

Vigilance and its complex synchrony in the red-necked pademelon, *Thylogale thetis*

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Several adaptive functions, including gaining information from other group members and detecting predators, are generally ascribed to vigilance in groups of animals subject to predation. Most studies of the effects of neighbors on vigilance have focused on individual vigilance. We investigated the effects of neighbors on vigilance in wild red-necked pademelons *Thylogale thetis* foraging at night in nonpersistent aggregations in a clearing in rain forest. Neither the total number of pademelons in the clearing nor the numbers at various distances around focal individuals affected the individual vigilance of focal animals. However, focal animals' individual vigilance did change with the distance to their nearest neighbor and also with distance to cover. Pairs of individuals closer than 10 m apart tended to synchronize their bouts of individual vigilance and foraging. The degree of synchrony within pairs increased with both distance to cover and the total number of pademelons foraging in the area and decreased with increasing distance to the pair's nearest neighbor but did not vary with the distance separating the members of the pair. Thus, despite their individual vigilance being unaffected by the number of other pademelons in the feeding aggregation, pademelons were nonetheless sensitive to the presence of conspecifics and adjusted their behavior in relation to their separation from neighbors. Thus, some vigilance benefits may be obtained from the presence of conspecifics even in species that aggregate only temporarily on food patches without forming more permanent social groups. **Key words:** antipredator behavior, independent scanning, neighbor effect, synchronization of vigilance, vigilance. [*Behav Ecol* 20:22–29 (2009)]

INTRODUCTION

In groups of prey species, vigilance activity is classically viewed as conferring protection against predators (Pulliam 1973; Lima 1987, 1995; Elgar 1989; Roberts 1996; Treves 2000), although it may also be beneficial for monitoring the behavior of conspecifics (Baldellou and Henzi 1992; Artiss and Martin 1995; Tchabovsky et al. 2001) and gaining information about food patches (Elgar 1989; Quenette 1990; Beauchamp 2001; Robinette and Ha 2001). Vigilance varies with predation risk, group size, sex, and social status of the focal individual (Bertram 1978; Pulliam and Caraco 1984; Lima and Dill 1990; Yaber and Herrera 1994; Roberts 1996; Hunter and Skinner 1998; Lung and Childress 2006).

The influence on vigilance of the presence or position of conspecifics within groups has been reported frequently. The effect of distance to neighbors has been theoretically investigated (Bahr and Bekoff 1999), and many empirical studies of mammals (e.g., Underwood 1982; Childress and Lung 2003) and birds (e.g., Rolando et al. 2001; Fernández-Juricic et al. 2007) have shown that the vigilance of a group member may be affected by the presence of neighbors. For example, in the quokka (*Setonix brachyurus*) and the yellow-footed rock-wallaby (*Petrogale xanthopus*), both small or medium-sized and moderately social macropodid marsupials, group size defined as the number of conspecifics within 10 m explained more variation in vigilance than group size defined as the number of conspecifics within 50 m (Blumstein, Daniel, and

Evans 2001; Blumstein, Daniel, and McLean 2001). Vigilance decreased with increasing numbers of close neighbors in coatis (*Nasua nasua*) (Di Blanco and Hirsch 2006) and several studied primates (e.g., black howler monkey, *Alouatta pigra*, Treves et al. 2001; tamarins, *Saguinus fuscicollis* and *Saguinus mystax*, Smith et al. 2004), whereas the reverse was found in brown capuchin monkeys, *Cebus apella* (Hirsch 2002). Most studies that have reported the effect of either the presence or the distance of neighbors on vigilance of focal animals have concentrated on vigilance at an individual level. The influence of nearby conspecifics on group vigilance (i.e., vigilance at a collective level) is still not well understood. Therefore, we set out to investigate the effects of neighbors on vigilance activity at both an individual and a collective level.

To predict the vigilance behavior that a group of individuals should adopt in response to the risk of being preyed upon, most studies of gregarious species have made 1 of 2 main assumptions. First, most theoretical models of vigilance (e.g., Pulliam 1973; Pulliam et al. 1982; Bednekoff and Lima 1998; Scannell et al. 2001) have simply assumed that group members should scan their environment independently of one another. Functionally, scanning that is independent among group members is considered an optimal solution as this avoids the high costs of organizing vigilance through coordination (Ward 1985; Bednekoff and Lima 1998). The second assumption (more theoretically than empirically supported) is that, in order to maximize benefit from their respective vigilance activities, group members should coordinate their scans in nonoverlapping 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 behavior). Modeling by Fernández-Juricic et al. (2004) suggests limits

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to the circumstances in which coordinated vigilance would be optimal; whether coordination of vigilance might be favored would depend on numerous factors such as group size and predation risk, visual perception, and information transfer.

In contrast to these 2 main theoretical assumptions (i.e., independence or coordination of vigilance), a tendency to synchronize bouts of vigilance and foraging between group members has been demonstrated in the greater rhea (*Rhea americana*) (Fernández et al. 2003), degu (*Octodon degus*) (Ebensperger et al. 2006), eastern gray kangaroo (*Macropus giganteus*) (Pays, Jarman, et al. 2007), and Defassa waterbuck (*Kobus ellipsiprymnus defassa*) (Pays, Renaud, et al. 2007). This pattern of synchronization of vigilance has not been predicted from theory. In order to better understand the synchronization of vigilance, we need to test whether the presence and the distance of nearby individuals can contribute to the emergence of synchronized vigilance in species that exhibit simple aggregations as well as those that form more persistent social groups, such as eastern gray kangaroos. In less social prey species that form nonpersistent aggregations, we predict independence of vigilance activity among conspecifics as is generally assumed in theoretical studies (Bednekoff and Lima 1998).

We tested this prediction by studying vigilance in a wild population of the red-necked pademelon (*Thylogale thetis*), a small forest-dwelling member of the kangaroo family, gathering data at night when animals emerged from cover onto a pasture to forage. Johnson (1980) reported that pademelons tolerate conspecifics within the nonpersistent aggregations that form on such food patches. In the continuum from living alone to living in social groups, the red-necked pademelon occupies an intermediate position, closer to solitary than group living (Johnson 1977). Group-size effects have previously been studied in this species with contrasting results. Wahungu et al. (2001) found that individual vigilance decreased with increasing group size, whereas Blumstein et al. (2002) reported that pademelons did not modify time allocated to vigilance as group size increased. It remains unclear whether an aggregation of several individual pademelons foraging simultaneously on a pasture should be characterized as a group because we do not know whether individuals maintain any social and spatial cohesion during nocturnal foraging. However, that does not prevent us investigating the effect of individuals in such aggregations on each other's vigilance.

To study vigilance at both individual and collective levels, we first investigated whether individual vigilance of focal pademelons in aggregations was affected by conspecifics. We tested for effects of the total number of conspecifics that foraged on the study area, the numbers of conspecifics inside and outside areas within radii of 5, 10, 15, or 20 m around the focal animal, and the distance to the focal animal's nearest neighbor. By testing for the effects of conspecifics on the individual vigilance of focal animals, we could test our prediction that pademelons place little reliance on the vigilance of conspecifics because they tend to be solitary and form only temporary aggregations. However, factors external to the aggregation could also influence the time an individual spent in vigilance. For example, Burger et al. (2000) reported that vigilance time in springbok (*Antidorcas marsupialis*) decreased with increasing distance to bushes. For other macropodid marsupial species, Blumstein, Davies, and Evans (2001; Blumstein et al. 2003) reported that quokkas were sensitive to their distance from cover but agile wallabies (*Macropus agilis*) were not. Therefore, we also investigated whether time of night and distance to cover affected individual vigilance. Second, we tested whether individuals scanned their environment independently of one another (Pulliam's assumption) or exhibited a collective pattern of vigilance (i.e., a tendency toward coordination or, conversely, synchronization) and what factors influenced these patterns.

METHODS

Study area and animals

Fieldwork was carried out in June 2007 at Binna Burra in the Lamington National Park (28°08'32"S, 153°06'55"E), a UNESCO World Heritage-listed wilderness situated in the Border Ranges of southern Queensland in Australia. The park is composed of a dense rain forest that blends into more open forest. At Binna Burra, several small areas of open pasture, adjacent to the rain forest and characterized by very short grass, are attractive to foraging pademelons and provide excellent conditions for observing them. The red-necked pademelon is one of the most abundant species in rain forest–pasture ecotones (Jarman and Phillips 1989). Pademelons emerge from cover at night and come onto the pasture (typically no more than 70 m from forest edge) to forage (Johnson 1980; Wahungu et al. 1999, 2001). Pademelons can form aggregations of up to several dozen individuals while feeding but do not form persistent associations (Johnson 1977). Predators of pademelons that occur at Lamington National Park include carpet pythons (*Morelia spilota*), red foxes (*Vulpes vulpes*), wedge-tailed eagles (*Aquila audax*), feral cats (*Felis catus*), and occasional dogs (feral dogs, dingoes and their hybrids; *Canis lupus* subsp.). At Binna Burra, animals are relatively habituated to the presence of humans.

Recording data

Individual sampling

At Binna Burra, we chose an area of pasture (about 70 × 40 m) adjacent to the rain forest that offered excellent conditions for observing all foraging animals simultaneously. To mark a grid to facilitate easy recording of the positions of animals, we placed branches on the ground to form a natural mark at each grid node, which we assumed would not disturb the behavior of the pademelons. The grid cells (measuring 15 × 15 m and visually subdivisible into 4 equal subunits) allowed the position of each animal to be easily and unambiguously recorded.

Data were collected at night with a night-vision scope (M.6121 Versatile Night Scope with a X3 lens and built-in infrared illuminator from Night Vision Australia, Sydney) from 1730 to 2300 h. Before each focal sample began, the observer recorded the positions of all animals on a map of the study area. He randomly selected one individual that was foraging and recorded its behavior during a 10-min sequence. It was important that no individuals entered or left the study area or moved more than several meters within it, during the focal sampling. After each focal 10-min sequence, the observer checked that animals had not moved during the sample. If that happened, the focal sample was abandoned and the observer began again until a 10-min sequence was achieved during which the number of individuals on the study area did not vary. A 10-min sequence proved long enough to sample sufficient instances of vigilance by each individual for our statistical comparisons without being too long to meet the requirement that the focal individual should forage in the same place throughout the sampled sequence. Adhering to this strict procedure, we sampled 61 focal animals. To investigate whether focal animals were affected by the behavior of their nearest neighbor, the observer also recorded the behavior (foraging vs. vigilance), during the 10-min sequence, of the focal animal's nearest neighbor present in the field of view of the night-vision scope at the same time as long as that neighbor was within 10 m of the focal individual. Twenty nearest-neighbor pairs of individuals were sampled. We gained no information on gender in this nocturnal study as it is difficult to distinguish males from females in this species on the basis of body size dimorphism. We use the term "pairs" for sampled nearest

neighbors regardless of gender. Pademelons form pairs only during the short period when males pursue periostrous females. The behavior of such pairs is distinctive and none of the nearest-neighbor pairs that we observed included estrous females.

Individuals were neither captured nor marked. To minimize the risk of sampling individuals more than once (i.e., to achieve statistical independence between samples), we observed aggregations of animals in different parts of the pasture on different nights and, while observing a single aggregation, we avoided resampling the same individual by shifting our focus to different focal individuals for each 10-min recording sequence. There were plenty of animals on our study site, and we are confident that the majority of our observations come from different individuals.

Recording behavior

The observer minimized his movements and made observations from a location (far from cover to avoid any bias triggered by the observer's position) where he did not detectably influence the animals' behavior. To characterize when a pademelon was vigilant, we used the same postures reported for kangaroos (Jarman 1987, Pays, Jarman, et al. 2007). Thus, we considered an animal as vigilant when it raised its head above horizontal, while either crouched or standing upright, and scanned its surroundings. No ambiguities were encountered in distinguishing a vigilant from a nonvigilant animal.

During the 10-min sequences, focal animals either fed or scanned their environment. The observer recorded the time that the focal animal spent in each activity. For analysis, the field-recorded 10-min sequences were converted to analytic sequences. For each individual, a binary sequence (0, foraging activity; 1, vigilant activity) was constructed reflecting its activity state precisely at each second for 600 s. Samples of nearest-neighbor pairs similarly yielded 2 simultaneous binary analytic sequences.

The position of each animal that was recorded during each focal sample allowed us to estimate several independent variables: the total number of conspecifics on the study area; the numbers of conspecifics inside and outside areas with radii of 5, 10, 15, or 20 m around the focal animal; the distance of the focal animal's nearest neighbor; and the distance of each animal to cover. For each nearest-neighbor pair sampled, we recorded the time of night, the distance to cover of the member of the pair closer to the forest, the distance separating the 2 individuals within the pair, and the shortest distance to the nearest neighbor outside the pair for either individual within the pair (the pair's nearest neighbor).

Data analysis

Individual vigilance

From the analytic sequences, we calculated for each individual the means (and variances) of the lengths of its scan durations and its interscan durations (the time between the end of one and the beginning of the next vigilant event) in seconds (from these can be derived the number of vigilant acts it performed during the 10-min sequence and the proportion of time it spent vigilant, but we do not report those derived variables here). For the assumptions of normality and homoscedasticity to be fulfilled, the 2 variables, scan duration and interscan duration, were log transformed. We investigated the relationships between these 2 dependent variables and the independent variables listed above using linear models. The variable time of night was categorized into 3 classes (before 1830 h, $N = 19$; between 1831 and 1930 h, $N = 20$; after 1931 h, $N = 22$). Moreover, as the relationships between variables describing individual vigilance and the other con-

tinuous independent variables could be nonlinear (i.e., polynomial), we included in each procedure the square of each factor.

Tests of independence of vigilance between individuals in focal pairs

To test whether nearest neighbors less than 10 m apart scanned independently of one another, we used Pearson's correlation coefficient to investigate whether bouts of vigilance and of foraging tended to occur independently between 2 neighbors or were correlated. For each observed pair, we calculated a Pearson's correlation coefficient between the 2 binary sequences (0 for foraging and 1 for vigilant activity) of the 2 individuals. This coefficient was compared with the zero value expected under the assumption that individuals scan independently of one another using a Wilcoxon T -test for paired samples. If individuals tended to act independently of one another, the observed values would not be statistically different to zero. If individuals tended to coordinate their bouts of vigilance in nonoverlapping bouts of vigilance, the observed coefficients would be significantly lower than zero, whereas if individuals tended to synchronize their vigilant bouts (i.e., tended to overlap in their vigilance), the observed coefficients would be significantly higher than zero.

Factors affecting the degree of synchrony between 2 individuals in a focal pair

Finally, we tested for factors affecting the degree of synchrony between individuals within pairs. Knowing the position of each individual in the study area at the time of sampling, we investigated whether synchronization was affected by the distance to cover, time of night, distance to the nearest neighbor of the pair, distance separating the 2 individuals within the pair, and the total number of individuals that were foraging on the sampled area. The correlation coefficient values were used as a response variable representative of the degree of synchrony. 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). We investigated the relationships between these independent variables and the degree of synchrony using a linear model with backward selection. Given the number of sampled pairs and the large number of independent variables, we could not perform a statistical model more complex than one assuming linear relationships between these factors and the degree of synchronization. Thus, we did not include in the procedure the square of each factor.

Statistical analyses were computed with R software (the R Foundation for Statistical Computing, 2005).

RESULTS

We observed between 2 and 26 pademelons on the studied pasture area at the same time.

Individual vigilance

Although we used backward selection to test for the effects of independent variables on each of the transformed dependent variables describing the focal animal's vigilance (scan duration and interscan duration), we present our results according to the effect of each factor rather than according to the backward selection's stages in each linear model procedure in order to increase the readability of the numerous results.

Time of night

There was no effect of the time of night on either of the individual vigilance variables ($F_{2,54-56} < 1.168$, $P > 0.319$).

Total number of conspecifics in the study area

Whatever the considered relationship, linear or polynomial, results showed no effect of the total number of conspecifics on the study area on either of the transformed variables ($F_{1,53-56} < 1.919$, $P_s > 0.712$).

Numbers of conspecifics inside and outside areas with radii of 5, 10, 15, or 20m around the focal animal

Whatever the considered relationship, linear or polynomial, neither of the variables describing focal animals' individual vigilance were affected by the numbers of conspecifics inside and outside areas around the focal animal with radii of 5 m ($F_{1,50-51} < 0.053$, $P_s > 0.819$), 10 m ($F_{1,50-51} < 0.043$, $P_s > 0.837$), 15 m ($F_{1,50-51} < 0.660$, $P_s > 0.421$), or 20 m ($F_{1,50-51} < 0.097$, $P_s > 0.757$).

Distance of the nearest neighbor

There were no polynomial relationships between either of the transformed individual vigilance variables and distance to the nearest neighbor ($F_{1,52-57} < 2.354$, $P_s > 0.131$). However, linear models computed on transformed data showed that the mean duration of individuals' vigilant acts increased when the distance to their nearest neighbors increased (coefficient \pm standard error [SE]: 0.023 ± 0.012 , $F_{1,59} = 4.001$, $P = 0.050$). Moreover, the mean interval between 2 successive vigilant acts (the interscan duration) decreased when the distance to the

nearest neighbor increased (coefficient \pm SE: -0.055 ± 0.013 , $F_{1,58} = 19.215$, $P < 0.0001$). Figure 1 shows the effects of the distance to the nearest neighbor on each individual vigilance variable.

Distance to cover

There were no polynomial relationships between either transformed individual vigilance variables and distance to cover ($F_{1,52-53} < 0.709$, $P_s > 0.404$). However, linear models computed on transformed data showed that the mean interval between 2 successive vigilant acts (the interscan duration) decreased when distance to cover increased (coefficient \pm SE: -0.014 ± 0.009 , $F_{1,58} = 6.921$, $P = 0.011$). The distance to cover did not affect the mean duration of vigilant acts of individuals ($F_{1,58} = 1.214$, $P = 0.275$). Figure 2 shows the effects of the distance to cover on each individual vigilance variable.

Bouts of vigilant and foraging activity of individuals within pairs

We tested whether bouts of vigilant and foraging activity of 2 neighboring individuals within 10 m of each other were independent of one another by estimating the correlation coefficients between the pairs of individual sequences. The observed correlation coefficients between individuals within pairs (mean \pm SE: 0.097 ± 0.033) were much higher than

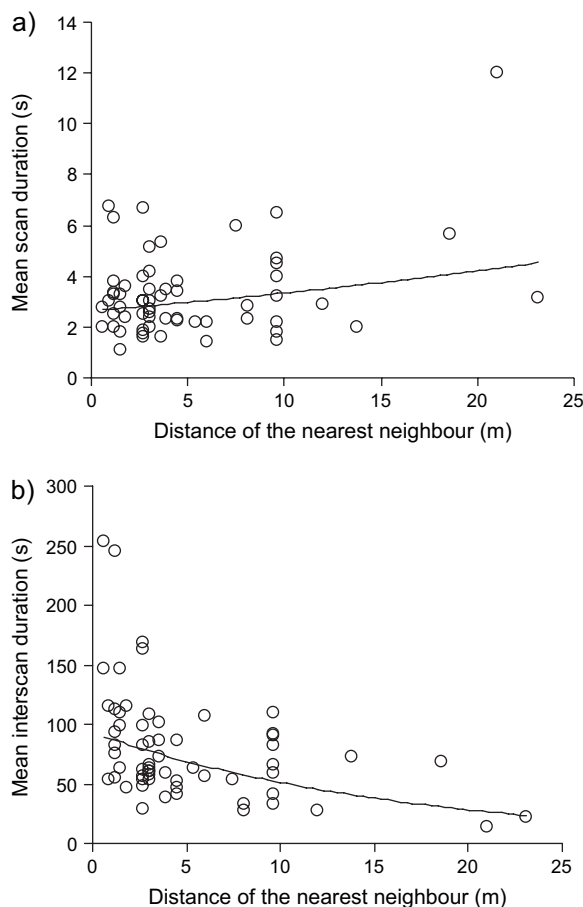


Figure 1

Effect of distance to the nearest neighbor on (a) the mean duration of individuals' vigilant acts and (b) the mean interval between 2 successive vigilant acts (interscan duration) (see Results for statistical details).

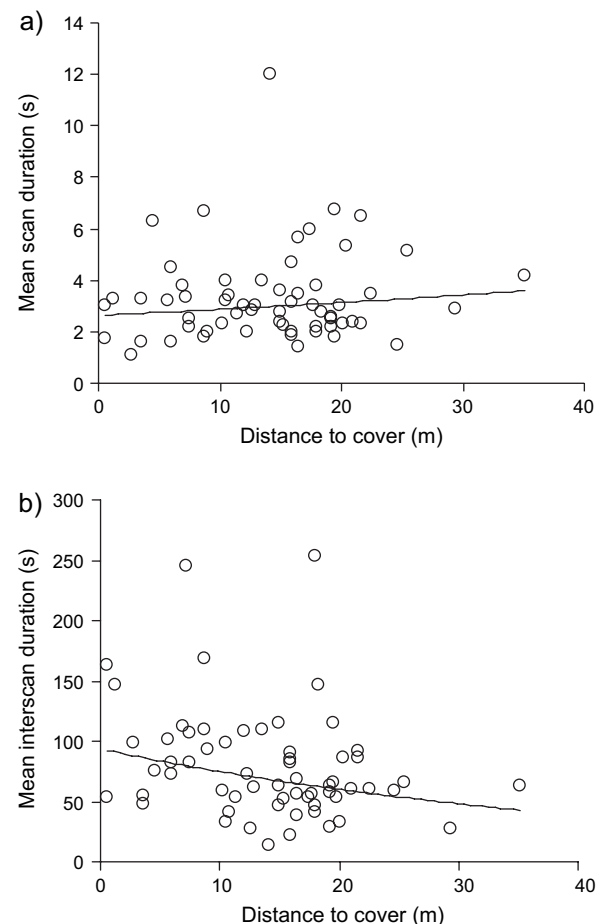


Figure 2

Effect of distance to cover on (a) the mean duration of individuals' vigilant acts and (b) the mean interval between 2 successive vigilant acts (interscan duration) (see Results for statistical details).

those expected under the assumption that individuals scanned independently of one another (mean equivalent to 0) (Wilcoxon test for paired samples: $T = 174$, $N = 20$, $P = 0.01$). Thus, bouts of individual vigilant and foraging activity tended to be synchronized within pairs.

Factors affecting the degree of synchrony between individuals within pairs

Here, we investigated factors that could affect synchronization of activities between pairs of individuals. Backward selection from a linear model showed that the degree of synchrony (i.e., the correlation coefficients between individuals within pairs) did not vary with time of night ($F_{2,13} = 2.678$, $P = 0.122$) or the distance separating the 2 individuals within the pair (which was limited to 10 m) ($F_{1,15} = 1.768$, $P = 0.203$). Table 1 shows the minimal model and the variables that affected the degree of synchrony. According to the sign derived for the distance to cover (Table 1), the degree of synchrony increased with the distance to cover (Figure 3a). The degree of synchrony also increased as the total number of individuals that foraged in the area increased (Table 1, Figure 3b). However, the degree of synchrony between 2 individuals decreased as distance to the pair's nearest neighbor increased (Table 1, Figure 3c).

DISCUSSION

Patterns of individual vigilance

Our results show that the mean duration of individuals' vigilant acts increased and the mean interval between 2 successive vigilant acts (interscan duration) decreased when the distances to their nearest neighbors increased. Therefore, pademelons seem to be influenced by the distance to their nearest neighbor as has been reported for some other species living in nonpersistent gatherings (Blumstein, Daniel, and Evans 2001; Cameron and Du Toit 2005). Our results thus seem to support models of vigilance derived from Pulliam's original prediction (e.g., McNamara and Houston 1992; Roberts 1996; Bednekoff and Lima 1998) that individuals benefit from grouping by reducing the amount of time spent in individual vigilance, while increasing time spent feeding, without affecting their probability of detecting a predator (Pulliam 1973). Our results show that pademelons are sensitive to the presence of conspecifics and adjust their behavior in relation to the distance separating them from their nearest neighbors. However, although this pattern of behavior has been described for other species in the literature, the proximate mechanism generating such regulation of individual vigilance activity with distance to the nearest neighbor is still unknown. In temporary aggregations characterized by unstable interindividual distances, such a mechanism would require continuous adjustment of the individual's vigilance activity. We thus need to know more about the internal processes directly related to

the computational capacity of individual's information processing in such species.

Individual pademelons appeared to react more to the distance to their nearest neighbor than to any measure of aggregation size that we investigated. The individual vigilance of pademelons seemed not to be affected by the total number of conspecifics that foraged on the same grassy area, nor by the numbers of conspecifics inside and outside areas with radii of 5 m, 10 m, 15 m, or 20 m around the focal animal. Thus, we found neither an aggregation nor a group-size effect on individual vigilance. These results pose questions about the presence of true grouping in this species for which the term 'group' has been used in the literature (Wahungu et al. 2001; Blumstein et al. 2002). Criteria for defining whether an individual does or does not belong to a group have been extensively discussed in methodologies of behavioral studies. Group has usually been defined on the spatial basis of interindividual distance with the additional criterion of maintenance of social and spatial cohesion of the group members. However, on this basis, 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; Pays, Benhamou, et al. 2007). Some authors studying grouping in mammalian species have used arbitrary interindividual distances to define groups (Alados 1985; Jarman 1987; Jarman and Coulson 1989; FitzGibbon 1990; Scheel 1993; Pays, Benhamou, et al. 2007), whereas others have offered no definition (Berger 1978; Risenhoover and Bailey 1985; Prins and Iason 1989). In the case of the red-necked pademelon, the lack of correlations between individual vigilance and the numbers of conspecifics within 5 m, 10 m, 15 m, or 20 m of the focal animal might challenge the notion that clusters of individuals formed groups at least on the basis of definitions that have been used in the literature. Our results suggest that it is possible for individuals in semisolitary species to be aware of nearby conspecifics and to respond to them in terms of synchronizing vigilance, yet not to build on that awareness to the point of reducing their vigilance with increasing numbers of nearby conspecifics. This illustrates that a group-size effect of reduced individual vigilance is not an inevitable outcome of associating with conspecifics and suggests that a species' typical form of sociality may play a role in determining what forms of antipredator benefits individuals may gain.

Theory predicts that pademelons should display a distance-to-cover effect on individual vigilance because they are vulnerable to both aerial predators, such as wedge-tailed eagles and terrestrial predators, which include snakes and dogs. Like many other species (Lima 1990), pademelons may perceive cover as being protective. If they suffer a high predation risk from aerial predators, it could be expected that pademelons would increase the time spent in vigilance when far from cover. This is indeed what we found; the 2 measures of vigilance showed an effect of distance to cover. Thus, our results differ from those of other studies of macropodid species,

Table 1

Minimal model showing the effects on the correlation coefficient values ($\tanh^{-1}(x)$ transformed) calculated between 2 individuals within a pair (<10 m apart) of distance to cover, the total number of individuals that foraged on the area, and the distance of the nearest neighbor of the pair

Variables	Coefficient	SE	numDf	denDf	F value	P
Intercept	-0.106	0.094	1	16	1.127	0.277
Distance to cover	0.015	0.005	1	16	5.913	0.027
Total number of individuals	0.010	0.005	1	16	4.638	0.047
Distance of the nearest neighbor	-0.007	0.003	1	16	5.970	0.027

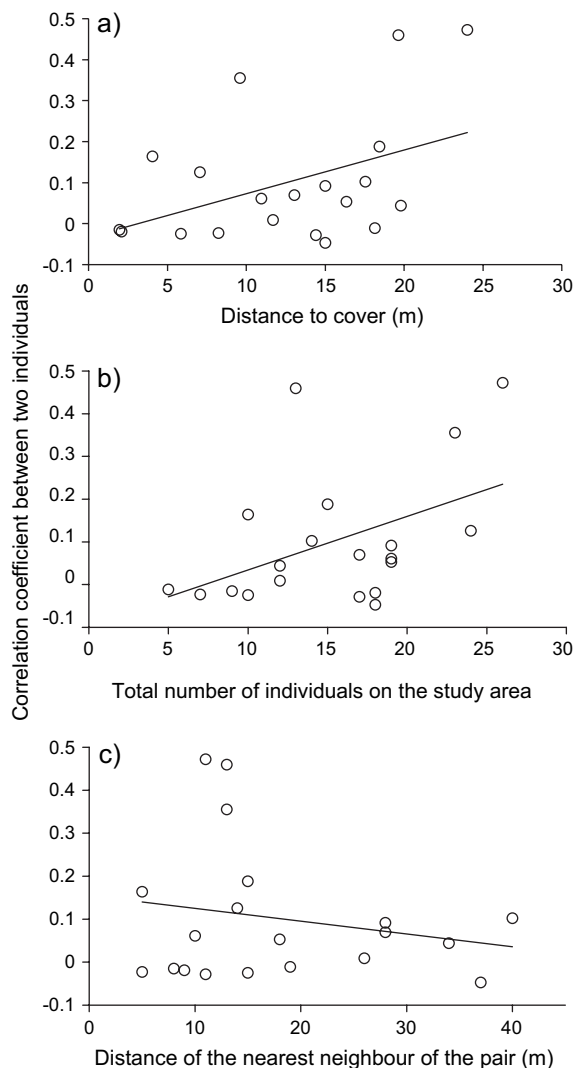


Figure 3
Effects of (a) distance to cover, (b) total number of individuals that foraged in the area, and (c) distance to the pair's nearest neighbor on the degree of synchrony between 2 individuals (see Table 1 for statistical details). The degree of synchrony was calculated from a Pearson's correlation coefficient between the 2 binary sequences (0 for foraging and 1 for vigilant activity) of the 2 individuals.

which have not detected any significant variation in individual vigilance with distance to cover (Blumstein et al. 2003).

Synchronization of vigilance among pairs of individuals

Contrary to our prediction that synchronization would not occur in a semisolitary species, we found that bouts of individual vigilant and foraging activities tended to be synchronized among pairs of neighbors that were less than 10 m apart. These results appear to show that individuals do not scan independently of one another and thus do not support Pulliam's (1973) assumption. This thus raised the question of how general patterns of synchronization of vigilance are; do they occur in many other semisocial and perhaps even more solitary species when individuals feed near each other? However, although bouts of individual vigilant and foraging activity appeared to be synchronized within pairs, the proportion of time that the pademelons spent in vigilance was only 0.042 (Pays O, unpublished data). This proportion is very low com-

pared with individuals in similarly sized groups in other mammalian species that form nonpersistent groups, such as rodents (Ebensperger et al. 2006; Fairbanks and Dobson 2007), marsupials (Jarman 1987; Blumstein, Daniel, and Evans 2001; Blumstein, Daniel, and McLean 2001), and ungulates (Risenhoover and Bailey 1985; FitzGibbon 1990; Cameron and Du Toit 2005). Indeed, this proportion is about one-fifth of the proportion of time individuals spent vigilant in groups of 2 individuals of eastern gray kangaroos (0.25; Pays, Jarman, et al. 2007), waterbucks (0.21; Pays, Renaud, et al. 2007), and degus (0.30; Ebensperger et al. 2006).

Two studies of synchronization of vigilance in species that spend very little time in vigilance compared with the time they spend feeding found contrasting patterns. Fernández et al. (2003) found that the proportion of time greater rheas spent in vigilance in group sizes similar to those in our study was 0.08 and that conspecifics tended to synchronize their vigilant activities. In contrast, Quenette and Gerard (1992) found that the proportion of time wild boar (*Sus scrofa*) spent in vigilance was about 0.06 but group members clearly scanned independently of one another. Thus, patterns of synchronization of vigilance between 2 individuals seem not to be directly related to the proportion of time spent in vigilance. However, we need more refined tests for detecting synchronization patterns when infrequent behaviors are being compared with frequent ones (Engel and Lamprecht 1997).

This apparent general synchronization of vigilance and foraging activities among pairs of neighboring pademelons that were less than 10 m apart does not tell us whether head-up acts were induced by neighbors' head-up acts (a copying effect) or whether both conspecifics responded to the same external stimuli. However, we propose that the synchronization of vigilance within pairs of pademelons was probably due to copying for 2 reasons. First, the presence of neighbors affected the individual vigilance activity of focal pademelons, with individual vigilance reduced when another conspecific was close. Second, the observer did not detect any external disturbances during the focal sampling.

Our results show that pairs of pademelons do not coordinate their behaviors to exhibit nonoverlapping bouts of vigilant activity. McGowan and Woolfenden (1989) suggested that such a pattern of nonoverlapping bouts of vigilance among conspecifics might confer an advantage by improving predator detection, but our results support the evidence for the rarity of such coordinated vigilance in nature (Elcavage and Caraco 1983). Coordination has been documented only in a few species of mammals and birds that display sentinel behavior (Bednekoff 1997, 2001; Clutton-Brock et al. 1999). Theoretical studies suggest that coordination might occur when it is inexpensive or extremely efficient, and social cohesion and ecological conditions allow efficient sharing of information about detected predators (Rodríguez-Gironés and Vásquez 2002). For these reasons, we did not expect coordination in pademelons, which forage in temporary, nonsocial aggregations.

Some synchronization of behavior among members of groups is essential for group cohesion (Keverne et al. 1978; De Ruiter 1986), and some studies suggest that such cohesion may be advantageous for the group members (Hamilton 1971; Pulliam 1973; FitzGibbon 1990; Mooring and Hart 1992). Under risk of predation, synchronization of vigilance and feeding activities among group members is not expected to provide optimum detection of predators because this pattern results in times when all individuals are feeding and none are vigilant. However, Pays, Renaud, et al. (2007) found that a pattern of synchronization among group members in Defassa waterbucks in their bouts of vigilance and foraging activities did not affect collective vigilance because the observed collective proportion of time during which at least one member of the group was

vigilant increased continuously with group size. Thus, the collective probability of predator detection may not to be impaired despite the synchronization reported in nonpersistent gatherings. Elgar et al. (1984) and Lima (1995) suggested that animals respond to an attack more quickly when they are already alerted than when they are feeding. Thus, it could be an adaptive strategy to copy the vigilant behavior of a neighbor as it may have detected a potential predator.

Factors affecting the degree of synchrony between individuals within pairs

Theory assumes that individuals should scan their environment independently of one another (Pulliam 1973; Bednekoff and Lima 1998). The lack of a pattern of coordinated vigilance among group members in nonpersistent gatherings is expected to be an efficient trade off between the detection of predators and the high cost required to organize vigilance through coordination. Under this assumption, we would predict that individuals would tend to develop more independent vigilant activity as their risk of being preyed on increased. Thus, in pademelons, the tendency of individuals to scan independently should increase with increasing distance from cover if the forest presents this species with a safer environment than the exposed pasture. However, our results show that the degree of synchrony between nearest neighbors increased with the distance to cover and the total number of conspecifics foraging on the grassy area and decreased when the distance to the pair's nearest neighbor increased. Therefore, the tendency toward synchronization was affected by both the presence and the distance of conspecifics and was sensitive to the size of the aggregation. This suggests that synchronization of vigilance between individuals is complex and may depend on several interrelated factors related to conspecifics (distance and density) and individuals' risk of predation.

Hirsch (2002) suggested that social and antipredator vigilance are totally compatible and might be efficiently combined. Although our study was not designed to distinguish social from antipredator vigilance, we believe that for species at risk of predation, group members may gain information about a detected danger by monitoring the behavior of conspecifics (via a copying strategy), facilitating escape from an attacking predator. Indeed, a group member that is alerted to danger by detecting another individual's reaction to an attacking predator could escape earlier and thus increase its individual probability of survival (Elgar et al. 1984; Lima 1995). More experimental and field studies investigating patterns of vigilance are now needed to investigate whether the degree of synchronization varies between genetically related and unrelated individuals and whether individuals that associate with familiar conspecifics might gain any benefits by coordinating their vigilance activity.

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