



## Predators, food and social context shape the types of vigilance exhibited by kangaroos



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Vigilance in prey species can serve many purposes, including predator detection and monitoring other group members, and is generally thought to impose a cost due to reduced food intake. However, previous studies have shown that herbivores are able to reduce the foraging cost of vigilance by chewing their food during vigilance bouts ('vigilance with chewing', as compared to 'vigilance without chewing'). How predation risk, food availability and competition affect both the functions and the foraging costs of vigilance remains an open question. We studied female eastern grey kangaroos, *Macropus giganteus*, during winter and summer, when available food supplies were poor and rich, respectively, to investigate how group size, distance to cover, proximity between foragers and food patch quality affected decisions of foraging female kangaroos to exhibit antipredator or social vigilance, distinguishing vigilance with and without chewing. The use of antipredator vigilance was mainly driven by the perception of predation risk, and antipredator vigilance without chewing decreased with increased group size whereas antipredator vigilance with chewing increased nonlinearly with group size in winter. Distance to cover affected both forms of antipredator vigilance in summer only but there was no effect of nearest-neighbour distance. Social vigilance was affected positively by group size, and distance between foragers affected social vigilance without chewing positively, particularly in winter, and social vigilance with chewing negatively. Finally, patch quality increased the use of social vigilance with chewing in both seasons and decreased the use of antipredator vigilance with chewing in winter. This study provides new information on how animals make decisions about the functions and foraging costs of vigilance and allows a better understanding of how social foragers respond to an ever-changing environment.

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Vigilance behaviour is crucial for prey in order to increase their safety. In gregarious species, this activity may also serve for the acquisition of social information (Beauchamp, 2001). Whatever its function, vigilance probably reduces the time an individual can allocate to other fitness-enhancing activities such as food acquisition, and may thus reduce energetic gains, particularly when prey have strong time constraints on foraging (McNamara & Houston, 1992). Therefore, gregarious prey should manage their use of vigilance carefully in order to balance the needs for safety, social information and food.

Although vigilance is thought to reduce food intake, the foraging cost of vigilance may be reduced in situations in which scanning and feeding are not incompatible (Cowlshaw et al., 2004; Illius & FitzGibbon, 1994; Spalinger & Hobbs, 1992). In fact, many species of birds and mammals are able to continue food ingestion by handling or chewing their food during vigilance periods (Baker, Stillman, Smart, Bullock, & Norris, 2011; Fortin, Boyce, Merrill, & Fryxell, 2004; Pays et al., 2012). In these species, it is therefore possible to distinguish a high-intensity form of vigilance in which the animal stops all activities and raises its head (hereafter termed 'vigilance without chewing') from a lower intensity form of vigilance during which the animal is vigilant while processing (i.e. handling or chewing) its food (hereafter termed 'vigilance with chewing') (e.g. Lima, Zollner, & Bednekoff, 1999; Meer, Pays, & Fritz, 2012; Pays et al., 2012; Robinson & Merrill, 2013). However, while

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differing in terms of their costs to foraging, these two types of vigilance may also differ in the quality of perception that they offer (Lima & Bednekoff, 1999). Carrying out multiple tasks simultaneously can reduce an animal's attention and efficiency with respect to predator detection (Dukas, 2002), and researchers have suggested that vigilance while handling food would reduce the chance of detecting a predator because of the noise resulting from the mastication process (Blanchard & Fritz, 2007; Fortin et al., 2004; Lima et al., 1999). The investment of social foragers in these two types of vigilance has been shown to vary with predation risk, food resource characteristics, group size and the distance between foragers (Benhaim et al., 2008; Fernández-Juricic, Beauchamp, & Bastain, 2007; Lima et al., 1999; Meer et al., 2012; Pays et al., 2012; Périquet et al., 2012).

Although vigilance has been mainly described as an antipredator behaviour, it can also function for the acquisition of social information in gregarious species (Beauchamp, 2001). Vigilance towards conspecifics (or social vigilance) may be used in various contexts such as monitoring competitors, searching for mates, protecting young or indirectly detecting predators (e.g. Burger & Gochfeld, 1994; Caro, 2005; Ellard & Byers, 2005; FitzGibbon, 1990). However, the function of social vigilance that has received the most attention is that it can allow social foragers to locate and assess the quality of food patches discovered by others (Barnard & Sibly, 1981; Smith, Benkman, & Coffey, 1999). This behaviour has been described in producer–scrounger models, which suggest that a forager can either search for food by itself (producer mode) or locate and exploit food patches discovered by its companions (scrounger mode) (Giraldeau & Beauchamp, 1999). Such behaviours have been observed in many taxa including birds, insects, fishes and mammals (see Beauchamp, 2014).

Vigilance is therefore a complex behaviour that can differ in terms of its foraging costs and be used for safety or social purposes. Foraging herbivores thus have different vigilance options and have to make choices between these in order to optimize the balance between their survival and resource acquisition. To further complicate the situation, an animal exhibiting either antipredator or social vigilance can use vigilance with or without chewing, and thus have the opportunity to moderate the cost of its social or antipredator bouts of vigilance by simultaneously processing its food. The factors that motivate individuals to invest in particular types of vigilance, considering both their functions and costs simultaneously, remain poorly documented, especially in herbivores. Predation risk, food quality and availability, and the occurrence and level of competition should all affect the vigilance tactics employed by foragers (Beauchamp, 2008; Favreau, Goldizen, & Pays, 2010; Fernández-Juricic & Kacelnik, 2004). A more nuanced understanding of the relationships between these two aspects of vigilance is therefore needed.

We studied wild female eastern grey kangaroos, *Macropus giganteus*, in Sundown National Park in southeast Queensland, Australia, to investigate how food resources, social context and perceived predation risk affected the decisions made by foraging individuals to exhibit particular types of vigilance (antipredator vigilance with or without chewing, and social vigilance with or without chewing). Using data from detailed behavioural monitoring of foraging females, we developed a statistical approach for modelling the probability of a kangaroo exhibiting a particular type of vigilance that allowed us to consider an individual's choices second by second. We chose this temporal scale to examine the drivers shaping the probability of an individual exhibiting a particular type of vigilance at the fine temporal scale at which such decisions can occur. We used this procedure to test whether group size, distance between the focal animal and its nearest neighbour, distance to cover and food patch quality affected the decisions of

foraging kangaroos to engage in a particular type of vigilance. We focused on females only because (1) they are known to exhibit different vigilance patterns from males (Pays & Jarman, 2008; Rieucou et al., 2012), (2) most males were less regularly observed at our study site, and (3) we wanted to avoid adding sex differences to our already complex analyses. As the grass eaten by kangaroos varies seasonally in abundance and quality in this part of Australia, we also investigated whether overall food conditions affected the behavioural decisions taken by kangaroos by studying their behaviour during two contrasting seasons, winter (offering the worst food conditions) and summer (offering the best food conditions).

Based on theoretical and empirical studies on social foragers, we made predictions on which factors should affect the probability of foraging kangaroos engaging in different types of vigilance. We predicted that kangaroos should invest part of their vigilance time in monitoring conspecifics in order to obtain social information. However, as prey, their time spent in vigilance should be mainly dedicated to antipredator vigilance (Favreau et al., 2010). Based on studies of other grazing herbivores, we also predicted that vigilance with chewing should be more common than vigilance without chewing (Pays et al., 2012), and that the investment in vigilance without chewing should increase with predation risk (Favreau, Pays, Goldizen, & Fritz, 2013). We thus predicted that female kangaroos should decrease their probability of using antipredator vigilance without chewing as their perceived risk of predation decreases. This occurs when animals forage in larger groups and closer to another individual because of the dilution of risk in such situations (Hamilton, 1971; Quinn & Cresswell, 2006), but also when closer to cover, as kangaroos seem to use cover as a source of protection against predators (Colagross & Cockburn, 1993). Also, because some species including eastern grey kangaroos use the vigilance of other group members as a clue to predation risk (FitzGibbon, 1990; Pays et al., 2009), and because vigilance with chewing is assumed to reduce detection abilities (e.g. Blanchard & Fritz, 2007), we predicted that individuals far from cover should increase their use of social vigilance without chewing. Because rich food patches are rare in winter, and kangaroos decrease their diurnal feeding in summer as a result of high temperatures (Jarman, 1984), causing them to experience a time constraint on foraging, they should reduce their vigilance time to increase their investment in food acquisition when foraging on rich food patches, as observed in other grazing herbivores (e.g. Pays et al., 2012). However, because rich patches should increase bite sizes, thereby increasing chewing time but decreasing searching time (Bradbury, Vehrencamp, Clifton, & Clifton, 1996; Spalinger & Hobbs, 1992), kangaroos should also have more spare time while chewing between bites and use it for vigilance with chewing (Fortin et al., 2004; Illius & FitzGibbon, 1994). Considering these two aspects, we predicted that kangaroos foraging on rich food patches should decrease their use of vigilance without chewing but increase their use of vigilance with chewing.

We made further predictions on how kangaroos should manage their social vigilance. Although there is no evidence that individual kangaroos assess the patches exploited by others (i.e. scrounging), this phenomenon has been observed in other mammals (see Beauchamp, 2014) and is assumed to increase when food is scarce and competition strong (Beauchamp, 2009). In kangaroos, competition is mainly exploitative, but interference can occur when food is scarce or when individuals are close (Jaremovic & Croft, 1991; Jarman, 1993). Therefore kangaroos maintain spacing during foraging, and tolerance of competitors at closer distances is reduced as a resource is more localized or valuable (Jaremovic & Croft, 1991). Consequently, we predicted that the probability of using social vigilance should increase with group size as more

group members need to be monitored (Favreau et al., 2010). If kangaroos use vigilance to scrounge, they should also increase their social vigilance when distances between foragers increase, because the quality of social information decreases when foragers are further apart (Fernández-Juricic & Kacelnik, 2004). For both predictions, this increase should be more pronounced in winter when food is scarce, and mainly involve vigilance with chewing to reduce the cost of this activity. However, when a competitor is too close, kangaroos may increase their social vigilance without chewing as there is a risk of an aggressive interaction (Jarman, 1993).

## METHODS

### *Study Site and Animals*

The study was conducted in Sundown National Park (Queensland, Australia, 28°9'S, 151°58'E) over 2 months in winter (July–August 2011) and 2 months in summer (November–December 2011). The 37.4 ha study area was composed of a mosaic of open pasture and mixed open forests primarily composed of eucalypts, *Eucalyptus melanophloia*, and pines, *Callitris intratropica*. Eastern grey kangaroos are gregarious and one of the most social species of marsupials. They form open-membership mixed-sex groups and exhibit fission–fusion social dynamics (Aureli et al., 2008; Clarke, Jones, & Jarman, 1995; Jarman, 1987). Kangaroos typically come onto the pasture to forage from the late afternoon to the early morning and rest during the daytime. The study area contained 240 females and notably fewer males (Best, Seddon, Dwyer, & Goldizen, 2013). Kangaroos' predators were occasionally observed or heard in the study area and included red foxes, *Vulpes vulpes*, and wedge-tailed eagles, *Aquila audax*, and possibly dingoes, *Canis lupus dingo*, although dingoes were rare if present at all. This research was approved by the University of Queensland's Animal Experimentation Ethics Committee, and conducted under a Scientific Purposes Permit from Queensland's Environmental Protection Agency.

### *Recording Data*

#### *Sampling of individuals*

We collected behavioural data by videotaping (video camera: Sony DCR-SR37, 60× optical zoom, Sony Corporation, Tokyo, Japan) selected focal adult females for 10 min periods during the few hours after dawn (summer: 0430–0730; winter: 0630–1030) and before dusk (summer: 1600–1830; winter: 1530–1730) when the animals came onto the pasture to forage. All field data were collected by the same observer (F.-R.F.). Kangaroos in this population have been intensively studied since 2009 and all resident females were identified, which allowed the observer to avoid resampling individuals more than once per day. Individuals were identified by a combination of personal features such as scars, facial markings, dark patches and ear shapes and tears (Best et al., 2013; Coulson, 1997; Jarman et al., 1989). For the purpose of this study, the observer selected 28 identified females from this population that were known to be present in the study area frequently and to be relatively easy to recognize. These selection criteria should not have biased our results in any way as they would not be related to an individual's vigilance behaviour.

The video sequences were used only if the size and composition of the group in which the focal animal was observed remained constant during the observation and group members stayed in the same location. Following Jarman's 'chain rule' (1987), we considered a group as a set of kangaroos that maintained social and spatial cohesion during focal sampling and whose most peripheral associate was within 15 m of another group member.

For our analyses, we used six randomly selected samples per female per season. Our analyses included observations of the 28 identified females in winter and 21 of these in summer, for a total of 168 focal samples in winter and 126 in summer, because we did not have enough observations for seven of the females in summer.

### *Recording behaviour*

Data were recorded on foot, keeping a minimum distance of 30 m between the focal individual and the observer to minimize disturbance. Owing to the nearly continuous presence of researchers and the occasional campers in the area, kangaroos were habituated to people and easy to approach. We characterized a kangaroo as vigilant if it raised its head above horizontal while either crouched or standing upright, and looked fixedly in one direction or scanned its surroundings (Jarman, 1987; Pays et al., 2007). To determine whether an animal was likely to be exhibiting antipredator or social vigilance, we used head orientation as an indicator of the target of the individual's visual attention. This method has been used in previous studies of birds (Fernández-Juricic, Siller, & Kacelnik, 2004), rodents (Quirici, Castro, Oyarzun, & Ebensperger, 2008) and eastern grey kangaroos (Edwards, Best, Blomberg, & Goldizen, 2013; Favreau et al., 2010). The eyes of macropodids have a frontolateral position, allowing them to have both wide lateral monocular vision and some forward binocular vision (Hume, Jarman, Renfree, & Temple-Smith, 1989). We also observed in the field that, when individuals were disturbed by other people or cars, they interrupted their activity to monitor the disturbance and their head direction followed the movement of the disturbance. We thus believe that kangaroos' head orientation is a good indicator of the target of their visual attention. Although we cannot be absolutely certain of the function of any particular vigilance bout, we assumed a female to be using antipredator vigilance when she oriented her head away from her group and to be mostly engaged in social vigilance when her head was oriented towards other group members. In addition, we followed the method developed by Favreau et al. (2010) for this species by only taking samples from females located on the periphery of groups for our analyses, as antipredator and social vigilance could not easily be distinguished for central individuals, and by using only groups of at least three individuals. To account for the cost/intensity of vigilance in our study, we distinguished vigilance with chewing (when an individual raised its head while chewing) from vigilance without chewing (when it raised its head without chewing) (Lima & Bednekoff, 1999; Unck, Waterman, Verburgt, & Bateman, 2009). Thus, the function (social or antipredator) and foraging cost (vigilance with or without chewing) of each bout of vigilance were recorded.

For each focal sample, we measured the following predictor variables. We recorded the group size, including all age–sex classes, and measured the distance between the focal animal and its nearest adult neighbour with a range finder at the beginning of the 10 min sample. To do this, we measured the distance between the observer and the focal female, the distance between the observer and the female's nearest neighbour and the angle between them using a protractor and then later calculated interindividual distances with trigonometric formulas. We similarly measured the distance between the focal animal and the nearest cover (i.e. distance to the edge of the forest) at the beginning of the observation. As already mentioned, we only analysed data from groups that stayed relatively immobile. However, if the distance between individuals or the distance to cover changed markedly during the observation period, we took a second measure at the end of the observation and averaged both distances.

At the end of each focal sample, the observer measured characteristics of the patch exploited by the animal to estimate patch

characteristics in terms of the quantity and quality of vegetation available on food patches. This procedure has been described in Favreau et al. (2013) and is summarized here. To measure patch quality, the observer put down a quadrat (90 × 90 cm) with 81 grid crossings at the spot where the animal had spent most of its time feeding during the observation, and recorded a greenness index for all plants under each grid crossing. This index comprised two categories, brown (plants with low energetic value) and green (plants with high energetic value) (Bradbury et al., 1996), and allowed us to estimate the percentage of plant material that was green for each food patch. To measure the quantity of vegetation in patches, we determined grass biomass using a pasture meter (Herbo-LIS Arvalis, Paris, France), an instrument that uses the height of a plastic plate that has fallen onto the vegetation from a standard height to estimate the standing crop of the vegetation. To convert the height of the pasture meter (PM) into biomass, we calibrated the pasture meter for each season by randomly selecting 60 patches of different heights. The relationship between PM height and biomass was measured by clipping, drying and weighing the plant biomass below the pasture meter (winter: biomass = 12.09 + 2.6634 × PM height,  $P < 0.001$ , adjusted  $R^2 = 0.87$ ,  $N = 50$ ; summer: biomass = 8.33 + 3.1131 × PM height,  $P < 0.001$ , adjusted  $R^2 = 0.86$ ,  $N = 51$ ).

From these two measures of patch characteristics, we established an index of patch quality (i.e. poor patch, medium patch or rich patch), reflecting the quality of the patch exploited by the kangaroo in relation to its digestibility (Table 1), and attributed a single patch quality index to the site of each focal observation. Kangaroos are short-grass grazers, and the relationship between greenness, biomass and food intake in such herbivore species is complex (Wilmshurst, Fryxell, & Colucci, 1999). Eastern grey kangaroos preferentially select green leaves of grass, preferring short grass and avoiding long dry grass (Bell, 1973; Clarke, Jones, & Jarman, 1989). Similar preferences for patches of low to intermediate biomass have been observed in other short-grass grazers of similar body size to the eastern grey kangaroo, such as sheep, antelopes and other kangaroo species (Bradbury et al., 1996; Short, 1985; Wilmshurst et al., 1999). Such a preference would arise because an increase in biomass increases fibre content but decreases digestibility for short-grass grazers (Fryxell, 1991). Therefore, for such species, a patch with a high biomass of green grass is of lower quality than a patch with a medium biomass of green grass as the former contains more fibre and is less digestible. Based on this framework, rich patches were those at and close to the optimum biomass and greenness (within 30% from the optimal patch)

**Table 1**  
Table of patch richness index for short-grass grazers in relation to patch biomass and greenness

Biomass (g/m <sup>2</sup> )	Percentage of green grass						
	0–40	>40–50	>50–60	>60–70	>70–80	>80–90	>90–100
0–5	Poor	Poor	Medium	Medium	Medium	Medium	Medium
>5–10	Poor	Poor	Medium	Rich	Rich	Rich	Rich
>10–15	Poor	Medium	Medium	Rich	Rich	Rich	Rich
>15–20	Poor	Medium	Rich	Rich	Rich	Rich	Rich
>20–25	Poor	Medium	Rich	Rich	Rich	Rich	<b>Rich</b>
>25–30	Poor	Medium	Rich	Rich	Rich	Rich	<b>Rich</b>
>30–35	Poor	Medium	Rich	Rich	Rich	Rich	Rich
>35–40	Poor	Medium	Medium	Rich	Rich	Rich	Rich
>40–45	Poor	Poor	Medium	Rich	Rich	Rich	Rich
>45–50	Poor	Poor	Poor	Medium	Medium	Rich	Rich
>50–55	Poor	Poor	Poor	Medium	Medium	Medium	Medium
>55–60	Poor	Poor	Poor	Medium	Medium	Medium	Medium

'Poor' means poor patch richness, 'medium' medium patch richness and 'rich' rich patch richness. Values for expected optimal patches are in bold.

for herbivores of kangaroo size, medium patches were those within 60% from the optimal patch, and poor ones were those further from the optimum.

#### Data Analyses

To evaluate the seasonal differences in food patch characteristics, we ran Kolmogorov–Smirnov two-sample tests to compare the distributions of the percentages of vegetation of different greenness and of different biomass between the two seasons.

We extracted from our data which activity was exhibited by the focal individual at each second during the 600 s sequences. First, we calculated the time spent by female kangaroos in each vigilance type (i.e. antipredator vigilance with and without chewing, and social vigilance with and without chewing), as well as the frequency and mean durations of the vigilance scans. For each season, we ran separate linear mixed-effect models (LME; 'lme' function of the 'nlme' R package; Pinheiro & Bates, 2000) for the proportion of time spent in vigilance, the mean frequency of vigilance and the mean scan duration as the response variables, including the type of vigilance exhibited, group size, distance to the nearest neighbour, distance to cover and patch quality as fixed effects and individual identity as a random factor. To satisfy assumptions of normality, the proportion of time spent in vigilance was logit transformed, and the mean frequency and duration of vigilance scans were log transformed in all models.

Then, because we wanted to explore how ecological and social contexts affected the decisions of foraging kangaroos to engage in different types of vigilance, we investigated which factors affected the probability of an individual exhibiting a particular type of vigilance at a given second, by adapting and extending the statistical procedure described in Pays et al. (2009). This analysis allowed us to investigate both the instantaneous decisions that an individual made (and the factors influencing these decisions) and the investment in vigilance (i.e. scan duration or frequency), because when the probability of being vigilant increased, both the scan durations and the mode of frequencies of vigilant acts were likely to increase. Pays et al. (2009) developed a statistical procedure to investigate an individual's decisions about whether to be vigilant or not. Our procedure allowed us to investigate an individual's decisions among five options (not vigilant or engaged in one of the four types of vigilance). As these five options were treated as the response variable, we ran multinomial logistic regression models using the package 'R2BayesX' using the function bayesx() in the R software (Umlauf, Lang, Kneib, & Zeileis, 2011). In this procedure, we fixed the level 'nonvigilant' of the response variable (corresponding mainly to foraging activity, see Results) as the reference, allowing us to model the probabilities of a kangaroo exhibiting the four types of vigilance when she was foraging. We included group size, distance between the focal animal and its nearest neighbour, distance to cover and patch quality (poor, medium, rich) as fixed factors and ran a model for each season. To consider potential nonlinear trends between the continuous variables and the probabilities of exhibiting the four types of vigilance, we also included the squares of group size, distance between the focal animal and its nearest neighbour and distance to cover as fixed factors.

We also had to consider temporal autocorrelation in our analyses. Pays et al. (2009) showed that the probability of a kangaroo exhibiting a vigilant behaviour was strongly affected by the behaviour of the focal animal at the previous second. Therefore we investigated whether there was autocorrelation in the individual sequences of 600 s. We used a partial autocorrelation function that provided an estimate of the correlation between observations separated by a lag of  $m$  time units, for  $m = 0, 1, 2, \dots, M$  (see Cryer & Chan, 2010 for more statistical details). We estimated the values of

the autocorrelation functions for all five behaviours (foraging, social and antipredator vigilance with chewing and without chewing) in the individual sequences using the function `pacf()` in R (Mairdona & Braun, 2007). For each season, there was an obvious and substantial serial correlation in individual sequences that occurred with a lag of 1 s. For lags greater than 1 s, the autocorrelation estimates fell inside the 95% confidence intervals, so we could assume that no serial correlation existed with a lag greater than 1 s (see Appendix Fig. A1). Consequently, to test whether the probabilities of a kangaroo exhibiting the four types of vigilance were affected by the environmental and social factors, we included its behaviour at the previous second as a fixed factor in the models (named 'Behaviour before' in the tables) to control for the serial correlation existing in our data set. To simplify the procedure, we grouped the four different types of vigilance together for the focal animal's activity at the previous second to consider only two states (nonvigilant versus vigilant). In contrast to Pays et al.'s (2009) study, it was not possible to consider the behaviour of other group members.

This analysis described a biological system in which a first-order Markov's assumption applies. The probability of a female being vigilant (whatever the type of vigilance), taking into account the past ( $t-1$ ,  $t-2$ ,  $t-3$  s, etc.), could be reduced to a law accounting for only the immediate past  $t-1$  s (see Meyn & Tweedie, 1993). Accepting Markov's assumption, we assumed that the probability of an individual exhibiting a vigilance act was affected by its own state at the previous second. When we included the behaviour at the previous second as an independent variable in the model, we observed almost no serial correlation in the residuals. It is crucial to understand here that a first-order process (i.e. a system considering a  $t-1$  s memory) does not preclude an individual maintaining its activity for several seconds. It considers only that the animal's state at  $t_0$  was dependent on the previous one at  $t-1$  s. Such an approach (represented by a first-order process) has been well documented and used to describe several ecological systems including animal behaviour (Franke, Caelli, & Hudson, 2004; McCowan, Hanser and Doyle, 1999; Nilsen, Chan, Huber, & Kravitz, 2004).

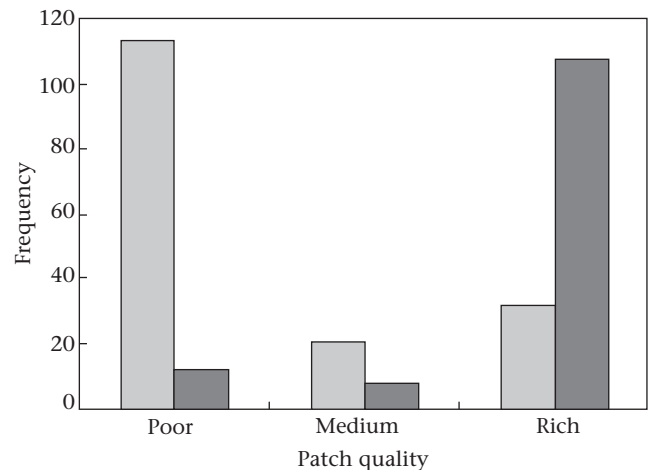
We ran the mixed-effects multinomial regression models including individual ID as a random factor. We also standardized the number of focal samples per individual by including only six focal samples for each female in a season (i.e.  $6 \times 10$  min = 3600 s). We avoided the nonindependence that would have been caused by sampling multiple individuals in the same group by including only one individual per group. Finally, model selection was AIC guided considering the potential curvilinear trends of continuous predictors (Appendix Table A1). From the best model, selected by AIC, the significance of each factor was tested using comparative deviance (chi-square test; Appendix Table A2).  $\beta$  coefficients with their standard errors (SE) were estimated using a bootstrap procedure.

The statistical analyses were performed with R version 3.0.2 (R Core Team 2013).

## RESULTS

### Seasonal Differences in Food Patch Characteristics

The percentage of vegetation that was green differed significantly between winter and summer (Kolmogorov–Smirnov two-sample test:  $D = 0.73$ ,  $N_1 = 168$ ,  $N_2 = 126$ ,  $P < 0.001$ ), as did the biomass of the vegetation at foraging patches (Kolmogorov–Smirnov two-sample test:  $D = 0.29$ ,  $N_1 = 168$ ,  $N_2 = 126$ ,  $P < 0.001$ ). Pastures were much greener but slightly lower in biomass during summer than winter. Consequently 'poor' patches were dominant in winter and 'rich' patches dominant in summer (Fig. 1).



**Figure 1.** Frequencies of patches used by female kangaroos that were poor, medium or rich in winter (pale grey,  $N = 168$ ) and summer (dark grey,  $N = 126$ ).

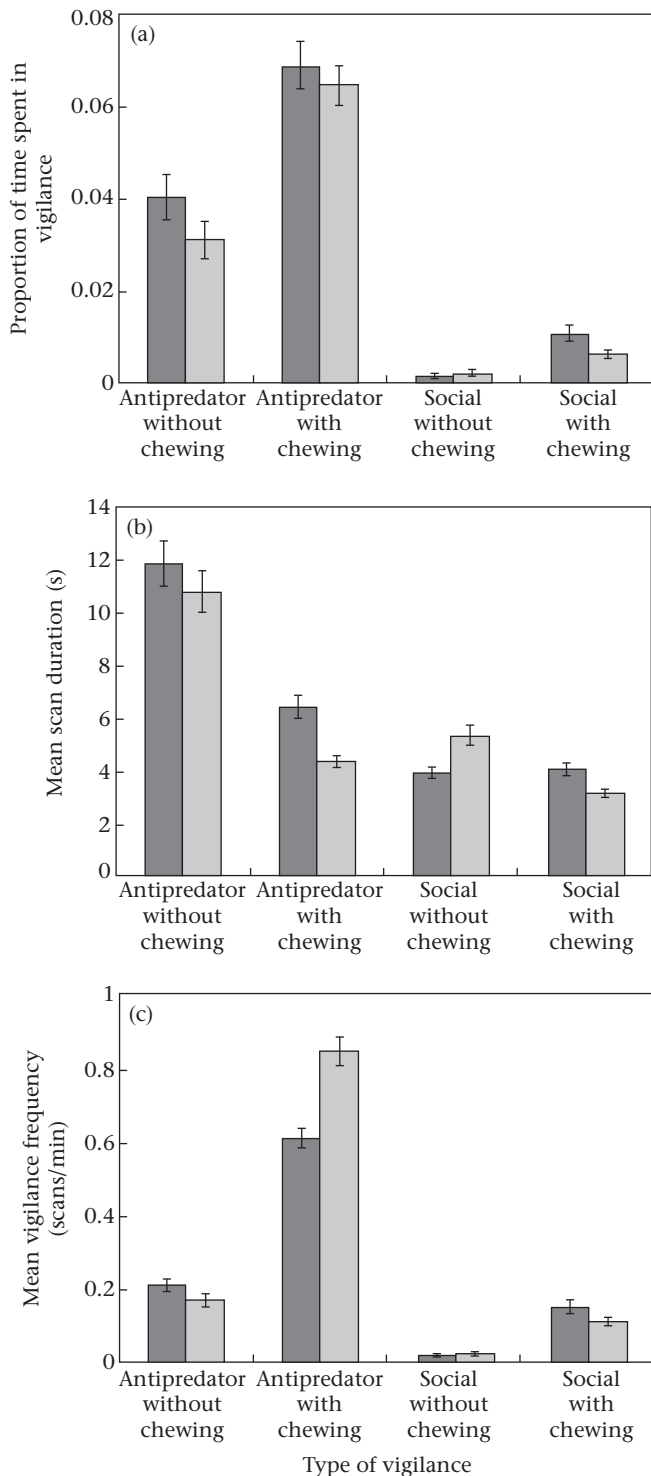
### Investment in Vigilance

Analysis of the 10 min video sequences showed that female kangaroos spent most of their time foraging (mean  $\pm$  SE:  $85.3 \pm 0.9\%$  in winter and  $86.7 \pm 0.8\%$  in summer) and between  $10.8 \pm 0.7\%$  (in summer) and  $12.9 \pm 0.8\%$  (in winter) of their time being vigilant. The time invested by female kangaroos in the four different types of vigilance varied in each season (Appendix Table A3). Analyses in which antipredator vigilance without chewing was used as a reference show that female kangaroos were more likely to engage in antipredator vigilance with chewing, less likely to engage in social vigilance with chewing and even less likely to engage in social vigilance without chewing (Appendix Table A3, Fig. 2a). Mean scan duration and frequency also varied according to the type of vigilance in both seasons (Appendix Tables A4, A5). Compared to the reference (antipredator vigilance scans with chewing), antipredator vigilance scans without chewing were longer, whereas social vigilance scans with and without chewing were shorter (Appendix Table A4, Fig. 2b). When antipredator vigilance without chewing was used as the reference, scans of antipredator vigilance with chewing were more frequent, whereas scans of social vigilance with chewing were less frequent, and scans of social vigilance without chewing even less frequent (Appendix Table A5, Fig. 2c). Tables A3–A5 also include the significance of the other predictor variables, including group size, distance to the nearest neighbour, distance to cover and patch quality; group size and distance to cover were the variables that had a significant effect on vigilance patterns.

### Factors Affecting Types of Vigilance Used

AIC-based model selection (Appendix Table A1) and deviance values between models (Appendix Table A2) show that group size, distance between the focal animal and its nearest neighbour, distance to cover, patch quality and whether females were vigilant at the previous second all affected the probabilities of exhibiting a particular type of vigilance.

Female kangaroos were more likely to be vigilant when they had already been vigilant at the previous second, whatever the season and the type of vigilance (Table 2). Figs. 3–5 show that when an animal was foraging, its probability of engaging in any particular type of vigilance was low and showed little variation in relation to the factors considered (horizontal curves near 0), whereas when it had been vigilant at the previous second, the probabilities of



**Figure 2.** (a) Proportions of time spent by female kangaroos in antipredator vigilance without and with chewing, and in social vigilance without and with chewing during winter (dark grey) and summer (pale grey). (b) Mean scan durations and (c) mean scan frequencies for the different types of vigilance exhibited by female kangaroos in winter (dark grey) and summer (pale grey). Means are given  $\pm$ SE.

vigilance showed more variation. These results are described here based on the significance of the coefficients derived for each factor (Table 2), and the trends shown in Figs. 3–5. Because female kangaroos spent most of their vigilance time in antipredator vigilance, their probabilities of exhibiting either type of social vigilance were generally low, as was the extent to which their social vigilance

varied in relation to the studied factors, even when they were significant.

An increase in group size affected the probability of females exhibiting antipredator vigilance with and without chewing in a nonlinear way, but this effect was different for each season (Table 2, Fig. 3a, e, i, and b, f, j, respectively). In winter, the probabilities of females exhibiting both types of antipredator vigilance were similar in small groups but strongly increased for vigilance with chewing and decreased for vigilance without chewing in larger groups. In summer, the probabilities of females exhibiting antipredator vigilance without chewing were higher than for vigilance with chewing in small groups but tended to be similar in large groups. The effect of group size on the probability of kangaroos exhibiting social vigilance without chewing was weak and nonlinear for both seasons (Table 2, Fig. 3c, g, k). An increase in group size had a positive effect on the probability of kangaroos exhibiting social vigilance with chewing in both seasons. However, in winter the probability tended to decrease in groups larger than eight individuals (Table 2, Fig. 3d, h, l).

In both seasons, the distance between the focal female and her nearest neighbour did not significantly affect the probability of her using antipredator vigilance (Table 2, Fig. 4). In winter, distance to the nearest neighbour affected the female's probability of exhibiting social vigilance without chewing positively and social vigilance with chewing negatively. The effect of this variable was nonlinear (Table 2) but extremely weak in summer (Fig. 4c, g, k and d, h, l), with the patterns opposite to those shown in winter owing to the significant effect of the square of the distance to the nearest neighbour.

The effect of distance to cover on the probability of kangaroos exhibiting antipredator vigilance in winter was not significant for vigilance without and with chewing (Table 2). In summer, the use of both types of vigilance was affected by distance to cover but in opposite directions. The use of vigilance without chewing increased from 0 to 60 m to cover and then decreased, whereas the use of vigilance with chewing decreased from 0 to 60 m, increased from 60 to 100 m and decreased again at greater distances (Table 2, Fig. 5a, e, i, and b, f, j). The effect of distance to cover on the probability of exhibiting social vigilance without chewing was also small and negative in winter only (Table 2, Fig. 5c, g, k). Its effect on the use of social vigilance with chewing was significant in both seasons and tended to increase at far distances (Table 2, Fig. 5d, h, i).

Finally, the quality of food patches had significant effects on the probabilities of kangaroos showing vigilance (Table 2, Figs. 3–5), but the effects of this variable were difficult to interpret in many cases because the signs differed when comparing poor and medium patches and poor and rich patches. Our analyses showed, however, that patch quality increased the use of social vigilance with chewing in both seasons and decreased the use of antipredator vigilance with chewing in winter.

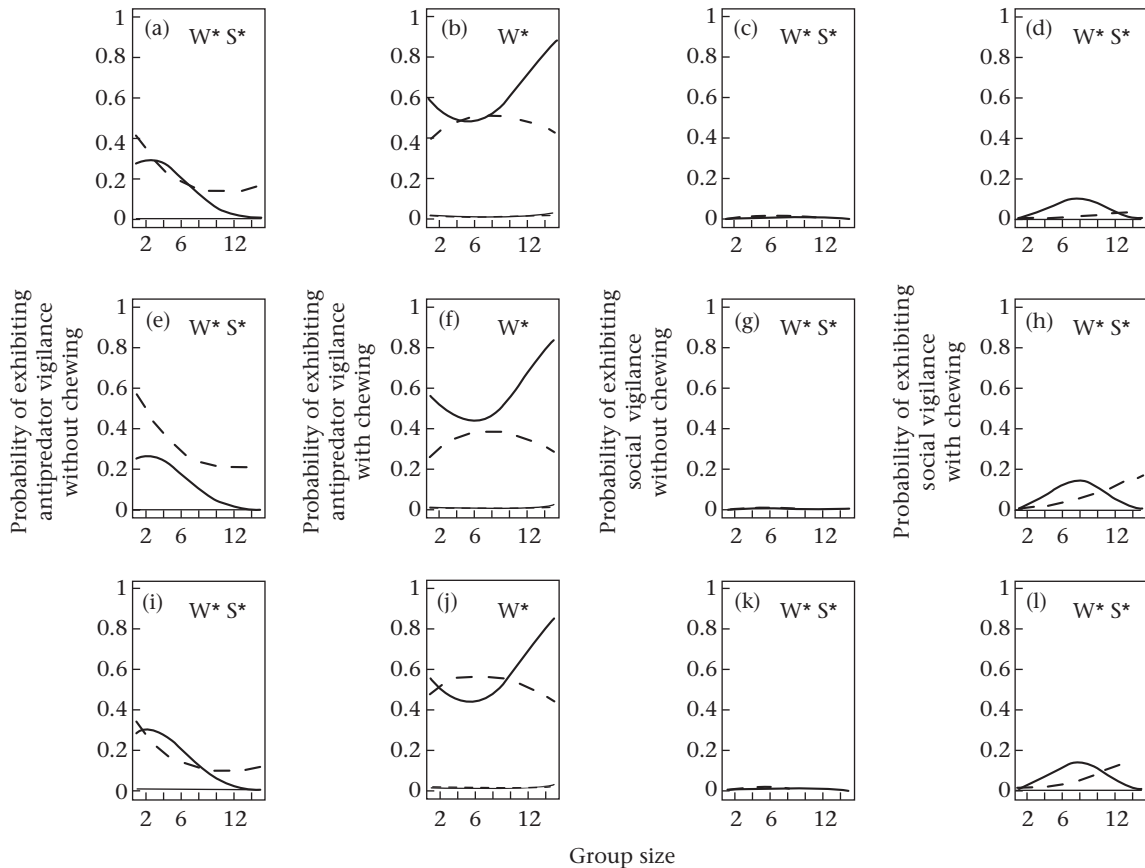
## DISCUSSION

Female kangaroos spent most of their time being vigilant looking outwards from their foraging groups and thus seemed to focus more on predator detection than on the acquisition of social information. A similar pattern had already been observed in this species (Favreau et al., 2010) and in other semisocial mammals (e.g. Le Roux, Cherry, Gyax, & Manser, 2009). In contrast, in highly social species such as primates, monitoring conspecifics can be the primary function of vigilance, as for example in brown capuchin monkeys, *Cebus apella*, for which social vigilance can represent up to 75% of vigilance time (Hirsch, 2002). For methodological reasons, in this study we focused only on peripheral females within foraging groups. However, peripheral animals are expected to be more

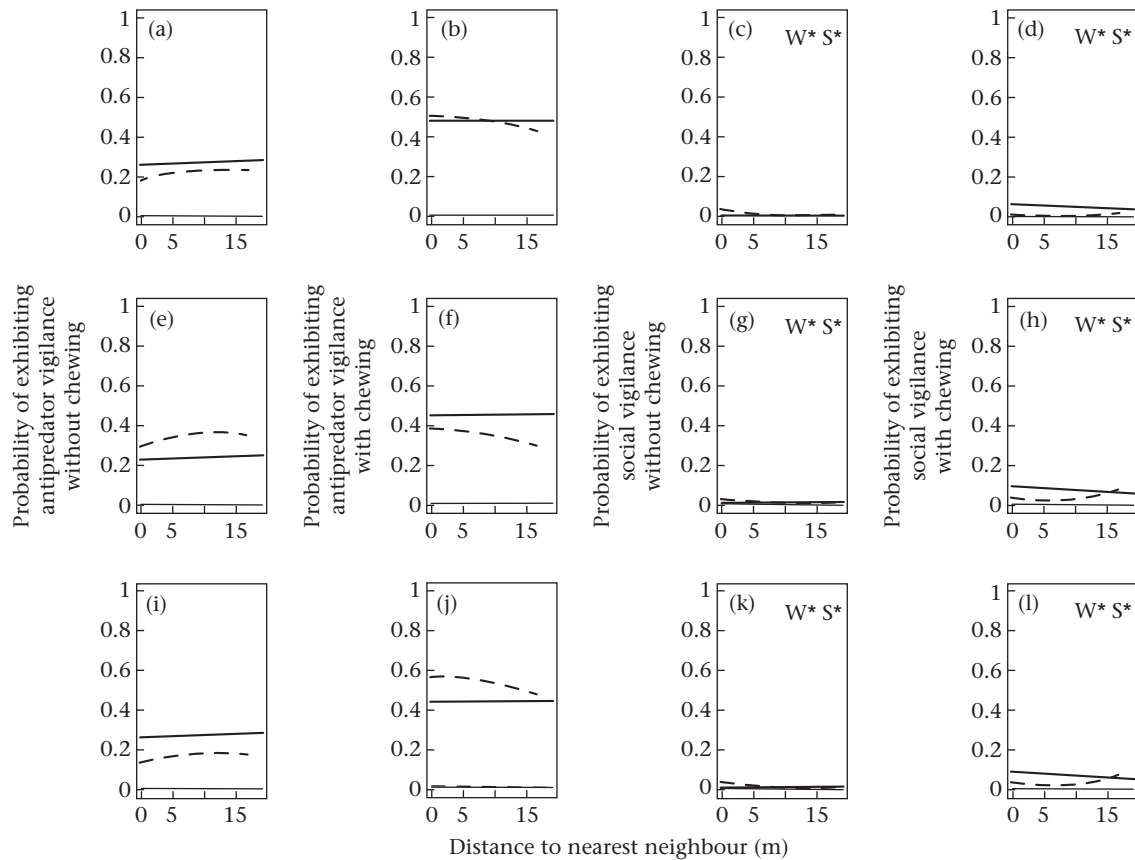
**Table 2**  
β coefficients and P- values for the factors influencing the probabilities that foraging female kangaroos used the four types of vigilance.

Factors	Antipredator vigilance without chewing			Antipredator vigilance with chewing			Social vigilance without chewing			Social vigilance with chewing		
	B	SE	P(t)	β	SE	P(t)	β	SE	P(t)	B	SE	P(t)
<b>Winter</b>												
(Intercept)	-5.103	0.146	<0.001	-3.532	0.095	<0.001	-9.547	0.57	<0.001	-7.036	0.204	<0.001
Behaviour before: vigilant	5.987	0.057	<0.001	5.326	0.04	<0.001	5.000	0.186	<0.001	4.987	0.076	<0.001
Group size	-0.035	0.060	0.280	-0.275	0.033	<0.001	0.516	0.183	0.002	0.613	0.075	<0.001
Group size <sup>2</sup>	-0.018	0.006	0.002	0.019	0.003	<0.001	-0.041	0.015	0.003	-0.041	0.006	<0.001
Distance to the nearest neighbour	0.007	0.007	0.191	0.002	0.006	0.348	0.047	0.023	0.019	-0.022	0.009	0.009
Distance to cover	-0.002	0.002	0.241	-0.001	0.002	0.301	-0.018	0.007	0.010	-0.031	0.003	<0.001
Distance to cover <sup>2</sup>	0.0001	0.00002	0.389	0.0001	0.00002	0.271	0.0001	0.00006	0.095	0.0002	0.00003	<0.001
Patch quality: medium rich	-0.267	0.057	<0.001	-0.199	0.077	0.002	0.383	0.285	0.09	0.271	0.109	0.006
	-0.078	0.062	0.104	-0.164	0.055	0.001	0.377	0.248	0.064	0.222	0.110	0.022
<b>Summer</b>												
(Intercept)	-5.073	0.163	<0.001	-3.997	0.117	<0.001	-9.174	0.724	<0.001	-7.998	0.442	<0.001
Behaviour before: vigilant	5.732	0.069	<0.001	4.944	0.041	<0.001	5.236	0.213	<0.001	4.570	0.118	<0.001
Group size	-0.338	0.045	<0.001	-0.029	0.028	0.151	0.871	0.229	<0.001	0.267	0.062	<0.001
Group size <sup>2</sup>	0.014	0.003	<0.001	-0.001	0.002	0.333	-0.077	0.022	<0.001	-0.005	0.004	0.078
Distance to the nearest neighbour	0.039	0.029	0.208	-0.002	0.018	0.453	-0.212	0.065	<0.001	-0.111	0.038	0.002
Distance to the nearest neighbour <sup>2</sup>	-0.002	0.002	0.356	-0.001	0.001	0.254	0.008	0.002	0.009	0.009	0.002	<0.001
Distance to cover	0.011	0.003	<0.001	-0.005	0.003	0.036	-0.014	0.009	0.062	-0.040	0.006	<0.001
Distance to cover <sup>2</sup>	-0.0001	0.00003	<0.001	0.0001	0.00002	0.031	0.0001	0.00008	0.185	0.0003	0.00005	<0.001
Patch quality: medium rich	0.525	0.161	<0.001	-0.218	0.118	0.032	-0.125	0.281	0.500	1.511	0.399	<0.001
	-0.141	0.112	0.107	0.242	0.083	0.002	0.106	0.519	0.419	1.447	0.363	<0.001

Values were extracted from multinomial logistic regression models run for winter and summer separately. Individual ID was included as a random factor. Group size, distance to the nearest neighbour and distance to cover were modelled as continuous variables. 'Behaviour before' (nonvigilant, vigilant) and 'patch quality' were categorical and 'nonvigilant' and 'poor' were used as the references, respectively. Significant P values are in bold.



**Figure 3.** Probabilities of female kangaroos exhibiting each type of vigilance studied when they had been vigilant (thick lines) or foraging (thin lines) at the previous second, in relation to group size and food patch quality in winter (unbroken lines) and summer (dashed lines). (a–d) Rich patches, (e–h) medium patches and (i–l) poor patches. The types of vigilance considered are (a, e, i) antipredator vigilance without chewing, (b, f, j) antipredator vigilance with chewing, (c, g, k) social vigilance without chewing and (d, h, l) social vigilance with chewing. Asterisks indicate whether the trends were significant for each season (W: winter; S: summer); see Table 2 for details. Curves are calculated using the mean distance to cover (W and S: 47 m) and distance to the nearest neighbour (W: 5.6; S: 4.3 m) extracted from our data set for each season.



**Figure 4.** Probabilities of female kangaroos exhibiting each type of vigilance studied when they had been vigilant (thick lines) or foraging (thin lines) at the previous second, in relation to the distance to their nearest neighbour and food patch quality in winter (unbroken lines) and summer (dashed lines). (a–d) Rich patches, (e–h) medium patches and (i–l) poor patches. The types of vigilance considered are (a, e, i) antipredator vigilance without chewing, (b, f, j) antipredator vigilance with chewing, (c, g, k) social vigilance without chewing and (d, h, l) social vigilance with chewing. Asterisks indicate whether the trends were significant for each season (W: winter; S: summer); see Table 2 for details. Curves are calculated using the mean group size (W: 4.3; S: 5.0) and distance to cover (W and S: 47 m) extracted from our data set for each season.

exposed to predation than central ones, and thus might allocate more time to antipredator vigilance. In addition, animals in the centre of groups would be expected to show higher levels of social vigilance as they are surrounded by more individuals. Our focus on peripheral females may partially explain why levels of social vigilance were low and why the factors studied had small effects on social vigilance.

Regardless of its function, the vigilance of female kangaroos was mainly composed of vigilance with chewing. Similar observations have been found in other grazing herbivores including impalas, *Aepyceros melampus* (Pays et al., 2012) and plains zebra, *Equus quagga* (Périquet et al., 2012), consistent with the hypothesis that foragers try to limit the foraging cost of their vigilance (Fortin et al., 2004). The vigilance scans of kangaroos with and without chewing also differed in their duration and frequency. Overall, vigilance scans without chewing were longer but less frequent than scans with chewing (Fig. 2), showing the greater intensity of this form of vigilance compared to vigilance with chewing.

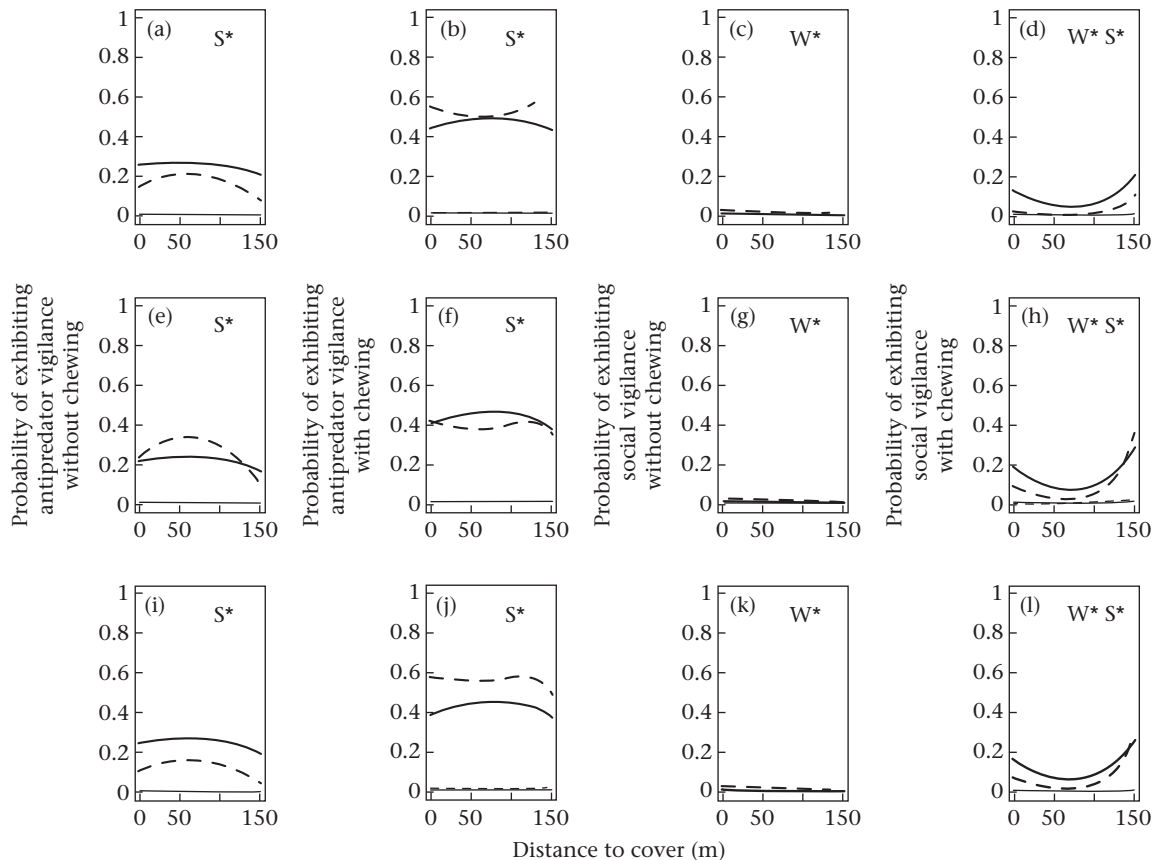
We also found that the probability of female kangaroos engaging in, and therefore investing more in, a particular type of vigilance varied in relation to group size, distance to their nearest neighbour, distance to cover and patch quality, and that these effects could also vary seasonally. For clarity, we only discuss here the strongest patterns observed.

The probability of kangaroos exhibiting antipredator vigilance without chewing decreased as group size increased, regardless of the season. This result supports the classical ‘safety in numbers’

hypothesis, which states that prey can reduce their vigilance in large groups because of collective detection (Pulliam, 1973), dilution (Hamilton, 1971) and confusion effects (Landeau & Terborgh, 1986). This ‘group size effect’ has already been observed in many taxa (Elgar, 1989; Roberts, 1996), including eastern grey kangaroos (Favreau et al., 2010; Jarman, 1987; Pays et al., 2007). Although other studies on birds and mammals have reported a reduction of both types of antipredator vigilance with group size (e.g. Beauchamp & Livoreil, 1997; Lima et al., 1999; Périquet et al., 2012), we found that antipredator vigilance with chewing tended to increase nonlinearly with group size in winter. The reduction of antipredator vigilance without chewing is likely to increase the individual’s intake rate, which should in turn increase chewing time available for performing vigilance with chewing, which is the lower cost form of vigilance. The stronger effect in winter probably occurred because most food patches were poor and composed of fibrous dry grass that required longer chewing time than soft green grass. An increase in group size also affected the investment of females in social vigilance, particularly by increasing their use of social vigilance with chewing. Although a positive effect of group size on social vigilance had been predicted by theory (Treves, 1999) and observed in eastern grey kangaroos (Favreau et al., 2010), these studies did not separate social vigilance into vigilance with and without chewing.

Distance to the nearest neighbour did not affect the investment of females in antipredator vigilance. This result does not support Hamilton’s ‘selfish herd theory’, which states that proximity





**Figure 5.** Probabilities of female kangaroos exhibiting each type of vigilance studied when they had been vigilant (thick lines) or foraging (thin lines) at the previous second, in relation to the distance to cover and food patch quality in winter (unbroken lines) and summer (dashed lines). (a–d) Rich patches, (e–h) medium patches and (i–l) poor patches. The types of vigilance considered are (a, e, i) antipredator vigilance without chewing, (b, f, j) antipredator vigilance with chewing, (c, g, k) social vigilance without chewing and (d, h, l) social vigilance with chewing. Asterisks indicate whether the trends were significant for each season (W: winter; S: summer); see Table 2 for details. Curves are calculated using the mean group size (W: 4.3; S: 5.0) and distance to the nearest neighbour (W: 5.6; S: 4.3 m) extracted from our data set for each season.

between prey decreases their personal 'domain of danger' and thus reduces the predation risk to an individual (Hamilton, 1971; Quinn & Cresswell, 2006). In contrast, distance to the nearest neighbour did affect the social vigilance of kangaroos. Although this effect was weak in summer, it was pronounced in winter but with contrasting patterns for the different types of social vigilance considered. Because food was scarce in winter, we interpreted these effects in relation to the acquisition of information about food patches or competitors. First, kangaroos increased their social vigilance without chewing as their nearest-neighbour distance increased. This result agrees with findings from bird studies showing that the quality of social information decreases when foragers are further apart, leading to an increase in vigilance time (Fernández-Juricic & Kacelnik, 2004; Pöysä, 1994). The fact that this pattern involved vigilance without chewing may be (1) because overall food quality is low in winter, reducing bite sizes and thus the probability of animals exhibiting vigilance with chewing, but also (2) because vigilance without chewing may allow individuals to acquire more accurate information (Lima & Bednekoff, 1999). Second, kangaroos increased their use of vigilance with chewing as the distance to their nearest neighbour decreased. Although interference competition is rare in this species, it has been shown to occur when food is scarce and individuals are too close to each other (Jaremovic & Croft, 1991; Jarman, 1993). We interpreted this increase in social vigilance with chewing as a way for kangaroos to maintain spacing and/or avoid aggression or displacement from their neighbours.

In winter, distance to cover did not affect a kangaroo's antipredator vigilance, whereas in summer it had opposing effects on the two types of antipredator vigilance. Although the overall level of antipredator vigilance changed only weakly as distance to cover increased, its components varied nonlinearly. The amount of vigilance without chewing increased from 0 to 60 m and then decreased, whereas the amount of vigilance with chewing decreased from 0 to 60 m and then increased. In prey, the relationship between distance to cover and vigilance can be positive, negative or nonexistent, depending on whether cover is perceived as obstructive or protective, which in turn varies according to their predators' hunting strategies (Lazarus & Symonds, 1992; Loarie, Tambling & Asner, 2013). For eastern grey kangaroos, cover has often been considered protective because (1) they flee into cover when alarmed, (2) they rest near or in cover and (3) they spend more time feeding close to cover when in risky habitats (Banks, 2001; Colagross & Cockburn, 1993). However, the lack of a relationship between vigilance and distance to cover has been reported in some studies of eastern grey kangaroos and other macropodid species (e.g. Evans, Elgar, & Handasyde, 2005; Favreau et al., 2010; Wahungu, Catterall, & Olsen, 2001). Kangaroos (particularly small individuals) are preyed by several predators using different hunting strategies (Evans et al., 2005). Terrestrial predators can hide in cover, whereas the hunting success of raptors is greatest in the open. The fact that kangaroos increased their use of intense vigilance at around 60 m from cover suggests that they may have been concerned about both terrestrial and avian

predators at intermediate distances. This pattern probably only occurred in summer because the vegetation was more developed in that season (F.-R. Favreau, personal observation), reducing visibility and predator detection (Burger, 2001). Distance to cover also negatively affected the investment of individuals in social vigilance without chewing in summer only. This effect may have been because there is less visual obstruction in the open and companions are easier to locate and monitor than in more closed habitats (Metcalf, 1984).

Except for social vigilance without chewing, patch quality influenced the probability of kangaroos exhibiting every type of vigilance in both seasons. In winter, the patterns were unambiguous, and, contrary to our predictions, patch quality was more likely to affect the function of vigilance than its cost. In this season, an increase in patch quality reduced the investment of females in antipredator vigilance. This pattern is consistent with previous findings in birds and mammals that animals invest more time in food acquisition and less time in predator detection in good food patches, especially when these are rare (LaGory, 1986; Pays et al., 2012; Repasky, 1996). However, some antipredator vigilance may have been replaced by social vigilance as patch quality increased; although kangaroos decreased their use of antipredator vigilance with patch quality, they simultaneously increased their use of social vigilance. This increase in social vigilance in good food patches at a time when food conditions were poor overall may have different explanations. First, a high-quality patch is a valuable resource that individuals should keep from potential competitors, which could lead to an increase in social vigilance. Second, because such patches were rare, kangaroos may have used their chewing time to detect other high-quality patches.

To conclude, this study provides new understanding about vigilance patterns in prey species by considering simultaneously the functions (antipredator and social) and the foraging costs (with or without chewing) of this behaviour. Our results show that individuals' decisions to use a particular type of vigilance are based on variation in both ecological and social contexts, including predation risk, competition for food and food resources, which are at the heart of the trade-off between food acquisition and safety. To improve our understanding of the adjustment of individuals' decisions in relation to their social context, it would be interesting to test for the effects on vigilance strategies of the positions of individuals within foraging groups or the social network, interindividual aggression and reproductive status. Finally, a major finding of our study is that vigilance with chewing was the main type of vigilance used in both social and antipredator contexts. Thus, our study does not support the idea that vigilance is automatically a costly activity.

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## Appendix

**Table A1**

AIC-based model selection to examine factors influencing the probabilities that foraging female kangaroos used antipredator vigilance with and without chewing, and social vigilance with and without chewing

Season	Model ID	Model structure	k	AIC	
Winter	1w	Behaviour before+Group size+Distance to the nearest neighbour+Distance to cover+Patch quality	28	50699.1	
	2w	1w+Group size <sup>2</sup>	32	50555.9	
	3w	1w+Distance to the nearest neighbour <sup>2</sup>	32	50701.2	
	4w	1w+Distance to cover <sup>2</sup>	32	50656.0	
	5w	1w–Group size	24	51178.7	
	6w	1w–Distance to the nearest neighbour	24	50711.6	
	7w	1w–Distance to cover	24	50743.0	
	8w	1w–Patch quality	20	50735.9	
	9w	1w–Behaviour before	24	95489.0	
	<b>Winter</b>	<b>10w</b>	<b>1w+Group size<sup>2</sup>+Distance to cover<sup>2</sup></b>	<b>36</b>	<b>50488.9</b>
	Winter	11w	1w+Group size <sup>2</sup> +Distance to cover <sup>2</sup> +Distance to the nearest neighbour <sup>2</sup>	40	50495.1
Summer	1s	Behaviour before+Group size+Distance to the nearest neighbour+Distance to cover+Patch quality	28	35025.0	
	2s	1s+Group size <sup>2</sup>	32	34957.8	
	3s	1s+Distance to the nearest neighbour <sup>2</sup>	32	35009.5	
	4s	1s+Distance to cover <sup>2</sup>	32	34938.6	
	5s	1s–Group size	24	35352.8	
	6s	1s–Distance to the nearest neighbour	24	35039.8	
	7s	1s–Distance to cover	24	35021.1	
	8s	1s–Patch quality	20	35123.9	
	9s	1s–Behaviour before	24	61951.5	
	Summer	10s	1s+Group size <sup>2</sup> +Distance to cover <sup>2</sup>	36	34874.6
	<b>Summer</b>	<b>11s</b>	<b>1s+Group size<sup>2</sup>+Distance to cover<sup>2</sup>+Distance to the nearest neighbour<sup>2</sup></b>	<b>40</b>	<b>34866.2</b>

Results are extracted from multinomial logistic regression models run for winter and summer separately. Individual ID was included as a random factor. Best models are in bold.

**Table A2**

Comparative deviance values (chi bootstrap) between the selected models (10w and 11s for winter and summer, respectively, see Table A1) and the same models without the tested factor on the probabilities that foraging female kangaroos used anti-predator vigilance without and with chewing, and social vigilance without and with chewing

Season	Model comparison	Chi bootstrap	df	P
Winter	10w versus 10w–Group size–Group size <sup>2</sup>	6132	8	<0.0001
Winter	10w versus 10w–Distance to the nearest neighbour	37.1	4	<0.001
Winter	10w versus 10w–Distance to cover–Distance to cover <sup>2</sup>	416.9	8	<0.0001
Winter	10w versus 10w–Patch quality	98.3	8	<0.0001
Winter	10w versus 10w–Behaviour before	49160	4	<0.0001
Summer	11s versus 11s–Group size–Group size <sup>2</sup>	3599.7	8	<0.0001
Summer	11s versus 11s–Distance to the nearest neighbour–Distance to the nearest neighbour <sup>2</sup>	135.2	8	<0.0001
Summer	11s versus 11s–Distance to cover–Distance to cover <sup>2</sup>	354.4	8	<0.0001
Summer	11s versus 11s–Patch quality	1098.1	8	<0.0001
Summer	11s versus 11s–Behaviour before	34907.6	4	<0.0001

**Table A3**

Effects of vigilance type on the proportions of time spent in vigilance by female kangaroos (logit transformed) for winter and summer separately, controlling for the effects of group size, distance to the nearest neighbour, distance to cover and patch quality, and including individual ID as a random factor

Factors	Numerator df	Denominator df	F	P	$\beta \pm SE$
<b>Winter</b>					
(Intercept)	1	612	4304.171	<0.001	
Vigilance type	3	612	180.676	<0.001	Antipredator vigilance with chewing: 1.291 $\pm$ 0.135 ( $P$ <0.001) Social vigilance without chewing: –1.740 $\pm$ 0.135 ( $P$ <0.001) Social vigilance with chewing: –0.806 $\pm$ 0.134 ( $P$ <0.001)
Group size	1	612	8.746	0.003	–0.054 $\pm$ 0.022
Distance to the nearest neighbour	1	612	2.667	0.103	
Distance to cover	1	612	4.966	0.026	–0.003 $\pm$ 0.001
Patch quality	2	612	0.130	0.878	
<b>Summer</b>					
(Intercept)	1	435	8367.595	<0.001	
Vigilance type	3	435	160.701	<0.001	Antipredator vigilance with chewing: 1.483 $\pm$ 0.148 ( $P$ <0.001) Social vigilance without chewing: –1.629 $\pm$ 0.147 ( $P$ <0.001) Social vigilance with chewing: –1.053 $\pm$ 0.148 ( $P$ <0.001)
Group size	1	435	3.847	0.051	–0.030 $\pm$ 0.015
Distance to the nearest neighbour	1	435	0.490	0.484	
Distance to cover	1	435	0.033	0.855	
Patch quality	2	435	1.895	0.152	

Vigilance type and patch quality were categorical and 'antipredator vigilance without chewing' and 'poor' were used as the references, respectively. Group size, distance to the nearest neighbour and distance to cover were modelled as continuous variables.

**Table A4**

Effects of vigilance type on the mean scan durations of female kangaroos (log transformed) for winter and summer separately, controlling for the effects of group size, distance to the nearest neighbour, distance to cover and patch quality, and including individual ID as a random factor

Factors	Numerator df	Denominator df	F	P	$\beta \pm SE$
<b>Winter</b>					
(Intercept)	1	354	995.943	<0.001	
Vigilance type	3	354	22.972	<0.001	Antipredator vigilance without chewing: 0.185 $\pm$ 0.042 ( $P$ <0.001) Social vigilance without chewing: –0.198 $\pm$ 0.073 ( $P$ =0.007) Social vigilance with chewing: –0.160 $\pm$ 0.042 ( $P$ <0.001)
Group size	1	354	4.866	0.028	–0.017 $\pm$ 0.008
Distance to the nearest neighbour	1	354	0.084	0.772	
Distance to cover	1	354	0.104	0.747	
Patch quality	2	354	2.069	0.128	
<b>Summer</b>					
(Intercept)	1	252	1029.438	<0.001	
Vigilance type	3	252	32.772	<0.001	Antipredator vigilance without chewing: 0.284 $\pm$ 0.043 ( $P$ <0.001) Social vigilance without chewing: –0.016 $\pm$ 0.071 ( $P$ =0.817) Social vigilance with chewing: –0.189 $\pm$ 0.046 ( $P$ <0.001)
Group size	1	252	4.457	0.036	–0.013 $\pm$ 0.006
Distance to the nearest neighbour	1	252	0.139	0.709	
Distance to cover	1	252	1.035	0.310	
Patch quality	2	252	0.062	0.940	

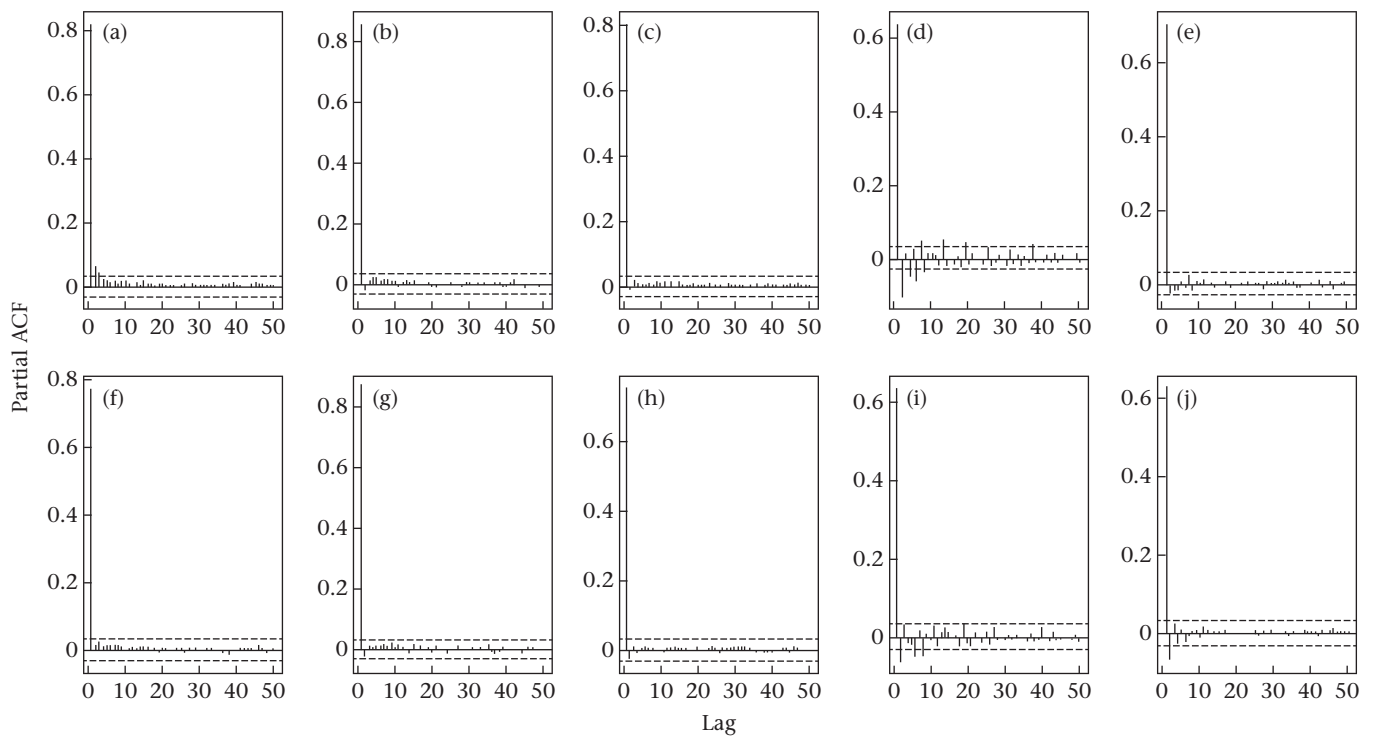
Vigilance type and patch quality were categorical and 'antipredator vigilance with chewing' and 'poor' were used as the references, respectively. Group size, distance to the nearest neighbour and distance to cover were modelled as continuous variables.

**Table A5**

Effects of vigilance type on the mean scan frequencies of female kangaroos (log transformed) for winter and summer separately, controlling for the effects of group size, distance to the nearest neighbour, distance to cover and patch quality, and including individual ID as a random factor

Factors	Numerator <i>df</i>	Denominator <i>df</i>	<i>F</i>	<i>P</i>	$\beta \pm SE$
<b>Winter</b>					
(Intercept)	1	354	664.774	<0.001	
Vigilance type	3	354	69.173	<0.001	Antipredator vigilance with chewing: $0.327 \pm 0.035$ ( $P < 0.001$ ) Social vigilance without chewing: $-0.294 \pm 0.064$ ( $P < 0.001$ ) Social vigilance with chewing: $-0.086 \pm 0.039$ ( $P = 0.029$ )
Group size	1	354	2.234	0.135	
Distance to the nearest neighbour	1	354	0.002	0.969	
Distance to cover	1	354	2.859	0.092	
Patch quality	2	354	0.311	0.733	
<b>Summer</b>					
(Intercept)	1	252	978.005	<0.001	
Vigilance type	3	252	116.134	<0.001	Antipredator vigilance with chewing: $0.569 \pm 0.039$ ( $P < 0.001$ ) Social vigilance without chewing: $-0.193 \pm 0.066$ ( $P = 0.003$ ) Social vigilance with chewing: $-0.003 \pm 0.045$ ( $P = 0.938$ )
Group size	1	252	0.212	0.645	
Distance to the nearest neighbour	1	252	0.001	0.971	
Distance to cover	1	252	2.271	0.133	
Patch quality	2	252	0.951	0.388	

Vigilance type and patch quality were categorical and 'antipredator vigilance without chewing' and 'poor' were used as the references, respectively. Group size, distance to the nearest neighbour and distance to cover were modelled as continuous variables.



**Figure A1.** Partial autocorrelation functions (partial ACF) estimated for each studied behaviour exhibited within individual sequences of 600 s and averaged across all kangaroos in winter (a–e) and summer (f–j). Behaviours are (a, f) foraging, (b, g) antipredator vigilance without chewing, (c, h) antipredator vigilance with chewing, (d, i) social vigilance without chewing and (e, j) social vigilance with chewing. The horizontal dotted lines provide an approximate 95% confidence interval for the autocorrelation estimate at each lag.