The effect of social facilitation on vigilance in the eastern gray kangaroo, *Macropus giganteus*

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The relevance of vigilance activity to predator detection has been demonstrated in numerous studies. However, few studies have investigated the effect of one group member being vigilant on the probability of others being vigilant in group-forming prey species. Thus, we studied vigilance activity of eastern gray kangaroos *Macropus giganteus* that still experience occasional predation. We video recorded the behavior of all group members simultaneously and investigated the probability of a focal group member being vigilant (or nonvigilant) in relation to other individuals’ vigilant and nonvigilant behaviors. Our results show that the decision of an individual to exhibit a vigilant posture depended on what it and other group members had been doing (scanning or foraging) at the second preceding and on group size. The probability of an individual being vigilant was positively affected by the proportion of companions that were vigilant at the previous second, confirming the existence in this species of a tendency for synchronization of individual vigilance. Group size affected individuals’ vigilance in 3 ways. First, individuals were more likely to be vigilant if the proportion of their group mates that was vigilant was high, and this was strengthened with increasing group size. Second, the effect of the individual’s own vigilance state (vigilant or not) at the previous second also increased with group size. Third, the probability of an individual being vigilant decreased with group size. These findings increase our understanding of the much-studied relationship between vigilance and group size. Key words: alleomimesis, group size, kangaroos, neighbor effect, probability of being vigilant, social facilitation, vigilance. [Behav Ecol 20:469–477 (2009)]

Numerous theoretical and empirical studies have demonstrated the importance of vigilance activity to the detection of predators (Lima 1995a, 1995b; Bednekoff and Lima 1998; Treves 2000). In social prey species, the vigilance behavior that group members adopt in response to the risk of being preyed on is assumed to have a strong effect on their survival. However, our understanding of the factors that motivate each group member to raise its head and scan its surroundings, and remain vigilant, is still limited for most wild species.

Although vigilance in group-forming species has already received considerable attention, this has been mostly in the context of changes in individuals’ vigilance rates with changing group size (Elgar 1989; Lima 1995b; Roberts 1996; Childress and Lung 2005), predation risk (Lima 1987; Hunter and Skinner 1998; Laundré et al. 2001; Lung and Childress 2006), or strength of intraspecific competition among group members (Baldellou and Henzi 1992; Robinette and Ha 2001; Tchabovsky et al. 2001; Hirsch 2002). Many studies, especially of mammal species, have demonstrated that a group member’s vigilance is affected by the presence of its neighbors, although the effect may differ between species forming open-membership and those forming persistent groups (Blumstein et al. 2001; Treves et al. 2001; Cameron and Du Toit 2005; Di Blanco and Hirsch 2006, Pays et al. 2008). In birds, some studies also show that the decision of an individual within a flock to be vigilant is partly dependent on the behavior of its close neighbors (Bekoff 1995; Fernández-Juricic and Kacelnick 2004; Fernández-Juricic et al. 2004, 2005). Several theoretical models have also assumed that the probability of an individual being vigilant will depend on other group members’ activities (Ruxton 1996; Bahr and Bekoff 1999; Jackson and Ruxton 2006; Sirot 2006; Sirot and Touzalin 2008). However, little empirical evidence exists in the literature on how the probability of an individual being vigilant varies with other group members’ vigilance activity and how this is affected by group size.

Synchronization of vigilance among group members has been shown in several avian and mammal species (Bertram 1980; Fernández et al. 2003; Ebensperger et al. 2006; Pays, Jarman, et al. 2007; Pays, Renaud, et al. 2007). In these species, vigilant and nonvigilant periods are positively correlated among group members and thus synchronized in phase. This synchronization of scanning periods among individuals produces a pattern of waves of collective vigilance during each of which several individuals are vigilant at the same time. Although such waves of vigilance may be caused by simultaneous detection of an approaching danger by group members, recent models have shown that reciprocal influences among individuals in the group may be sufficient to generate them. In particular, individuals surrounded by neighbors displaying high levels of vigilance may perceive a high predation risk, through the process of social information transfer, and respond by increasing their own vigilance, even if no predator is present (Sirot 2006). Furthermore, when predators display marked preferences for stragglers in an attack, it also becomes adaptive for an individual to copy the vigilance of its
neighbors, in order not to react too slowly and lag behind them whenever an attack occurs (Sirot and Touzalin 2008). In both situations, vigilance in the group may then become contagious, as a result of an adaptive response to the vigilance attitude of companions and relatively independently of the real level of risk in the environment (see also Giraldeau et al. 2002).

In a previous study of eastern gray kangaroos *Macropus giganteus*, Pays, Jarman, et al. (2007) demonstrated that both the onset and the end of individuals’ scanning bouts, as well as bouts of nonvigilant activity, tended to be synchronized, producing waves of collective vigilance. However, although the methods in that study allowed the detection of synchronization of vigilance activity between group members, they did not allow the determination of the causes of this observed collective pattern. Waves of collective vigilance were likely triggered by several causes, including proactive vigilance (i.e., the focal animal raised its head without any intra- or extragroup stimulus) and re-active vigilance (i.e., either several group members raised their heads because they had independently detected the same disturbance outside the group at the same time or 1 individual raised its head and that action alerted other group members without their having independently seen the disturbance themselves).

Although the idea that individuals monitor their environment while foraging has received experimental support (Quirici et al. 2008), the proximate mechanisms and rules that trigger collective patterns of vigilance (such as coordination or synchronization) are still unknown. We investigated the emergence of collective patterns of synchronization in wild eastern gray kangaroos. Our aims were to test 1) whether the probability of a focal individual being vigilant is positively affected by the proportion of companions that are vigilant and 2) whether this effect is affected by group size. We address these aims by using a new statistical method to quantify, as precisely as possible, the influence of companions’ activity (scanning or foraging) on a focal group member’s vigilance behavior. We studied 10-min behavioral sequences of foragers in groups during which the observer did not detect any evident extragroup disturbances (i.e., presence of predators or other heterospecifics, human disturbance, etc.). Thus, we tried to exclude as much as possible collective synchronized vigilance events during which several group members raised their heads simultaneously yet independently of one another because they reacted to the same extragroup disturbances. As we recorded the behavior of all group members simultaneously, we analyzed the probability of a focal group member being vigilant in relation to other group members’ behaviors.

### MATERIALS AND METHODS

#### Study areas and animals

Fieldwork was carried out in Australia, at Newholme (30°25'S, 151°38'E) near Armidale, New South Wales, in July 2005 and at Elanda Point (26°15'S, 152°59'E) in southeast Queensland in March 2007. More extensively described in a previous study (Pays, Jarman, et al. 2007), the first study site comprised eucalypt forest, woodland, and open pastures of predominantly native species. The second area was located on the edge of Lake Coohtharaba and completely surrounded by bush within Great Sandy National Park. In this area, observations of eastern gray kangaroos were conducted within an approximately 25-ha area of cleared and semicleared land within the national park. Animals were not marked for individual recognition at either site. We tested for an effect of study area on vigilance activity of group members, controlling for group size in our data set, and did not find any significant differences between the 2 sites (linear models of effect of site on Logit-transformed proportion of time individual spent vigilant, $P > 0.09$). Therefore, we pooled the data from the 2 field sites.

#### Recording data

To study the pattern of collective vigilance arising from the individual behaviors of group members, we collected behavioral data by video recording all members of focal groups of eastern gray kangaroos for 10-min periods. During sampling, all group members were in the camera’s field of view. Data were collected by 1 observer (OP) who kept a minimum distance of 100 m between himself and the focal group. When filming animals, the observer did not move and was hidden in the landscape. Only groups whose predominant activity was foraging and that did not move far during recording were considered. Furthermore, only groups whose size and composition did not change during recording were retained in the analysis. Identifying groups on the basis of 30-m maximal separation between members and the maintenance of social and spatial cohesion of members during the whole focal sample (Jarman and Coulson 1989) produced no ambiguous cases. We began the video sequence when all animals displayed feeding behavior. When analyzing video sequences, the observer sought to identify whether he might have triggered group members’ scans by looking at the orientation of animals’ head-up stances. No group was filmed more than once a day to ensure that sampled groups were independent of each other; in fact, individuals change their group membership many times each day, and sometimes even many times in an hour. We considered an animal as vigilant when it did not move its feet but raised its head above horizontal, scanning its surroundings. No ambiguities were encountered in distinguishing a vigilant from a nonvigilant animal. Nonvigilance corresponded predominantly to feeding. The position of each group member during the 10-min sequences was not recorded because the dynamics of individual movements led individuals to change their positions constantly within groups.

As we wished to study whether synchronization of vigilance occurs that is not triggered by individuals independently responding to an external stimulus, we did not wish to include in the analyses behavioral sequences of groups within which at least 2 individuals reacted to the same extragroup source of disturbance. We therefore reviewed video sequences, rejecting from analysis any in which several group members, evidently reacting to an extragroup source of disturbance, raised and oriented their heads in the same direction at the same second. There was only one such case in 124 groups studied, which we have not included in our analyses; we are confident that in all other cases, individuals were not independently responding to the same external stimulus.

For analysis, video sequences were converted to analytic sequences. For each individual within each group, a binary sequence was constructed reflecting its activity state (nonvigilance activity: 0 and vigilant activity: 1) precisely at each second for 600 s. All individual binary video sequences were aligned within groups, and thus, we recorded at precisely the same time the activity of each group member.

Following this strict procedure, we studied 510 individuals at the 2 study sites that were in 123 groups ranging from 2 to 15 individuals (see Table 1 for details). No groups of 13 individuals were recorded in our study.

#### Data Analyses

Our main focus in this paper is to investigate whether the probability of a group member being vigilant was affected by the proportion of other group members already vigilant ($P_{\text{non}}$).
We analyzed each group size separately for 2 main reasons. First, group size and group geometry might be linked, and some studies have shown that group geometry may affect the individual vigilance of group members (Hamilton 1971; Elgar 1989; Bahr and Bekoff 1999; Di Blanco and Hirsch 2006). Second, even if equal proportions of companions were vigilant at the previous second, the effect on a focal individual’s vigilance activity of 1 vigilant companion in a group of 2 might be different to that of 2 vigilant individuals in a group of 4 or 5 vigilant individuals in a group of 6, and so on.

To test whether the probability of a focal group member being vigilant was affected by the proportion of vigilant individuals among its companions at the previous second ($P_{hu}$), we first investigated whether there was autocorrelation in individual sequences of 600 s. Whenever data are collected over time, there may be correlations between successive observations. Therefore, we first checked whether autocorrelation existed in our data set, and then we used a statistical procedure that took into account time correlation in the data set. We used an autocorrelation function that provided an estimate of the correlation between observations separated by a lag of $m$ time units, for $m = 0, 1, 2, \ldots, M$ (see Priestley 1982 for more statistical details). We estimated the value of the autocorrelation function on all of the individual binary sequences of vigilance and nonvigilance behaviors. Figure 1a demonstrates the presence of serial correlation. If no autocorrelation estimate (given by the vertical lines for positive lags) had fallen outside the strip defined by the 2 dotted lines, we could safely assume that no serial correlation existed. However, Figure 1a shows values far outside those limits and thus that substantial serial correlation existed in individual sequences. Therefore, a vigilant act displayed by a focal individual seemed to be affected by its behavior at the previous second, that is, with a lag not only at 1 s but also at 2, 3, 4 s, and so on. Consequently, to test whether the probability of a focal group member being vigilant was affected by the proportion of companions that were vigilant at the previous second ($P_{hu}$), we needed to use a statistical procedure that controlled for serial correlations.

Because the response variable, the focal individual’s behavior (vigilant: 1 or not vigilant: 0), had a binomial distribution, we used generalized linear mixed-effects models (binomial, link function: logit) fitted by PQL (penalized quasi-likelihood,
Breslow and Clayton 1993), including $P_{hu}$ (the proportion of companions that were vigilant at the previous second) as an independent variable. According to the link function, the probability of being vigilant ($P_1$) was Logit transformed in the procedure (i.e., $\text{Logit}(P_1) = \ln(P_1/(1-P_1))$). Thus, the computed model in this case assumed that the relationship between the probability of being vigilant ($P_1$) and the proportion of companions vigilant at the previous second ($P_{hu}$) was $\text{Logit}(P_1) = \alpha + \beta P_{hu} + e$, where $\alpha$ was the intercept; $\beta$, the estimated coefficient derived for the effect of $P_{hu}$; and $e$, errors. Moreover, we considered the hierarchical nature of our data set including individuals and groups as 2 nested random effects.

We also had to control for autocorrelation in the statistical procedure. As shown before, the behavior of a focal individual was affected by its behavior in the previous seconds, that is, lag not only at $t-1$ s but also at $t-2$ s, $t-3$ s, and so on. We considered Markov’s assumption that the probability of being vigilant taking into account the past ($t-1$, $t-2$, $t-3$ s, etc.) can be reduced to a law accounting for only the immediate past $t-1$ s (see Meyn and Tweedie 1993). Accepting Markov’s assumption, we assumed that the probability of a focal group member being vigilant was affected by its own state at the previous second (state 0: nonvigilant and state 1: vigilant). Thereafter, we included this independent variable in the model.

To summarize, the complete model included 2 fixed variables, focal individual state at the previous second ($S$) and the proportion of companions that were vigilant at the previous second ($P_{hu}$), and could be represented by the following simplified algorithm: $\text{Logit}(P_1) = \alpha + \beta P_{hu} + \delta S + e$, where $\alpha$ was the intercept; $\beta$ and $\delta$, estimated coefficients; and $e$, errors. To check whether autocorrelation had been controlled correctly, we used the same procedure as the one applied to the individual sequences (the previous autocorrelation function modeling procedure) but on the residuals of the model that included the individual state of the focal animal at the previous second, generating the results shown in Figure 1b.
For each group size (GS), the probability of a focal group member being vigilant in relation to the proportion of companions that were vigilant at the previous second ($P_{hu}$): (a) for GS from 2 to 8 individuals, (b) for GS from 9 to 15, when the focal animal was already vigilant at the previous second ($P_{11}$), (c) for GS from 2 to 8, and (d) for GS from 9 to 15, when the focal group member was nonvigilant at the previous second ($P_{01}$). See Table 1 for the coefficients attributed to each factor in the algorithms of each group size. For example, for a group of 2 individuals (GS 2), $P_{11} = \exp(1.973 + 0.357Phu)/(1 + \exp(1.973 + 0.357Phu))$ and $P_{01} = \exp(-3.274 + 0.357Phu)/(1 + \exp(-3.274 + 0.357Phu))$. When the group size (from 2 to 15), the probability of an individual being vigilant was affected by its own individual state at the previous second. An individual that was vigilant at the previous second had a higher probability of being vigilant than if it had been nonvigilant. Moreover, according to the positive sign derived from Phu, the probability of an individual being vigilant was positively affected by the proportion of companions that were vigilant at the previous second (Table 1).

The statistical procedure allowed us to compute 2 different algorithms from the results in Table 1 for the probability of being vigilant for each group size. For example, according to the coefficient derived for each factor in Table 1, for a group of 2 individuals, the probability ($P_{11}$) of being vigilant for a group member that was already vigilant at the previous second was given by: Logit($P_{11}$) = $-3.274 + 5.247 + 0.357Phu$. As Logit($P_{11}$) = $\ln(P_{11}/(1-P_{11}))$, $P_{11} = \exp(1.973 + 0.357Phu)/(1 + \exp(1.973 + 0.357Phu))$. Furthermore, the probability ($P_{01}$) of being vigilant for a group member that was nonvigilant at the previous second was given by Logit $P_{01} = -3.274 + 0.357Phu$. So, $P_{01} = \exp(-3.274 + 0.357Phu)/(1 + \exp(-3.274 + 0.357Phu))$. From these algorithms, we then calculated the probability of a focal group member being vigilant when the focal animal was or was not already vigilant at the previous second in relation to the proportion of companions that were vigilant at the previous second ($P_{hu}$) within each group size (Figure 2). Figure 2 shows 2 major points. First, given that Figure 2a,c corresponds to small groups (2 ≤ GS ≤ 8 individuals) and Figure 2b,d to larger ones (9 ≤ GS ≤ 15), global group size effects exist for both the

Figure 2

RESULTS

First, for each group size, we tested whether the probability of a focal group member being vigilant was affected by the proportion of companions that were vigilant at the previous second ($P_{hu}$) as well as by the focal animal’s own state (vigilant or not) at the previous second. Results are presented in Table 1.

All of the statistical analyses were computed using R software (the R Foundation for Statistical Computing, 2007).

For each group size, we obtained an estimate of each coefficient derived for the effect of $P_{hu}$ (proportion of companions that were vigilant at the previous second) and S (focal individual state at the previous second). Then we tested whether the effects of the proportion of companions that were vigilant and the individual state of the focal animal at the previous second varied among group sizes using linear model procedures. We compared whether a linear, second-degree polynomial or exponential function best fitted the coefficients $\beta_i$ derived for $P_{hu}$ and $\delta_i$ derived for S, using Akaike’s criterion (AIC) statistics (Akaike 1974). However, as the quotients between the number of observations and the number of parameters in models were less than 40, we used corrected Akaike’s criterion AICc statistics (Hurvich and Tsai 1995). The model with the smallest AICc statistic was considered the best (Burnham and Anderson 2002).

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probability that an individual would be vigilant when it had already been vigilant and the probability that it would be vigilant when it had not been vigilant, at the preceding second. When group size increased, both these probabilities tended to decrease. Second, the highest values of the 2 probabilities of being vigilant did not correspond to groups of 2 individuals but to groups of 3, 4, and 5 individuals. These calculations gave us, for each group size, the coefficients for the effects of $P_{hu}$ (proportion of companions that were vigilant at the previous second) and $S$ (focal individual state at the previous second) on the probability of an individual being vigilant. We then tested for group size effects on these coefficients by investigating whether linear, second-degree polynomial or exponential functions best fitted the coefficients $\beta$, derived for $P_{hu}$ and $\delta$, derived for $S$. Table 2 shows that the effect of $P_{hu}$ was positively affected by group size. When group size increased, the effect of $P_{hu}$ on the probability of an individual being vigilant increased. Moreover, as can be seen by the value of AICc, this increase was characterized by an exponential function (Figure 3a). Table 2 also shows that the effect of the focal individual’s state at the previous second ($S$) was positively affected by group size through a linear relationship (Figure 3b).

### DISCUSSION

Our main findings in this article were that an individual’s probability of being vigilant was positively affected by the proportion of group members that had been vigilant at the previous second and was affected in 3 ways by group size. First, individuals were more likely to be vigilant if the proportion of their group mates that was vigilant was high, and this effect was strengthened with increasing group size. Second, the effect of the individual’s own vigilance state (vigilant or not) at the previous second also increased with group size. Third, the probability of an individual being vigilant, in contrast, decreased with group size.

Our results show that the effect of the behavior of an individual on its probability of being vigilant at the following second was positively affected by group size in a linear way. Thus, the higher the group size, the greater the effect of the focal animal’s previous activity (foraging or scanning) will be on its own probability of being vigilant at the following second. Thus, our analyses suggested that the decision that an individual made about being vigilant depended on both group size and what it was doing previously (scanning or foraging). However, multiple other factors (Beauchamp 1998) such as the individual’s energetic state (McNamara and Houston 1986), predation pressure (Hunter and Skinner 1998; Laundré et al. 2001), or the presence of competitors (Baldellou and Henzi 1992) may also play key roles in a group member’s decision to be vigilant, and this combination of factors complicates our understanding of vigilance.

An individual kangaroo that was already vigilant at the previous second had a higher probability of being vigilant than if it had been nonvigilant (foraging) at the previous second. This result may be related to the durations of scan and interscan bouts. Jarman (1987) and Pays, Jarman, et al. (2007) found that for small groups (2–5 individuals) of eastern gray kangaroos, the mean duration of individual bouts of vigilance (scanning) was about 10 s and the mean duration of bouts of foraging (interscan) was about 40 s. Thus, analyzing individual activity at each second, there were finite intrinsic probabilities that an individual’s previously recorded activity state (vigilant or foraging) would persist.

The probability of an individual being vigilant was also positively affected by the proportion of companions that were vigilant at the previous second, which confirms the tendency for synchronization of individual vigilance that has been previously described in this species (Pays, Jarman, et al. 2007) as well as some other marsupial species (Pays et al. 2008), rodents (Ebensperger et al. 2006), ungulates (Pays, Renaud, et al. 2007), large flightless birds (Bertram 1980; Fernández et al. 2003), and passerines (Lazarus 1979; Bekoff 1995; Fernández-Juricic et al. 2004). Moreover, when group size increased, the effect of the proportion of companions that were vigilant at the previous second on the probability of an individual being vigilant increased. This is a novel finding and is particularly interesting given that we avoided collecting data in situations in which group members raised their heads because all individuals had simultaneously detected the same extragroup disturbance. Our results thus tend to show that reciprocal influences among neighbors play an important role in the determination of individual vigilance, which may be, in part, independent of external cues.

Considerable methodological challenges occur in the study of behavioral synchronization (Ward 1985; Engel and Lamprecht 1997; Pays, Jarman, et al. 2007). Here, we have used a new method of analysis to show that the probability of a group member being vigilant was strongly affected by the proportion of other group members that were vigilant at the preceding second. This statistical method has many other applications in behavioral ecology studies in which temporal autocorrelations exist. Indeed, it can be used for any binary

### Table 2

<table>
<thead>
<tr>
<th>Models</th>
<th>$\gamma$</th>
<th>$\zeta$</th>
<th>$\eta$</th>
<th>LogLik</th>
<th>k</th>
<th>AIC</th>
<th>AICc</th>
<th>$\Delta$AICc</th>
<th>$w_I$</th>
</tr>
</thead>
<tbody>
<tr>
<td>(1) $\beta P_{hu} = \gamma + \zeta S$</td>
<td>0.008</td>
<td>0.188</td>
<td>0</td>
<td>-6.187</td>
<td>3</td>
<td>18.375</td>
<td>18.437</td>
<td>5.000</td>
<td>0.095</td>
</tr>
<tr>
<td>$\beta P_{hu} = \gamma + \zeta S + \eta S^2$</td>
<td>-0.128</td>
<td>0.225</td>
<td>-0.002</td>
<td>-6.142</td>
<td>4</td>
<td>20.286</td>
<td>20.390</td>
<td>10.453</td>
<td>0.059</td>
</tr>
<tr>
<td>$\beta P_{hu} = \gamma + \zeta S^2$</td>
<td>0.661</td>
<td>0.01</td>
<td>0.047</td>
<td>-7.585</td>
<td>3</td>
<td>21.171</td>
<td>21.233</td>
<td>11.296</td>
<td>0.047</td>
</tr>
<tr>
<td>$\beta P_{hu} = \exp(\gamma + \zeta S)$</td>
<td>-0.932</td>
<td>0.144</td>
<td>-1.937</td>
<td>3</td>
<td>9.875</td>
<td>9.937</td>
<td>0.000</td>
<td>0.799</td>
<td></td>
</tr>
</tbody>
</table>

The best models with the lowest AICc are in boldface. $\gamma$, $\zeta$, and $\eta$ are coefficients. LogLik is the Loglikelihood, $k$ is the number of estimated parameters, AIC and AICc are Akaike’s criterion and the corrected criterion, $\Delta$AICc is the difference of AICc between the model and the best one, and $w_I$ is the weight of the model.
behavioral sequences between individuals to investigate whether the probability that an individual will exhibit a behavior depends on the behavior exhibited by other group members.

Previous studies that investigated patterns of synchronized vigilance could not differentiate between the proximate mechanisms that triggered the observed synchronization of vigilance among group members. Our study showed that the probability of a group member being vigilant was affected by the numbers of vigilant and nonvigilant companions at the previous second, which suggests that animals might often react to the behavior of other group members by considering those individuals’ head-up acts as information about potential risks outside the group. Thus, our results improve our understanding of the processes that motivate individuals to scan their environment. Successive head-up acts seem to emerge progressively in the group because of the contagious effect triggered by individuals reacting to each others’ behavior. First, 1 individual might raise its head proactively (i.e., without a stimulus from either inside or outside the group) or because of an extragroup stimulus. This individual’s vigilant act may or may not initiate a wave of collective vigilance (Pays and Jarman 2008). Such single, proactive vigilant scans might occur independently between group members and randomly through time, as assumed by Pulliam’s (1973) model. Second, an alleloimetic copying phenomenon might emerge, triggering an overlap of vigilance between the initiator and at least one other group member. These other group members might exhibit reactive vigilance, reacting to the initiator’s head-up act or vigilant state. In group-forming prey species in which information passes between group members, a communication signal (e.g., an alarm call or the sudden departure of that individual, Pulliam 1975; Davis 1975; Lazarus 1979) might commonly induce such a pattern. Studying bird flocks under attacks, several authors have recorded that if an individual fleeing because it has detected a predator communicates this information to its group mates, this triggers an immediate departure of other birds in a few seconds, increasing their chance of escaping (Hilton et al. 1999; Cresswell et al. 2000; Quinn and Cresswell 2005). It has also been suggested that birds alerted by the flight of their companions first take some time to assess the real level of threat before taking off (Quinn and Cresswell 2005). It could thus be that vigilance, as well as flight, induces antipredatory behavior among members of a group.

The relationship between group size and the influence of companions’ alertness at the previous second on the probability of an individual being vigilant in the subsequent second followed an exponential function (Figure 3). This provides evidence of an amplification effect when the proportion of companions that are vigilant increases. Amplification processes in which collective behaviors emerge because 1 individual’s behavior is amplified by the action of many other individuals (positive feedback) have been reported for a very wide range of group-forming organisms (Parrish and Edelstein-Keshet 1999; Krause and Ruxton 2002; Couzin and Krause 2003) such as social insects (Deneubourg and Goss 1989; Bonabeau et al. 1997; Dussutour et al. 2005), birds (Jackson et al. 2008), and mammals (Meunier et al. 2008). For example, studying the effect of social facilitation on foraging success in Gyps vultures, Jackson et al. (2008) reported that vultures rely heavily on cues from conspecifics to locate carcasses via local enhancement. The probability of a vulture finding a carcass is a function of vulture density in the habitat and carcass numbers, following a sigmoid relationship. Thus, these authors highlighted an amplification process with the probability of foraging success increasing exponentially (at least for the first stage of the curve) with the density of vultures close to the carcass.

We found that individuals in smaller groups were more vigilant than those in larger groups, as has been found in many studies (e.g., Jarman 1987); however, the increase with group size of the effect on vigilance of the proportion of group members that were vigilant suggests that synchronization of vigilance would be greater at larger group sizes. However, we might have expected that group members would act more synchronously in smaller groups than in larger ones because of the geometry of such groups, in particular the clustering of neighbors, as an individual would synchronize better with its proximate neighbors than with more distant group members. Thus, we need more studies to understand the relationships

Figure 3
(a) Relationship between group size and the influence of companions’ alertness at the previous second on the probability of the focal animal being alert and (b) relationship between group size and the influence of the focal individual’s alertness at the previous second on the probability of the focal animal being alert. See Table 1 for the values (± standard error [SE]) of the coefficients β attributed to P0, and P to S for each group size and Table 2 for statistical details for the relationship.
between group size, group geometry, degree of synchrony of vigilance and foraging activity, and the amplification process among group members. In our study, we used a lag of 1 s to investigate synchronization of vigilance for statistical reasons (particularly to control temporal autocorrelation) and because we have observed that individuals often react to each other’s head-up acts with a very short delay. However, it is clear that individuals will not always respond to their neighbors’ actions that quickly. Our analysis used Markov’s assumption that the probability of being vigilant taking into account the past \( (t - 1, t - 2, t - 3, s) \), etc. can be reduced to a law accounting for only the immediate past \( t - 1 \) s (see Meyn and Tweedie 1993); thus, we partially considered the history of correlations in behaviors during the previous seconds. However, our procedure did not allow us to test whether the probability of vigilance was affected by the companions’ behavior and the focal individual’s previous state using lag times of over 1 s (e.g., 2 or 3 s previously) or lag periods greater than 1 s in duration (e.g., the previous 1–5 s). We suggest that such analyses should be done. Experimental studies are also needed to analyze and quantify the delay shown by a group member in reacting to an alerted neighbor and to determine the efficacy of the communication signals that exist in large mammalian herbivores and more generally in other prey species.

**FUNDING**

Laboratoire Paysages et Biodiversité d’Angers, France.

We acknowledge M. Curkpatrick for permission to use the Newholme Field Laboratory at the University of New England. We would like to express our thanks to Brian Mays and the staff who allowed us to study kangaroos at Elanda Point and provided logistical support. This research was approved by the University of Queensland’s Animal Experimentation Ethics Committee and carried out under a Scientific Purposes Permit from Queensland’s Environmental Protection Agency. We are also grateful to Mike Speed and F. Stephen Dobson for their comments on an earlier version of this article.

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