RESEARCH PAPER

Collective Vigilance in the Greater Kudu: Towards a Better Understanding of Synchronization Patterns

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Abstract

Collective detection of predators is one of the main advantages of living in groups in prey species. However, the mechanisms linking individual and collective vigilance remain largely unknown. Here, we investigated individual and collective vigilance in a natural population of greater kudu (*Tragelaphus strepsiceros*), a gregarious ruminant living under high predation risk. Controlling for environmental, individual and group factors, we show that the proportion of time during which at least one individual was vigilant increased with group size, whereas individual investment in vigilance decreased. We also show that individuals tended to synchronize both vigilance and feeding activities. More generally, and whatever the considered group size, we demonstrate how the independent scanning assumption underestimated both the proportion of time during which no individual was vigilant and the proportion of time during which all individuals were simultaneously vigilant, but overestimated the proportion of time during which one vigilant individual only was present. Our results thus contrast with the point of view that the alternative to independent vigilance is coordinated vigilance and plead for a better description of the processes whereby reciprocal influences between individuals shape collective patterns of vigilance.

Introduction

Living in groups, a widespread behaviour in prey species, is an efficient anti-predator strategy (Krause & Ruxton 2002). Starting from the assumption that information about predators spreads in the group, Pulliam (1973) proposed a mathematical model showing how an individual can decrease its own vigilance as a response to an increase in group size, while enjoying a constant probability of escaping predators. Pulliam's model relies on two important assumptions. First, it assumes that predator detection by at least one individual insures successful escape for all group members. Second, it considers two levels of randomness in the scanning process, namely independent scanning between group members and randomness in individual scan initiation rate (see Pays et al. 2010).

Pulliam's model has been a pioneering work in the field of anti-predatory vigilance, and collective detection has remained a cornerstone of vigilance models and, thus, in the study of prey-predator interactions (e.g. McNamara & Houston 1992). Nevertheless, the assumptions underlying the original model have been challenged by field observations and experimental results. In particular, it has been shown that, in case of predator detection, the individuals that do not detect the predator by themselves tend to lag behind detectors when under an attack (Hilton et al. 1999). Concerning temporal patterns of vigilance, the independent scanning hypothesis has been rejected by a significant number of studies as, in many situations, the proportion of time when no individual in the group is vigilant is larger than expected under the independence hypothesis

(e.g. Fernández-Juricic et al. 2004; Ebensperger et al. 2006). To understand why this unexpected pattern is so common, it becomes necessary to investigate it with more scrutiny, within an appropriate adaptive framework.

Vigilance coordination is indeed generally presented as the adaptive alternative to independent scanning, because it reduces the proportion of time where no vigilant individual is present in the group. It has been addressed by several theoretical models (Ward et al. 2000; Sirot & Touzalin 2009), and some conditions for its evolutionary stability have been identified (Rodriguez-Gironés & Vàsquez 2002). However, the opposite tendency to imitate the vigilance of other group members can also be explained via adaptive decision rules. One possible explanation is that individuals observing vigilant companions may infer a rising level of risk and respond by increasing their own vigilance, thereby creating an informational cascade effect (Giraldeau et al. 2002; Sirot 2006). Another explanation is that, although the probability of predator detection increases with the number of vigilant individuals, an individual mostly surrounded by vigilant neighbours may also be at a considerable risk, as these neighbours might leave immediately when under attack, leaving the focal individual as a preferential target for the predator. The best approach for this individual can thus be to imitate the vigilance of its companions (Sirot & Touzalin 2009).

Actually, few studies have attempted to quantify collective vigilance, that is, the actual time during which one individual at least is vigilant (da Silva & Terhune 1988). However, measuring collective vigilance is crucial to fully understand the benefits that grouping confers to each individual, as group members are assumed to be more vulnerable to predation when no one in the group is vigilant. This measure is not sufficient, however, because the situation where at least one individual is vigilant does in reality encompass different situations, ranging from the situation where one individual only is vigilant to the situation where the whole group is in alertness.

To explore collective vigilance in more details, we studied vigilance activity in a natural population of greater kudu (*Tragelaphus strepsiceros*), a browsing ruminant living under high levels of predation risk in our study area. We recorded individual vigilance for each group member and calculated collective vigilance. We tested for the effects of individual (age–sex class), group (group size) and environmental factors (distance to cover) on individual vigilance,

as these variables are known to affect vigilance levels in large herbivores (e.g. Burger & Gochfeld 1994; Hunter & Skinner 1998). Animals in a vulnerable situation, such as mothers with calves or members of small groups, are indeed expected to increase their vigilance. Vigilance is also expected to vary with the proximity of vegetion cover, which may either offer protection for the prey or shelter ambushing predators (Ingrum et al. 2010). Therefore, to study how individual attitudes finally shape collective patterns of vigilance, we examined divergences between the observed and theoretical patterns of collective vigilance expected under the independent scanning hypothesis, by calculating for each group the observed time during which exactly 0, 1 and all individuals were simultaneously vigilant, respectively. The situations where 0 and all individuals are vigilant allow us to assess copying tendencies for feeding and vigilance, respectively, while the situation where only one individual is vigilant informs us on how each individual is inclined to initiate vigilance when no one else does.

Methods

Study Area and Animals

The fieldwork was conducted from Mar. to Jul. 2009 around the Main Camp area of Hwange National Park (19°00′S, 26°30′E) in Zimbabwe (HNP) (see Valeix et al. (2009) for more details on the vegetation and climate of HNP). Approval for the study was obtained from the Zimbabwe Parks and Management Wildlife Authority.

From 1999 to 2005, the population of kudus (mean density $\pm$ SD) was estimated to be 0.92 $\pm$ 0.36 animals/km^2 in the early dry season (May/-Jun.) (Chamaillé-Jammes et al. 2009). The predation pressure on kudu is very high in the Main Camp area, as kudu is the first or second prey of the main large carnivores lions (*Panthera leo*), leopards (*Panthera pardus*), African wild dogs (*Lycaon pictus*) and occasionally spotted hyaenas (*Crocuta crocuta*) (Drouet-Hoguet 2007; Loveridge et al. 2007a,b; Rasmussen 2009).

Although foraging strategies and population dynamics in kudus have received attention (Owen-Smith 1994; Owen-Smith & Mason 2005), we know little on social organization in this species. Perrin (1999) reports that it is based on a cow social unit, with closed matriarchal kinship groups consisting of several cows and their offspring. Bulls leave maternal groups when 2 yr old and form loose temporary

associations with peers. Dominance hierarchies are established within these bachelor groups. Adult bulls tend to become increasingly solitary with age and form temporary associations with cows.

Recording Data

We studied groups of kudus visiting salt licks. Salt licking is a necessary part of the foraging activity for ungulates because minerals (such as sodium and phosphorus) are limited in plants from most of soils worldwide (Ceacero et al. 2009). We collected behavioural data by videotaping (video camera: Sony DCR-SR30 (Sony Corporation, Tokyo, Japan), 20× optical zoom) all members of a focal group of kudus for a 5-min period. During sampling, all group members were in the camera field of view. Only groups whose predominant activity was licking the soil and that did not move away during the recording were considered. Only groups whose size and composition did not change during the recording were retained in the sample. We identified a group on the spatial basis of 50-m maximal separation between adjacent members and on the maintenance of social and spatial cohesion of the group members during all focal sampling. No ambiguities were encountered in defining a group as we observed very small inter-individual distances (i.e. about several decametres).

An animal was considered as vigilant when it did not move its feet and raised its head above horizontal, scanning its surroundings. No ambiguities were encountered in distinguishing a vigilant from a non-vigilant animal. We did not observe aggressive movements of any kind between the individuals, which could have affected time devoted to vigilance and to salt licking and artificially induce a synchronization of these activities. We also recorded group size, age–sex class of each individual (adult male, adult female and young, respectively, easily recognizable from their morphology), position of each individuals within its group (peripheral, central or mixed i.e. an individual that moved between peripheral and central positions during the 5-min sequence), date, time of day (morning or afternoon) and salt lick name (seven different locations). Finally, we measured the distance to cover, that is, the distance separating the centre of mass of groups from cover, using a range finder. As groups were licking salt and never moved far during the 5-min video recordings, the distance to cover was constant during each recording and relatively easy to assess. Distance to cover was categorized into four levels: 0–50, 51–100, 101–200, >200 m. Forty-six groups with group sizes ranging from two to 12 individuals were sampled, corresponding to a total of 200 individuals.

Data were collected using a four wheel vehicle, respecting a minimal distance of 200 m between the focal group and the observer to minimize disturbance. Although animals were not marked for individual recognition, we tried to minimize individual re-sampling by studying groups that were foraging in seven different salt licks distant on average by about 18 km, allowing us to ensure spatial independence between groups sampled in the day session. On the rare occasions where two groups were filmed in the same lick one after another, the observer paid special attention that no group flux occurred between these two studied groups during or between the video recordings. The observer changed the order of the sampled licks every day. Finally, we did not observe any correlation between group size and salt lick name (ANOVA: $F_{6,32} = 0.714$, p = 0.640) and group size and chronology of sampling session (Spearman's rank correlation: $r_s = 0.061$, p = 0.681). We filmed 11 groups including adult males and females (and potentially young), five groups including only adult males and 30 groups composed of females and young only.

For the analyses, video sequences were converted into analytic sequences. For each individual within each group, a binary sequence (0, non-vigilance and 1, vigilance) was built to reflect the activity state of the individual at each second precisely and for a total period of 300 s. We recorded the activity of each group member at precisely the same time, to be able to quantify both individual and collective levels of vigilance in a continuous way.

Data Analyses

For each analytic sequence, corresponding to a particular group, we computed individual vigilance as the proportion of time spent vigilant by this individual. Collective vigilance ($ColP_{obs}$) was calculated as the proportion of time when at least one member of the group was vigilant.

We first investigated whether group size affected collective vigilance, controlling for distance to cover. For the assumptions of normality and homoscedasticity to be fulfilled, we applied a logit transformation to the observed proportion of time $ColP_{obs}$. We computed a linear mixed-effects model including group size, distance to cover, time of day and the interactions between these variables as fixed factors and two nested random factors, salt lick location nested in date.

We then tested for the effects of individual, group and environmental factors on the time that each group member spent in vigilance. We computed a linear mixed-effects model including group size, distance to cover, age–sex class, time of day and the interactions between these variables as fixed factors and three nested random factors, group identity in salt lick location in date.

Then, we studied whether the observed temporal patterns of vigilance were compatible with the hypothesis that scans and interscans were initiated in an independent way by group members. We used a general approach that allowed us to study how each individual adapted its vigilance to the level of vigilance displayed by its companions. Thus, we did not consider only the situation where at least one individual was vigilant (i.e. using the common assessment of collective vigilance), but we calculated for each group the observed time (in the 300 s sequences) during which exactly 0, 1 and all (N) individuals were simultaneously vigilant, respectively. Thus, we looked for situations that were encountered with all group sizes, making comparisons possible.

To perform a statistical test of the independent scanning hypothesis, we derived, for each group, a theoretical distribution of the times during which exactly 0, 1, and all (N) individuals should have been simultaneously vigilant, under the hypothesis of independent behaviours between group members, using Monte Carlo simulations. To achieve these simulations, we performed random permutations of interscans and scans within all individual sequences of vigilance in the group. In such a way, we kept constant the proportion of time devoted to vigilance by each individual. Then we computed, within each set of permuted sequences, the simulated times during which exactly 0, 1 and all individuals were simultaneously vigilant. We performed 1000 runs of permutations per group and determined the proportion of these runs for which the simulated times when 0, 1 and all individuals were simultaneously vigilant, respectively, were smaller than the observed value. Thus, we obtained, for group i, an estimated probability p_i, measuring the likelihood of occurrence of the observed value under the independence hypothesis. We could thus see, for each group, whether the times when no, one and all individual was vigilant were reasonably compatible with independent scanning hypothesis.

Finally, we used a meta-analysis test to bring together the p_i values measured for all groups, and to determine whether, over all groups, there were consistent differences, indicating that, 'on average', individuals tended not to behave independently of one another. The analysis was performed independently for each of the three studied situations (i.e., 0, 1 and all individuals simultaneously vigilant, respectively), to better describe behavioural tendencies. We used a Fisher's combined probability test (Fisher 1932) using the following statistics: $\chi^2_{obs} = -2 \sum_{i=1}^{k} \ln(p_i)$, where p_i is the p-value for each group and k, the number of groups. Thus, we compared that χ^2_{obs} to an expected value for df = 2×46. As these probably should be regarded as three tests of the same hypothesis (independence in scanning), we corrected for multiple comparisons accepting $\alpha = 0.01$ (i.e. $\chi^2_{th} = 126.46$) as a significance threshold value.

Statistical analyses were performed using R 2.10.1 (R Development Core Team, 2010, Vienna, Austria. R is available from http://www.r.project.org).

Results

The average ($\pm$SE) scan duration of kudus was 12.62 ± 1.30 s, and interscan duration was 25.25 ± 1.41 s. The mean frequency of vigilant acts was 1.90 ± 0.10/min. Finally, the mean proportion of time during which a kudu was vigilant was 0.31 ± 0.01. At a group level, the mean proportion of time during which at least one individual was vigilant in the group (i.e. collective vigilance) was 0.68 ± 0.03.

Collective Vigilance

Statistical analyses of factors influencing collective vigilance are presented in Table 1. They show that group size affected significantly the observed proportion of time during which at least one individual was vigilant. According to the coefficient derived for group size (coef $\pm$ SE = 0.212 ± 0.085), collective vigilance increased with group size (Fig. 1) and neither distance to cover, nor time of day, nor the interactions between all variables affected this proportion of time.

Individual Vigilance

Analyses show that group size and age–sex class significantly affected individual vigilance (Table 2). According to the coefficients derived for each factor, individual vigilance decreased with group size and young were less vigilant than adults, while no signif-

Table 1: Factors influencing the logit-transformed collective vigilance, that is, the proportion of time during which at least one individual spent in vigilance. Date and salt pan location were included as two nested random factors. Group size was considered as continuous and distance to cover (0–50, 51–100, 101–200, *>200 m*) and time of day (*morning* or afternoon) were categorical (classes used as references are italicized). All interactions were not significant (p > 0.05) and are not presented. Adjusted *R*-square = 0.43. NumDf is Numerator degrees of freedom and DenDf is Denominator degrees of freedom

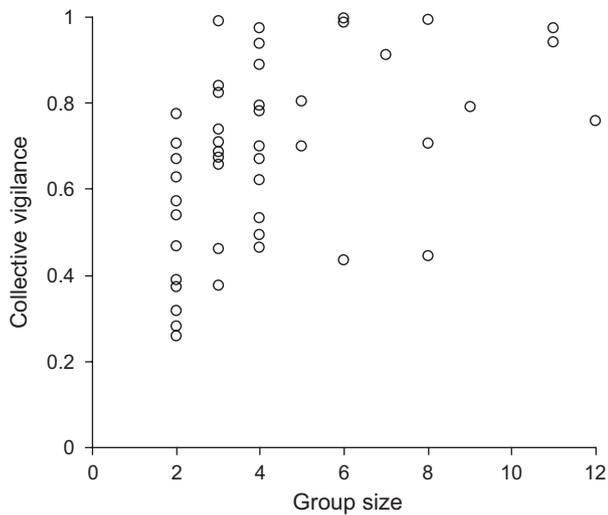| Factors	NumDf	DenDf	F	p	Coef ± SE
Intercept	1	26	9.029	0.006	
Group size	1	8	9.751	0.014	0.212 ± 0.085
Distance to cover	3	8	0.681	0.588	
Time of day	1	8	0.010	0.922	

Fig. 1: Group-size effect on collective vigilance, that is, the proportion of time during which at least one group member is vigilant (see Table 1 for statistical details).

icant difference was detected between adult males and females. However, in the 11 mixed-sex groups, controlling for the effects of group size and distance to cover, males were more vigilant than females (coef ± SE = 1.190 ± 0.327, $F_{2,61} = 7.737$, p = 0.001). Finally, neither the position of the individual within the group, nor distance to cover, nor time of day, nor the interactions between all variables significantly affected individual vigilance.

Divergence from the Independent Scanning Hypothesis

For each group, we derived distributions for the times during which exactly 0, 1 and all (N) individuals were expected to be simultaneously vigilant, under the hypothesis of independent vigilance, using Monte Carlo simulations. Then we used Fisher's combined probability test to determine whether, over all groups, there were consistent trends with respect to the position of the observed value relative to the theoretical distribution. χ^2_{obs} corresponding to the situations where exactly 0, 1 and all individuals were simultaneously vigilant were respectively 156.84, 170.38 and 245.57. Comparing these observed values to $\chi^2_{th} = 126.46$ (α = 0.01 and df = 92) shows that observed times were highly unlikely under the independent scanning hypothesis, which indicates that group members did not act independently of one another. Figure 2 illustrates the mean divergences between the observed proportions of times and the mean values for the durations obtained with the simulations. From the sign of these divergences, we conclude that individuals synchronized both their vigilance and foraging bouts more than expected by chance (i.e. tended to scan their environment and forage at the same time), while the situation where
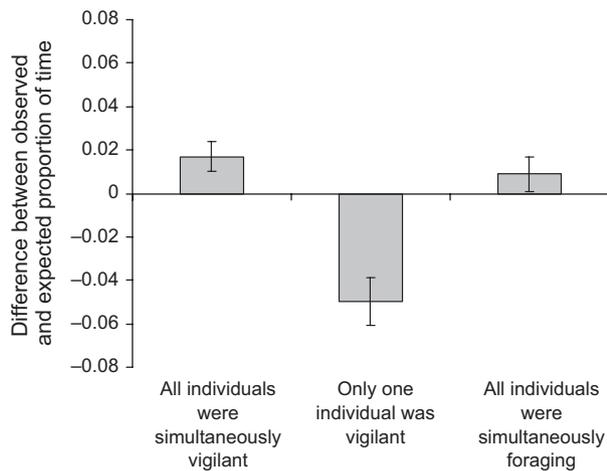
Table 2: Factors influencing individual vigilance. Group identity, date and salt pan location were included as three nested random factors. Group size was considered as continuous and distance to cover (0–50, 51–100, 101–200, *>200 m*), time of day (*morning* or afternoon), age–sex class of each individual (adult male: M, *adult female: F* and young: Y), position of the individuals within groups (peripheral, *central*, or mixed i.e. individuals that moved between peripheral and central positions during the 5 min sequence) were categorical (classes used as references are italicized). All interactions were not significant (p > 0.05) and are not presented. Adjusted *R*-square = 0.72. NumDf is Numerator degrees of freedom and DenDf is Denominator degrees of freedom

Factors	NumDf	DenDf	F	p	Coef ± SE
Intercept	1	133	50.743	<0.0001	−0.997 ± 0.245
Group size	1	20	7.332	0.014	−0.113 ± 0.051
Position of the individual within group	2	133	0.554	0.576	
Age–Sex class	2	133	3.189	0.044	Y: −0.269 ± 0.142 ($p_{Y \text{ vs. } F}$ = 0.045) M: 0.191 ± 0.197 ($p_{M \text{ vs. } F}$ = 0.333)
Distance to cover	3	20	2.456	0.093	
Time of day	1	20	0.010	0.921	

Fig. 2: Difference ($\bar{x} \pm$ SE) between the observed times when exactly n individuals were vigilant and the theoretical times simulated under the independent scanning hypothesis. The graph depicts the situation where all individuals were simultaneously foraging (licking salt), only one individual was vigilant and all individuals were simultaneously vigilant, respectively.

only one vigilant individual was present in the group was less frequent than expected.

Discussion

Collective vigilance, that is, the proportion of time during which at least one group member is vigilant was on average 0.7 in kudus. In accordance with previous studies in other mammal taxa (Ebensperger et al. 2006; Pays et al. 2007b) and in birds (Bertram 1980), collective vigilance increased with group size (exceeding 0.9 in large groups), in spite of reduced individual vigilance. Such high levels of vigilance may certainly be explained by the high level of risk that prevails in the area. Indeed, a previous study in HNP showed that buffalos, giraffes and kudus are the preferred prey for lions in this area (Loveridge et al. 2007a), and ungulate species that endure high levels of risk in the African savannah usually display high vigilance (Hunter & Skinner 1998; Pays et al. 2007b). We suspect that population dynamics of kudus is largely affected by predation, as kudu's body size is close to threshold (150 kg) below which predation is expected to have a greater effect than resource in limiting ungulate populations (Fritz & Duncan 1994; Sinclair et al. 2003). Concurrently, we expect these animals to modify their behaviour as a response to predation risk (Lima & Dill 1990). Kudus do indeed avoid waterholes when lions are in the vicinity (Valeix et al. 2009). Nevertheless, gregarious

animals should contribute to collective vigilance only if this improves their own fitness to some extent, and the overall collective patterns reflect the expression of cumulated individual selfish strategies (Beauchamp 2007).

Several factors contribute to explain the variation of individual investment in vigilance. First, young invest less in vigilance than adults. This result might be explained by the fact that growth is of paramount importance for juveniles, as it increases escape capabilities. Thus, juveniles should devote much time to foraging to maintain a high growth rate. Besides, maternal care in ungulates generally involves an increased vigilance, allowing the juveniles to spend more time feeding (Lung & Childress 2006). Although we did not detect any overall difference in vigilance between males and females, males were significantly more vigilant than females in mixed-sex groups. Males have been reported to be more vigilant than females in a wide range of primate (Steenbeek et al. 1999) and mammal species (Burger & Gochfeld 1994). This result might be related to the intra-specific competition hypothesis whereby, in gregarious species, direct competition between males (e.g. for territoriality or for access to females) requires them to spend time scanning to assess their rivals' presence and activities (Reboreda & Fernández 1997).

Second, when kudus used salt licks in daylight, individual vigilance seemed to not be affected by distance to cover. However, the role played by cover is ambiguous. Plants surrounding the salt licks are indeed a potential source of danger because lions, the main predators of kudus, spend most of their daytime in this habitat to ambush their prey (Hopcraft et al. 2005), but kudus may also perceive cover as being protective, as they usually live hidden in this closed habitat to feed on bushes. Thus, the lack of distance-to-cover effect in daylight might be the result of two compensating effects (i.e. protective and obstructive). More studies are needed to understand the effect of cover on anti-predator behaviour in kudus.

Our results show significant divergences between the observed times where exactly no, one and all individuals were vigilant and the corresponding theoretical times calculated under the independent scanning hypothesis. Thus, kudus did not behave independently of one another. More precisely, calculations made under the independence hypothesis underestimated both the time during which no kudu was vigilant and the time during which all individuals were vigilant, but overestimated the time during

which only one individual was vigilant. For purely mechanistic reasons, it is important not to consider synchronization for feeding and for vigilance in an independent way. As we studied kudus in situations where these two activities were exclusive (0 licking vs. 1 vigilance), any one cause of non-independence will indeed lead to more than one deviation because the deviations from randomness – independence scanning hypothesis – must sum to zero. This is why we separated, in our analysis, the situations where 0, 1 and all (N) individuals were simultaneously vigilant, respectively. Here, we develop the idea that different kinds of reasons may explain the synchronization of vigilance and feeding.

Vigilance synchronization has already been reported in both birds and mammals (Pays et al. 2007a,b; Beauchamp 2009) and it has been shown that individuals were more likely to be vigilant if the proportion of their group mates that were already vigilant was high (Pays et al. 2009; Michelena & Deneubourg 2011). In the present study, such a synchronization might be triggered by several processes. First, kudus could sometimes independently raise their heads at the same second in reaction to the same external stimulus (presence of predator). However, the observer did not detect any disturbance during the video recordings. It seems thus unlikely that such events were responsible for vigilance synchronization. Second, the contagion of vigilance may be caused by a possibly incorrect use of public information (Giraldeau et al. 2002; Sirot 2006) or the need to complete the information gleaned after observing others' behaviour by a personal scanning of the environment (Lima 1995). Lastly, individuals may imitate the alertness of their companions in order not to lag behind them whenever an attack occurs (Sirot & Touzalin 2009), and this tendency is enhanced if predators preferentially attack non-vigilant prey (FitzGibbon 1989).

Similarly, the time during which no individual in the group was vigilant was found to be greater than predicted by the independence hypothesis, indicating a tendency for feeding synchronization, which results in a reduced level of collective vigilance and converges with the conclusions of several other studies in birds and mammals (Fernández et al. 2003; Ebensperger et al. 2006).

Sirot & Touzalin (2009) argue that, if predators preferentially attack individuals that do not detect them immediately, the level of risk endured by an individual having only feeding companions may decrease, allowing it to feed as well. Additionally, social information among feeding companions should mostly indicate safety, which will reinforce the tendency of each individual to feed (Sirot 2006). Thus, both of these mechanisms might be involved in the present situation and contribute to explain feeding synchronization.

Another hypothesis may be proposed related to strategies for individual investment in collective vigilance and their shaping by natural selection. Indeed, if we assume that collective detection is efficient, individuals having one or a few vigilant neighbours may keep on feeding while enjoying a high probability of escaping predators. Thus, they will have no benefit of becoming vigilant and the vigilant individuals will carry the burden of vigilance for the whole group. The tendency to initiate vigilance will thus be easily parasitized by sneakers, so it will be counterselected. Individuals will thus be less prone to initiate collective vigilance and, as a consequence, the proportion of time during which no individual in the group is vigilant will become larger and the proportion of time where one single vigilant individual is present will decrease, which is what we observe in the present study. Such uncooperative behaviour is indeed possible in social interactions where individuals have the possibility to influence others' behaviour by adopting a defecting attitude (McNamara et al. 1999), with, as an outcome, a reduced efficiency at the group level (here, a reduced level of collective vigilance).

Acknowledgements

Literature Cited

Beauchamp, G. 2007: Vigilance in a selfish herd. Anim. Behav. **73**, 445—451.

Beauchamp, G. 2009: Sleeping gulls monitor the vigilance behaviour of their neighbours. Biol. Lett. **5**, 9—11.

Bertram, B. C. R. 1980: Vigilance and group size in ostriches. Anim. Behav. **28**, 278—286.

Burger, J. & Gochfeld, M. 1994: Vigilance in African mammals: differences among mothers, other females, and males. Behaviour **131**, 53—169.

Ceacero, F., Landete-Castillejos, T., García, A. J., Estévez, J. A., Martinez, A., Calatayud, A., Gaspar-López, E. & Gallego, L. 2009: Free-choice mineral consumption in Iberian red deer (*Cervus elaphus hispanicus*) response to diet deficiencies. Livest. Sci. **122**, 345—348.

Chamaillé-Jammes, S., Valeix, M., Bourgarel, M., Murindagomo, F. & Fritz, H. 2009: Seasonal density estimates of common large herbivores in Hwange National Park, Zimbabwe. Afr. J. Ecol. **47**, 804—808.

Drouet-Hoguet, N. 2007: Influence des activités anthro-pogéniques sur le régime alimentaire et la réponse numérique de la hyène tachetée en savane arborée dystrophique dominée par l'éléphant. Doctorate thesis, l'Université Claude Bernhard – Lyon1, Lyon, France.

Ebensperger, L. A., Hurtado, M. J. & Ramos-Jiliberto, R. 2006: Vigilance and collective detection of predators in degus (*Octodon degus*). Ethology **112**, 879—887.

Fernández, G. J., Capurro, A. F. & Reboreda, J. C. 2003: Effect of group size on individual and collective vigilance in greater rheas. Ethology **109**, 413—425.

Fernández-Juricic, E., Siller, S. & Kacelnick, A. 2004: Flock density, social foraging: an experiment with starlings. Behav. Ecol. **15**, 371—379.

Fisher, R. A. 1932: Statistical Methods for Research Workers. Oliver and Boyd, Edinburgh.

FitzGibbon, C. D. 1989: A cost to individuals with reduced vigilance in groups of Thomson's gazelles hunted by cheetahs. Anim. Behav. **37**, 508—510.

Fritz, H. & Duncan, P. 1994: On the carrying capacity for large ungulates of African savanna ecosystems. Proc. R. Soc. Lond. B **256**, 77—82.

Giraldeau, L. A., Valone, T. J. & Templeton, J. J. 2002: Potential disadvantages of using socially acquired infor-mation. Philos. Trans. R. Soc. Lond. B Biol. Sci. **357**, 1559—1566.

Hilton, G. M., Cresswell, W. & Ruxton, G. D. 1999: Intra-flock variation in the speed of response on an attack by an avian predator. Behav. Ecol. **10**, 391—395.

Hopcraft, G. J. C., Sinclair, A. R. E. & Packer, C. 2005: Planning for success: Serengeti lions seek prey accessibil-ity rather than abundance. J. Anim. Ecol. **75**, 559—566.

Hunter, L. T. B. & Skinner, J. D. 1998: Vigilance behaviour in african ungulates: the role of predation pressure. Behaviour **135**, 195—211.

Ingrum, J., Nordell, S. E. & Dole, J. 2010: Effects of habi-tat complexity and group size on perceived predation risk in goldfish (*Carassius auratus*). Ethol. Ecol. Evol. **22**, 119—132.

Krause, J. & Ruxton, G. D. 2002: Living in Groups. Oxford Series in Ecology and Evolution. Oxford Univ. Press, New York.

Lima, S. L. 1995: Collective detection of predatory attacks by social foragers: fraught with ambiguity? Anim. Behav. **50**, 1097—1108.

Lima, S. L. & Dill, L. M. 1990: Behavioural decisions made under the risk of predation: a review and prospectus. Can. J. Zool. **68**, 619—640.

Loveridge, A. J., Davidson, Z., Hunt, J. E., Valeix, M., Elliot, N. & Stapelkamp, B. 2007a: Hwange Lion Project Annual Report 2007. Zimbabwe Parks and Wildlife Management Authority, Zimbabwe.

Loveridge, A. J., Searle, A. W., Murindagomo, F. & Macdonald, D. W. 2007b: The impact of sport-hunting on the lion population in a protected area. Biol. Conserv. **134**, 548—558.

Lung, M. A. & Childress, M. J. 2006: The influence of conspecifics and predation risk on the vigilance of elk (*Cervus elaphus*) in Yellowstone National Park. Behav. Ecol. **18**, 12—20.

McNamara, J. M. & Houston, A. I. 1992: Evolutionarily stable levels of vigilance as a function of group size. Anim. Behav. **43**, 641—658.

McNamara, J. M., Gasson, C. E. & Houston, A. I. 1999: Incorporating rules for responding into evolutionary games. Nature **401**, 368—371.

Michelena, P. & Deneubourg, J. L. 2011: How group size affects vigilance dynamics and time allocation pat-terns: the key role of imitation and tempo. PLoS ONE **6**, 1—9.

Owen-Smith, N. 1994: Foraging responses of kudus to seasonal changes in food resources: elasticity in con-straints. Ecology **75**, 1050—1062.

Owen-Smith, N. & Mason, D. R. 2005: Comparative changes in adult vs. juvenile survival affecting popula-tion trends of African ungulates. J. Anim. Ecol. **74**, 762—773.

Pays, O., Jarman, P. J., Loisel, P. & Gerard, J. F. 2007a: Coordination, independence or synchronisation tendency of individual vigilance in the eastern grey kangaroo? Anim. Behav. **73**, 595—604.

Pays, O., Renaud, P. C., Loisel, P., Petit, M., Gerard, J. F. & Jarman, P. J. 2007b: Prey synchronize their vigilant behaviour with other group members. Proc. R. Soc. Lond. B **274**, 1287—1291.

Pays, O., Goulard, M., Blomberg, S. P., Goldizen, A. W., Sirot, E. & Jarman, P. J. 2009: The effect of social facilitation on vigilance in the eastern gray kangaroo, *Macropus giganteus*. Behav. Ecol. **20**, 469—477.

Pays, O., Blomberg, S. P., Renaud, P. C., Favreau, F. R. & Jarman, P. J. 2010: How unpredictable is the individual scanning process in socially foraging mammals? Behav. Ecol. Sociobiol. **64**, 443—454.

Perrin, M. R. 1999: The social organization of the greater kudu *Tragelaphus strepsiceros* (Pallas 1766). Trop. Zool. **12**, 169—208.

Pulliam, H. R. 1973: On the advantages of flocking. J. Theor. Biol. **38**, 419—422.

Rasmussen, G. S. A. 2009: Anthropogenic Factors Influencing Biological Processes of the Painted Dog *Lycaon pictus*. Doctorate thesis, Oxford Univ., Oxford, UK.

Reboreda, J. C. & Fernández, G. J. 1997: Sexual, seasonal and group size differences in the allocation of time between vigilance and feeding in the greater rhea, *Rhea americana*. Ethology **103**, 198—207.

Rodriguez-Gironés, M. A. & Vàsquez, R. A. 2002: Evolutionary stability of vigilance coordination among social foragers. Proc. R. Soc. Lond. B **269**, 1803—1810.

da Silva, J. & Terhune, J. M. 1988: Harbour seal grouping as an anti-predator strategy. Anim. Behav. **36**, 1309—1316.

Sinclair, A. R. E., Mduma, S. & Brashares, J. S. 2003: Patterns of predation in a diverse predator-prey system. Nature **425**, 288—290.

Sirot, E. 2006: Social information, antipredatory vigilance and flight in bird flocks. Anim. Behav. **72**, 373—382.

Sirot, E. & Touzalin, F. 2009: Coordination and synchronization of vigilance in groups of prey: the role of collective detection and predators' preference for stragglers. Am. Nat. **173**, 47—59.

Steenbeek, R., Piek, R. C., van Buul, B. & van Hooff, J. A. R. A. M. 1999: Vigilance in wild Thomas's langurs (*Presbytis thomasi*): the importance of infanticide risk. Behav. Ecol. Sociobiol. **45**, 137—150.

Valeix, M., Fritz, H., Loveridge, A. J., Davidson, Z., Hunt, J. E., Murindagomo, F. & Macdonald, D. W. 2009: Does the risk of encountering lions influence African herbivore behaviour at waterholes? Behav. Ecol. Sociobiol. **63**, 1483—1494.

Ward, J. F., Austin, R. M. & Macdonald, D. W. 2000: A simulation model of foraging behaviour and the effect of predation risk. J. Anim. Ecol. **69**, 16—30.