\chi^2 > 3.03$, $df=2$, $P < 0.05$; Table 1), no differences between females in female-only groups and in mixed-sex groups appeared in the durations of bouts of vigilance and of inter-scan bouts and in the proportion of individual vigilance time (t value < 1.39 , $df=2$, $P > 0.17$). Table 1 shows that the overall effect of group composition on these three variables was due to a general sex-difference between males and females. Indeed, according to the respective signs of the coefficients of the three variables derived for males in mixed-sex groups, females were more vigilant than males. Therefore, the sex-specific characteristics of vigilance in female kangaroos differ from those in males but appear to be unaffected by the presence of males. Lastly, no effect of sex upon the frequency of vigilant acts (females, mean \pm SE = 1.1 ± 0.04 ; males, mean \pm SE = 1.0 ± 0.10 acts/minute) was revealed in this analysis ($\chi^2 = 1.918$, $df=2$, $P = 0.159$). Figure 1 compares the durations of vigilance and inter-scan bouts of non-vigilance, the frequency of vigilant acts and the proportion of time spent in vigilance between females and males.

Applying linear mixed-effects models to data from mixed-sex groups only, to analyse whether the individual vigilance of females differed from that of males in such groups, backward selection revealed effects on the four

individual vigilance variables of neither the interaction group-size \times composition ($\chi^2 = 1.120$, $df=1$, $P = 0.303$) nor group size ($\chi^2 = 0.717$, $df=1$, $P = 0.422$). Moreover, no difference between females and males was apparent in the durations of bouts of vigilance and the frequency of vigilant acts ($\chi^2 < 2.687$, $df=1$, $P > 0.139$). However, relative to the coefficient derived for males (coef \pm SE = -0.647 ± 0.233), the proportion of time that a female spent in vigilance in such groups was higher than that of a male ($\chi^2 = 5.911$, $df=1$, $P = 0.015$); and, relative to the coefficient derived for males (coef \pm SE = 0.035 ± 0.149), the duration of inter-scan bouts was lower for females ($\chi^2 = 5.464$, $df=1$, $P = 0.029$).

Effect of group composition and group size on collective vigilance

As for the individual vigilance, we tested for the effect of group size and group composition (mixed-sex group vs single-sex group of females) on the four collective vigilance variables (duration and frequency of collective bouts of vigilance, duration of collective inter-scan bouts and proportion of collective vigilance time, i.e. when at least one individual within a group was vigilant). For each variable, backward selection from the complete model revealed no effect of the interaction group-size \times composition (linear models: $\chi^2 < 1.076$, $df=1$, $P > 0.307$). The

Table 1 Minimal models selected from complete models including one of the four individual vigilance variables (ln-transformed duration of bouts of vigilance, ln-transformed duration of inter-scan bouts, ln-transformed frequency of vigilant acts and the logit-transformed proportion of time spent in vigilance), group size, sex and group composition of the individual (male, female in mixed-sexes group and female in female-only group, this last used as the reference) and their interactions

Minimal models	Coef.	S.E.	denDf	t value	P
(1) Duration of bouts of vigilance					
Intercept	2.460	0.088	79	27.882	<0.0001
Group composition					
Female in mixed-sex groups	-0.252	0.181	79	-1.392	0.168
Male	-0.526	0.217	79	-2.428	0.018
(2) Duration of bouts of inter-scan					
Intercept	3.671	0.067	79	54.852	<0.0001
Group composition					
Female in mixed-sex groups	-0.007	0.137	79	-0.050	0.960
Male	0.359	0.166	79	2.167	0.033
(3) Frequency of vigilant acts					
Intercept	0.422	0.165	81	2.557	0.012
Group size	-0.133	0.050	38	-2.742	0.009
(4) Proportion of time spent in vigilance					
Intercept	-1.306	0.144	79	9.063	<0.0001
Group composition					
Female in mixed-sex groups	-0.248	0.287	79	0.864	0.390
Male	-0.891	0.322	79	2.769	0.007

A minimal model was backward-selected using a linear mixed effect model with group as a random effect. Males were always in mixed-sex groups in our analysed sample

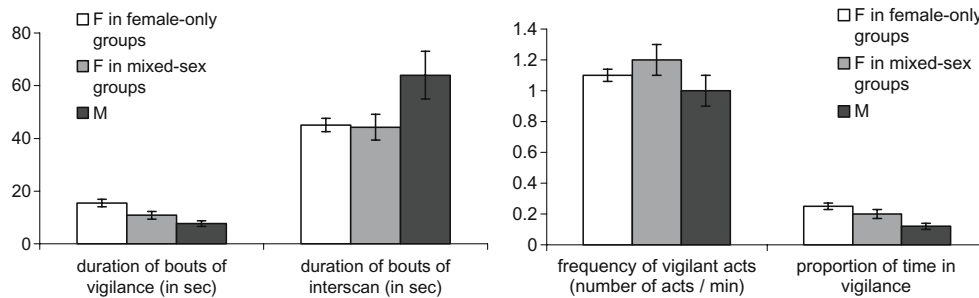


Fig. 1 Duration of bouts of vigilance, duration of inter-scan bouts, frequency of vigilant acts and proportion of time spent in vigilance, during the sampled 10-min sequences, performed by a female in a

female-only group (in white; $N=85$), a female in a mixed-sex group (in grey; $N=24$) or a male (in dark grey; $N=12$). Error bars are the standard errors

analyses revealed no group-size effect on the duration of bouts of collective vigilance and the frequency of collective vigilant acts ($\chi^2 < 0.875$, $df=1$, $P > 0.350$). However, relative to the negative coefficient (coef \pm SE = -0.147 ± 0.06), the duration of collective inter-scan bouts decreased when group size increased ($\chi^2 = 6.075$, $df=1$, $P = 0.018$). This effect appeared to be significant enough to lead to a group-size effect on the proportion of collective vigilance (the time when at least one individual in the group was vigilant) ($\chi^2 = 3.81$, $df=1$, $P = 0.05$). Indeed, relative to the sign of the coefficient (coef \pm SE = 0.28 ± 0.145), this proportion of time increased with group size. For each collective variable, the analyses revealed no effect of group composition ($\chi^2 = 0.144$, $df=1$, $P = 0.707$). Thus, no difference existed between the collective vigilance of mixed-sex and female-only groups.

Effect of group composition on degree of synchronisation

We tested for any difference, in the degree of synchrony in the observed correlation coefficients, between female–female pairs (mean \pm SE = 0.141 ± 0.016) and female–male pairs (mean \pm SE = 0.097 ± 0.039) in groups. The analysis revealed no difference between the two composition pairs (Mann and Whitney test: $U=1,090$, $N_1=113$, $N_2=23$, $P=0.224$). Thus, mixed-sex groups seemed to be neither more nor less synchronous than single-sex groups of females. We applied the same analysis comparing female–female pairs in single-sex vs mixed-sex groups to test whether the presence of males affected the degree of synchrony of females. The means of the observed correlation coefficients between female–female pairs in single-sex groups (mean \pm SE = 0.150 ± 0.0180) and female–female pairs in mixed-sex groups (mean \pm SE = 0.073 ± 0.030) did not significantly differ (Mann and Whitney test: $U=518$, $N_1=99$, $N_2=14$, $P=0.127$). Thus, males seem not to affect the degree of synchrony between females.

Effect of sex on frequencies of unique and non-unique vigilant acts, and of copied and uncopied unique acts

We considered whether the sex of the actor affected the probability that a vigilant act might be unique or not, and whether a unique vigilant act would be copied. In the sampled video sequences of mixed-sex groups, we noted 369 vigilant acts: 156 were not unique and 213 were unique. Of the latter, 75 were copied and 138 were not copied. Thus, 66% of vigilant acts were unique (performed when no other kangaroo was alert), and only about one unique vigilant act in every three (35%) induced a collective wave of vigilance.

Considering only the 10 mixed-sex groups (containing, in total, 12 males and 24 females), we investigated the relationship between sex and performance of unique vigilant acts (i.e. acts performed when no other kangaroo was currently vigilant and, by definition, the only vigilant acts that could be copied). Of the 213 unique acts, 161 were displayed by females and 52 by males. The average female performed 6.7 unique and 4.4 non-unique acts, and the average male 4.3 unique and 4.7 non-unique acts, during the average 10-min recording period. The proportions of vigilant acts that were unique were 60% for females but only 46% for males. Analyses of the unique vigilant acts, however, showed that the sexes differed little in the rates at which their unique vigilant acts were copied (i.e. induced a wave of vigilance): 34% for males and 38% for females.

Discussion

Effect of group size on vigilance

Other studies have reported group size effects on individual vigilance in eastern grey kangaroo (Jarman 1987; Pays et al. 2007a), in other macropodid species (Blumstein et al. 1999) and in several other mammalian species (e.g.

Underwood 1982; Burger and Gochfeld 1992; Illius and FitzGibbon 1994; Childress and Lung 2003). However, the only group-size effect on individual vigilance revealed in our study was a decrease in frequency of vigilant acts with increasing group size. The lack of correlation between group size and all other parameters of individual vigilance may be due to our sampling only a limited range of group sizes (1–6 individuals). However, it might also be explained by the balance between the two main functions of this activity. Our recorded vigilance (as in most studies) combined extra-group scanning (individual vigilance against predators), which should decrease with increasing group size, and intra-group scanning (individual vigilance towards conspecifics), which might increase as group size increases. Changes with group size in these two types of scanning might cancel one another. However, our study was not designed to separate the effects of these two sources of vigilance.

We found that the proportion of time during which at least one group member was vigilant (i.e. when the group showed collective vigilance) increased with group size. This trend would be individually adaptive if it increases the probability of detecting a potential predator without diminishing the individual's time allocated to feeding (Pulliam 1973). In a previous study, we showed that the collective proportion of time spent in vigilance increased with increasing group size up to seven members; however, above this group size, this proportion of time decreased (Pays et al. 2007a). Some studies that quantified collective vigilance have shown that it increased with group size (Bertram 1980; Ebensperger et al. 2006), while others have found that it did not vary with group size (Fernández et al. 2003).

Effect of sex on vigilance

Although females did not display vigilant acts more frequently than males, a female kangaroo spent a higher proportion of time vigilant than a male. In our study this was the product of females displaying longer vigilant bouts and shorter non-vigilant bouts (i.e. shorter inter-scan intervals) than males. Our results for eastern grey kangaroos contrast with many studies, particularly of several African large mammal herbivores (Prins and Iason 1989; Burger et al. 2000; Burger and Gochfeld 1994), that have reported that males are more vigilant than females.

Although inter-male rivalry might oblige males to monitor each other continuously (Baldellou and Henry 1992; Rose and Fedigan 1995) by spending time scanning to assess rivals' presence and activities (Hart et al. 1992; Reboreda and Fernández 1997), intra-specific competition seems not to explain our results. However, intra-specific competition is likely to have the most effect only when several males are present within the group. We could not

include this variable in the analyses because we could not evaluate a range of mixed-sex groups of kangaroos in which the proportion of males varied consistently.

The eastern grey kangaroo exhibits pronounced sexual body-size dimorphism (Jarman 1989), and our results are compatible with the expectations of the body-size-dimorphism hypothesis that males must spend more time feeding (and thus less time vigilant) than females (Clutton-Brock et al. 1982; Illius and Gordon 1992). Our finding that males generally do not scan as long as females is consistent with males facing greater time constraints (because of their greater food requirements) and therefore needing to reduce scanning time to increase foraging time. Ginnett and Demment (1997) reported that males of the highly dimorphic giraffe *G. camelopardalis* were less vigilant than females during the wet season when food is short. Our study was conducted in winter, a season when low food quality and availability forces kangaroos to extend their time spent feeding each day (Clarke et al. 1989), hence, when body-size effects might have an impact particularly upon males.

Another possible consequence of body-size dimorphism that might predict greater female vigilance is that females may be more vulnerable to predators or disturbance than males. Male kangaroos, taller than females both when crouched and especially when standing upright, should be able to detect an approaching predator at greater range. Additionally, the larger males, unlike females, are able to defend themselves actively against attack by dingoes (Jarman and Wright 1993), their largest predators other than humans. The historical presence of dingoes on the study site, and current exposure to dogs, may have contributed to sex differences in anti-predator vigilance. Future study of sex effects on vigilance should test whether the presence of juveniles affects not only the vigilance of females but also the group's collective vigilance. Any delay that a female experiences in escaping a surprise attack through her need to alert her young-at-foot or retrieve her pouch-young temporarily out of the pouch, or the handicap of carrying a large pouch-young, might make time spent on vigilance more profitable for a female than for a male.

The proportion of time that a female in a mixed-sex group spent vigilant and the frequencies and durations of her vigilant and non-vigilant bouts did not differ from those of a female in a single-sex group. Thus, females seemed unaffected in their vigilance activities by the presence or absence of males and appear not to have compensated in any way for the presence of less vigilant males. However, these analyses were not optimal because of the small number of groups sampled in our study. The open-membership groups of eastern grey kangaroos can change size and composition very frequently with departures and/or arrivals of one or several individuals (Southwell 1984; Jarman and Coulson 1989). Finding mixed groups stable

enough for sampling (i.e. where all of group members stayed together and in the field of view of the camera during 10-min video sequences) proved relatively difficult.

Possible effects upon behaviour of interactions between sex classes in temporary aggregation of eastern grey kangaroo have been discussed by Jarman and Southwell (1986) and Jarman and Coulson (1989). Given male–male competition for reproductive opportunities (Hart et al. 1992; Reboreda and Fernández 1997), the presence of males might well generate instability in groups, affecting female activities and increasing the females' vigilant acts when males continuously approach and attempt to sniff at them (particularly when an oestrous female is being sought). Individuals in groups of eastern grey kangaroos are generally clumped with inter-individual distances typically of 5–8 m (Jarman and Coulson 1989). In a closely clumped group, a female may not need to raise her head above the horizontal to monitor approaching males. Because we considered an individual as vigilant only when it raised its head above horizontal, the less overt vigilance behaviour required to monitor males might have been underestimated in our study.

Sex and patterns of collective vigilance

We found no effect of group composition on collective vigilance. Because group size, but not composition itself, affected collective vigilance, it may matter little (for vigilance) with what sexes an individual associates in a group, a finding that accords with the freely mixing nature of kangaroo groups (Jarman and Southwell 1986). Most theoretical models of vigilance assume independent scanning by group members (Pulliam 1973; Pulliam et al. 1982; Bednekoff and Lima 1998; Scannell et al. 2001), predicting that group members should scan their environment independently of one another to minimise the cost of vigilance in response to the risk of being preyed upon. However, a tendency to synchronise bouts of vigilance and foraging between group members has previously been demonstrated in eastern grey kangaroos (Pays et al. 2007a), Defassa waterbuck *K. defassa* (Pays et al. 2007b), greater rhea *Rhea americana* (Fernández et al. 2003) and degu *O. degus* (Ebensperger et al. 2006). Thus, the theoretical assumption of independent scanning seems not to be fully supported by field studies. Although individuals are influenced by the behaviours of other group members, they appear to copy them rather than to exhibit the opposite activity (i.e. vigilance vs foraging), as the coordination assumption would have predicted. Moreover, the tendency towards synchronisation might also be explained by social vigilance, during which individuals obtain information on other group members. We found neither an effect of sex on the degree of synchrony between female–female and female–

male pairs nor an effect of the presence of males on the degree of synchrony of females. However, if direct competition requires males to be vigilant to assess rivals' presence and activities (Reboreda and Fernández 1997), social vigilance ought to differ between the sexes, and the presence of males in a group might affect the behaviour and degree of synchronisation of females. We suggest that this assumption should be tested in other species.

Our data suggested that a higher proportion of the vigilant acts of females than of males were unique; but the significance of that could not be tested effectively. It would be valuable to investigate in a future study whether vigilant acts by females are significantly more likely than those by males to occur when no other kangaroo is currently alert. Only about a third of unique acts were copied, with little difference between the sexes in the probability that one of their unique acts would be copied. At times, several unique acts were needed to generate a similar act by at least one other group member. Future studies might take into account the duration of vigilance bouts in relation to sex and to the probability of the act inducing a wave of vigilance.

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