Different Forms of Vigilance in Response to the Presence of Predators and Conspecifics in a Group-Living Mammal, the European Rabbit

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Abstract

In group-living mammals, the major functions of vigilance are to detect the presence of predators and to monitor the movements of conspecific competitors, i.e. of potential opponents in agonistic encounters. The minimum distance to such a conspecific competitor that an animal considers safe is usually lower than to a predator, whereas the frequency of encounters with conspecifics is higher. Therefore, the acquisition of information about a predator or about a conspecific could lead to the existence of at least two different modes of vigilance behaviour. The aim of the present study was to describe and compare different forms of vigilance behaviour that European rabbits, *Oryctolagus cuniculus*, display in anti-predator and social contexts. We conducted an observational study on individually marked animals from a field enclosure population. We recorded social interactions of the animals, the presence of aerial predators (common buzzard *Buteo buteo*), and the vigilance behaviour of the rabbits. We distinguished between two forms of vigilance of different intensity: subtle and overt. The frequencies of both forms of vigilance displayed by the rabbits differed significantly in occurrence, duration, and distribution over time. Females and males showed higher frequencies of overt but not subtle vigilance when buzzards were present. In contrast, the presence of conspecifics in close proximity affected the display of subtle but not overt vigilance: males increased the frequency of subtle vigilance when other males were close. Females increased subtle vigilance in proximity of males and females; however, this effect was only apparent in females with a more unstable social situation. In conclusion, European rabbits differentially increased two different forms of vigilance behaviour in social and anti-predator contexts.

Introduction

The outcome of an interaction between a prey and a predator largely depends on the timing of detection of the predator by the prey. To attain information about nearby predators, animals are vigilant by scanning the environment and numerous studies have focused on vigilance as an anti-predator behaviour (Elgar 1989; Lima & Dill 1990; Kavaliers & Choleris 2001; Caro 2005). The presence of conspecifics can modify the display of vigilance behaviour of an animal. In fact, many group-living animals show a negative relationship between individual vigilance and group size (Pulliam 1973; Elgar 1989; Roberts 1996; Treves 2000; Childress & Lung 2003; Fairbanks & Dobson 2007), and the sharing of anti-predator vigilance has been suggested to be a driving force in the group formation in many species (Hamilton 1971).

Nevertheless, living in social networks also carries costs for the individual. Animals, in particular individuals of the same sex, frequently compete for resources, and agonistic interactions among them are part of the daily social life in almost all group-living mammals (von Holst 2001). Especially subordinate individuals or animals in an unstable social situation are prone to attacks by other group members (Waite 1987; von Holst 1998, 2001). Consequently, animals should also direct their vigilance towards conspecific competitors, as it has been shown in mammals (McDonough & Loughry 1995; Blumstein et al. 2001; Cameron & du Toit 2005; Lung & Childress 2007) and birds (Catterall et al. 1992; Pravosudov & Grubb 1999; Fernández-Juricic et al. 2005).

Animals display different types of vigilance which might differ in the intensity and in the costs associated, depending on whether feeding is interrupted or not (McDonough & Loughry 1995; Lima & Bednekoff 1999). Furthermore, the form of the display might differ, e.g. bipedal vs. quadrupedal vigilance in nine-banded armadillos (*Dasypus novemcinctus*) and degus (*Octodon degus*) (McDonough & Loughry 1995; Ebensperger et al. 2006). The display of overt vigilance, such as adopting an upright posture, might enable the animal to spot more far away objects but could also serve as a signal to the predator deterring its attack (e.g. FitzGibbon 1989; Scannell et al. 2001). However, predators and conspecifics do not represent the same threat, so it might be speculated that less conspicuous displays are sufficient to monitor conspecifics in proximity.

Studies on European rabbits (*Oryctolagus cuniculus*), which live in social groups of variable sizes (Parer 1977; Cowan 1987), revealed that social factors also influence the display of vigilance behaviour in this lagomorph (Roberts 1988). During our studies on behaviour of European rabbits (Monclús et al. 2005; Rödel et al. 2008) we found that the animals display two distinct forms of vigilance, an overt and a subtle one (unpubl. data).

The principal goal of this study was to investigate whether these different forms of vigilance were displayed by European rabbits in different contexts: either in response to conspecifics or to predator presence. We conducted our study on individually marked animals of a European rabbit population living under semi-natural conditions. We first described differences between subtle and overt vigilance regarding the frequency and length of the scans, and the distribution over time. We secondly compared the animals' display of both forms of vigilance (a) when a predator was present or not, and (b) when conspecifics were in close proximity or not. We additionally considered the stability of the animals' social situation, which may modify their responses.

Methods

Study Population

The study was conducted on animals from a population of European rabbits living in a 20 000-m^2 field enclosure of the University of Bayreuth (Franconia, Germany). Vegetation consisted of grassland interspersed with groups of trees and bushes, which represents an adequate habitat structure for the European rabbit (Corbet 1994).

The population consisted of descendents of animals that had been caught in the wild (Bavaria, Germany) in 1984. At the onset of the study period in early Jul. 2006, the population consisted of seven different social groups with a total of 23 adult females and 14 males. According to field data, the density in our enclosure was high but still within the range for wild rabbit populations (e.g. Wallage-Drees & Michielsen 1989; Caruso & Siracusa 2001; Palomares 2001). During our long-term study, we found no signs of inbreeding such as changes in body mass, juvenile survival, or reduced fecundity of females. For further details on the study population see von Holst et al. (2002).

All animals were individually marked with aluminium ear-tags and the composition of the social groups was known by prior behavioural observations. A double electric fence widely prevented terrestrial but not aerial predators from accessing the enclosure.

Behavioural Observations

We recorded behavioural data from two outlook towers from where the whole enclosure could be observed. The study was conducted during the mid-late breeding season (mid Jul. to mid Oct. 2006; see Rödel et al. 2005), and all observations were done by the same observer. We collected data from 15 adult females and 13 adult males by means of focal sampling techniques (Martin & Bateson 1993). The observations were conducted during the last 3 h before twilight, when rabbits usually show the peak of their daily activity (Wallage-Drees 1989).

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The animals were observed while feeding, so any display of vigilance could be unequivocally recorded. We observed every animal for 5 min (continuous recording) in 12 different sessions resulting in a total observation time of 1 h per animal. These 12 sessions per individual were evenly distributed over the 3 months of the study. During every 5-min session, we recorded the duration and frequency of any behavioural sign of vigilance. Only one animal was recorded per session by the observer (only one person was conducting all the observations), and the data were entered directly into a portable computer with the software OBSERVER (version 3.0 for DOS, Noldus Inc., Wageningen, The Netherlands). We also recorded the occurrence of agonistic interactions and the number and identity of all rabbits within a 5-m radius around the focal animal.

Behavioural Variables

Vigilance

Rabbit vigilance consisted of two different behaviours, defined as follows:

Subtle vigilance: low intensity response; the animal only raises the head above shoulder maintaining the feeding posture (the ventral region remains close to the ground) without interrupting its feeding activity.

Overt vigilance: high intensity response; the animal adopts an upright posture, either quadrupedal (the ventral region is perpendicular to the ground) or bipedal, lifts the ears, and stops all current activities (i.e. feeding).

Stability of an individual's social situation

The social system of the rabbit is characterised by sex-specific linear rank hierarchies (Mykytowycz 1959; Cowan 1987). Intrasexual aggression reaches the maximum at the beginning of the breeding season, when the social ranks are established among the members of the social group (von Holst et al. 1999). However, rank hierarchies are not always stable and intrasexual agonistic interactions are common all over the season. To determine the stability of an individual's social situation, we summed up the number of escalated agonistic interactions that the animal experienced over the 12 five-min observation sessions, and calculated the total frequency of interactions per hour. The agonistic interactions considered were chasing or being chased by other individuals of the same sex. Ritualized agonistic behaviours such as displacements were not considered. We performed a median cut over all values of the animals of the same sex, and defined animals with values higher than the median as being in an unstable social situation while the social situation of animals with smaller values was considered stable. In females, the frequency of total agonistic interactions ranged between 0 and 10 interactions per hour, and the median was 2. In males, the frequency of agonistic interactions per hour ranged from 0 to 5 interactions per hour and the median was 3.

Proximity of Conspecifics

During all 5-min observational sessions, we determined whether the focal animal was in close proximity (i.e. within a 5-m radius) to adult conspecifics or not. We chose 5 m because, because of the structural characteristics of the enclosure, animals within that radius were surely in visual contact with the other group members. Five-meter intervals could be assessed by the aid of a grid system made out of wooden sticks, which was fixed all over the study area.

We considered that an individual was in close proximity to the focal animal only if it stayed for more than 1 min of the 5-min observational session within a distance of 5 m. The status of each focal animal (i.e. to be alone or with conspecifics) was assigned for each of the 12 observational sessions.

For every focal animal, we considered two different grouping situations that could explain the vigilance response. We determined whether same sex animals or animals from both sexes in close proximity were correlated with the vigilance elicited. Based on this, females were considered to be in close proximity to adult conspecifics in 49% of cases and they were in close proximity to other females in 29% of cases. Males were with other conspecifics in 15% of cases whereas they were with other males in 56% of the occasions.

Furthermore, we measured the total number of animals (adults of both sexes plus juveniles) which were in close proximity (<5 m) to the focal animal. This was done for females as well as for males. This variable is hereafter referred to as group size. In case the number of close conspecifics changed during the 5-min session, we used the mean value of the number of animals present during five 1-min intervals.

Predator Presence

The animals of the enclosure population were regularly in contact with wild common buzzards (*Buteo buteo*), which frequently arrived in the late afternoon and circled over the enclosure, or sat on the trees inside the enclosure. Adult rabbits react to buzzards by behavioural signs of alertness but not or hardly to kestrels (*Falco tinnunculus*) or carrion crows (*Corvus corone corone*) (pers. obs.). We did not observe the presence of other diurnally active aerial predators during our study.

For every 5-min observation session, we recorded whether a buzzard was present or not. To determine predator presence, we recorded any visual or auditory signs of the buzzard. Regular scans for buzzards were done before starting the daily observations and every 5 min when changing the focal animal. In total, buzzards were present during 32.2% of the 5-min observation sessions.

Data Analysis and Sample Sizes

Differences between the two types of vigilance

We tested whether the two types of vigilance (subtle or overt vigilance), differed in the frequency and the mean duration of the bouts when the animals showed one of the two behaviours. Furthermore, we compared the coefficient of variation based on the frequencies recorded during the twelve observation sessions of each animal. This measure provides information about the evenness of the distribution of the two different behavioural variables over time.

Effects of predator presence and social factors

The major goal of our study was to test whether the presence of a predator (common buzzard) or different social factors affected the display of the two different behavioural types of the rabbits' vigilance. Frequency and duration of both types were highly collinear (subtle vigilance; averaged values per animal over all 12 observation sessions: $r^2 = 0.70$, $n = 28$, $p < 0.001$; overt vigilance: $r^2 = 0.71$, $n = 28$, $p < 0.001$). We only present the results of the analyses using the frequencies of subtle and overt vigilance as response variables, nevertheless we also ran all tests using the total duration and obtained the same results.

We analysed our data in two steps. First, we tested whether the presence of a predator explained the display of either subtle or overt vigilance. Therefore, we split the data in two sets: one set consisted of the averaged values measured for each individual when the predator was present. The other set consisted of data from the same individuals when the predator was absent. Using these data, we calculated repeated measurements ANOVAS where we included the factor sex and the interaction of both factors to consider sex-specific differences in the response to predator presence (see Fig. 1a). This statistical model was calculated separately for the frequencies of both subtle and overt vigilance. In total, we ran the analysis with the complete set of focal animals ($n_{females} = 15$, $n_{males} = 13$). In a further step, we only considered the data when the predator was present and tested if there was a sex-specific effect of group size (number of rabbits in close proximity to the focal animal) on the display of subtle and overt vigilance by ANCOVA. We included the interaction of sex with the covariate: group size. If non-significant, the covariate interaction term was removed and the model was recalculated (see Engqvist 2005). Group size did not differ significantly between situations when the predator was present or absent (paired t-test: $t_{27} = 0.23$, $p = 0.82$).

Second, we split the data for each individual with respect to the presence or absence of conspecifics in close proximity (<5-m distance). European rabbits

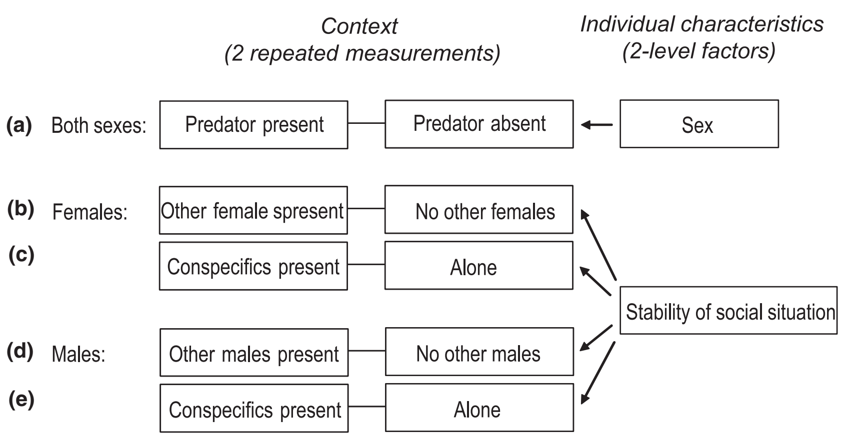

Fig. 1: Outline of the data analysis with respect to (a) the presence of predators (common buzzard) and (b–e) conspecifics. Response variables are the frequencies of subtle and overt vigilance.

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show sex-specific linear rank orders (Mykytowycz 1959; von Holst et al. 1999), i.e. intraspecific competition mainly takes place within sexes. Therefore, we ran the analyses separately for females and males (see Fig. 1b,c): for males and females, we considered the presence/absence of other adult conspecifics of the same sex as potential social factors triggering the display of vigilance behaviour, but also tested the presence/absence of the total number of conspecifics (adult males + females) in another model (Fig. 1c,e). Again, we used repeated measurements ANOVAS and tested for differences between both situations. For both sexes, we additionally used the individual's social situation as fixed factor with two levels (unstable/stable). We always considered the interaction between this factor and the respective repeated measurements of the model (Fig. 1). Eight females were in an unstable situation whereas seven were in a stable social situation. In males, six were in an unstable situation and five were in a stable situation. For this second step, we could only use a lower sample size of males ($n_{males} = 11$), since two of the males were never observed to be in close proximity to another male and were removed from all the analysis, as described in Fig. 1d,e.

Statistical Analysis

Prior to the use of parametric statistics, we ensured that the distribution of the data was approximately normal (checked by Shapiro Wilk test and normal probability plots) and that variances were homogenous (checked by Levene test). If these pre-conditions were not fulfilled the data were transformed. In all of these cases, we used a log-transformation to normalise the right-skewed distribution of the data. Analyses were done with SPSS 14.0 (SPSS Inc., Chicago, Illinois, USA).

Results

Differences Between Two Types of Vigilance

In our study, we distinguished between two different types of vigilance behaviour displayed by the rabbits: subtle and overt vigilance. Both behavioural variables were not correlated significantly (r = 0.26, n = 28, p = 0.18). Compared to overt vigilance, subtle vigilance was displayed in a much higher frequency (paired t-test: $t_{27} = 17.47$, $p < 0.001$; Fig. 2a) and consisted of shorter bouts (Wilcoxon's signed rank test: $Z_{27} = -4.53$, $p < 0.001$; Fig. 2b). Furthermore, subtle vigilance was more evenly distributed over time, which was apparent by the comparatively lower coefficient of variation (paired samples t-test: $t_{27} = -8.08$, $p < 0.001$; Fig. 2c).

Effects of Predator Presence

Subtle vigilance

The presence of buzzards did not modify the frequency of subtle vigilance displayed by the rabbits (repeated measurements ANOVA: $F_{1,26} = 1.02$, p = 0.32; Fig. 3a). There were no significant differences between sexes ($F_{1,26} = 0.35$, p = 0.56) and no significant interaction between predator presence and sex ($F_{1,26} = 0.11$, p = 0.74).

Overt vigilance

Predator presence significantly increased the frequency of overt vigilance by on average 87% (repeated measurements ANOVA: $F_{1,26} = 15.76$, p = 0.001; Fig. 3b). The response did not differ between males and females ($F_{1,26} = 1.21$, p = 0.28) and the interaction term predator presence × sex was not statistically significant either ($F_{1,26} = 2.60$, p = 0.12).

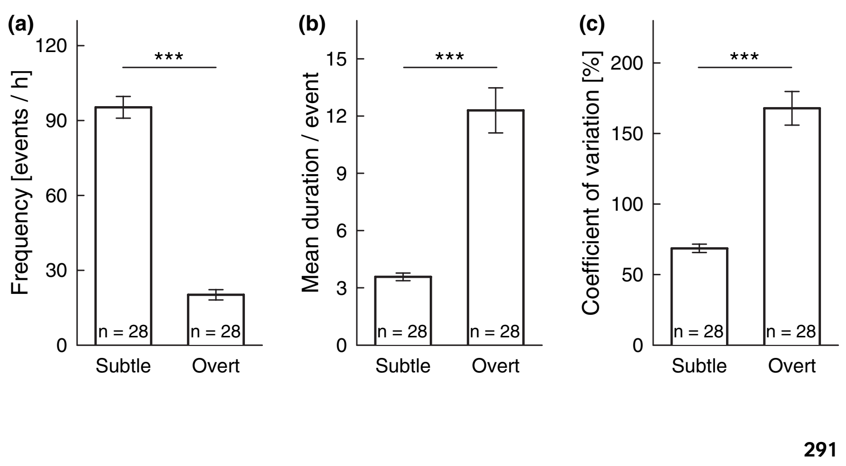

Fig. 2: Comparison of subtle and overt vigilance displayed by adult European rabbits by means of (a) the frequency of occurrence, (b) the mean duration of the bouts and (c) the coefficient of variation. Data (given as means ± SE) represent repeated measurements of the same individuals; sample sizes are shown in the bars. Statistically significant differences are indicated by asterisks; see text for statistics.

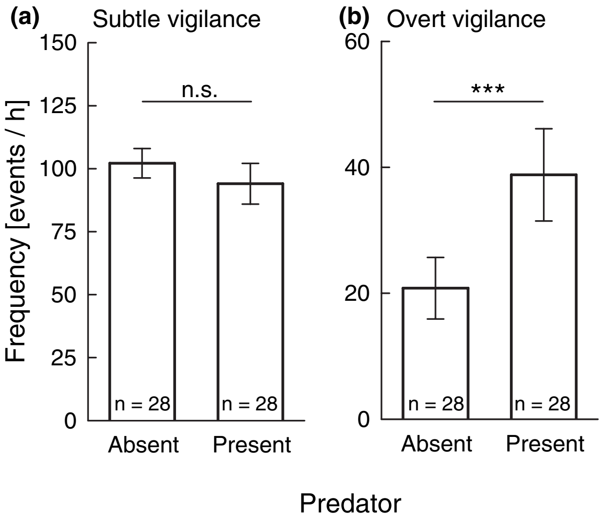

Fig. 3: Effects of the presence of common buzzard on the frequency of (a) subtle and (b) overt vigilance displayed by adult European rabbits. Data (given as means ± SE) represent repeated measurements of the same individuals; sample sizes are shown in the bars. Statistically significant differences are indicated by asterisks; see text for statistics.

Only considering the cases when a predator was present, we tested for the effects of group size (i.e. the presence of conspecifics within a distance of 5 m) on the frequency of overt vigilance. However, no significant effect of this variable was apparent (ANCOVA: $F_{1,25} = 0.11$, $p = 0.74$) and there were no differences between males and females ($F_{1,25} = 1.81$, $p = 0.19$). The covariate interaction term group size × sex was not significant ($F_{1,24} = 0.64$, $p = 0.43$) and was removed from the final model.

Effects of Social Factors

Subtle vigilance of females

The proximity of individuals of the same sex did not have a significant effect on the females' display of subtle vigilance, either in individuals with an unstable or stable social situation (Table 1a). However, the presence of adult conspecifics in close proximity affected the display of subtle vigilance (see significant interaction in Table 1b). Females, which were in a more unstable social situation showed a significantly higher rate of subtle vigilance when conspecifics were close (paired t-test: $t_7 = -2.41$, $p = 0.047$; Fig. 4a). In contrast, females in a more stable social situation did not show statistically significant differences between both situations (paired t-test: $t_6 = 1.40$, $p = 0.21$; Fig. 4b).

Subtle vigilance of males

The frequency of subtle vigilance displayed by males was significantly higher in situations when other

Table 1: Effects of different social factors on subtle and overt vigilance of female (a, b: n = 15) and male (c, d: n = 11) European rabbits (repeated measurements ANOVA). Repeated measurements were taken when the animals were alone or in close proximity (<5 m) to other adult individuals of the same sex (a, c), or adults of both sexes (b, d). The stability of the individuals' social situation (stable/unstable) is included as a factor. The data for (d) were log-transformed prior to analysis. Statistically significant effects are highlighted in bold letters

Source of variation		Subtle vigilance		Overt vigilance	
		$F_{1,12}$	p	$F_{1,12}$	p
Females					
(a)	Proximity to other females	0.002	0.96	1.164	0.30
	Stability of social situation	0.002	0.96	0.006	0.94
	Proximity × stability	1.18	0.30	0.051	0.82
(b)	Proximity to conspecifics	0.06	0.81	0.098	0.76
	Stability of social situation	0.23	0.64	0.152	0.70
	Proximity × stability	6.64	0.023	0.039	0.85
Males					
		$F_{1,9}$	p	$F_{1,9}$	p
(c)	Proximity to other males	7.26	0.025	0.075	0.79
	Stability of social situation	3.15	0.11	1.70	0.23
	Proximity × stability	0.002	0.97	1.98	0.19
(d)	Proximity to conspecifics	1.98	0.19	0.051	0.83
	Stability of social situation	1.29	0.29	0.080	0.78
	Proximity × stability	0.54	0.48	1.83	0.21

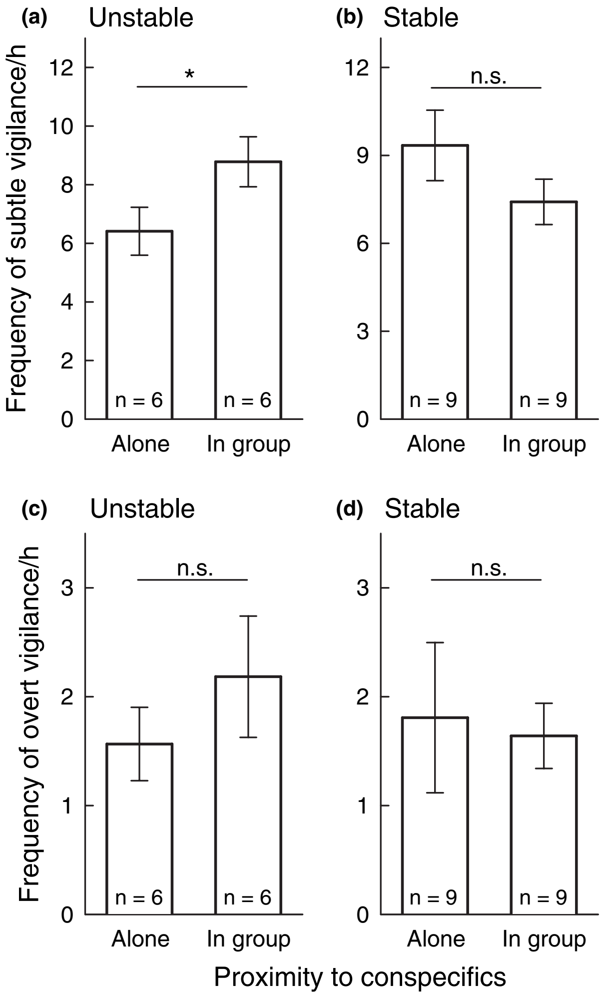

Fig. 4: Effects of the presence of conspecifics (adult males and females) in close proximity (<5 m) on the frequency of subtle (a, b) and overt vigilance (c, d) displayed by adult female European rabbits. Individuals with an unstable (a, c) and stable (b, d) social situation are tested. Data (given as means ± SE) represent repeated measurements of the same individuals; sample sizes are shown in the bars. Statistically significant differences are indicated by asterisks; see text for statistics.

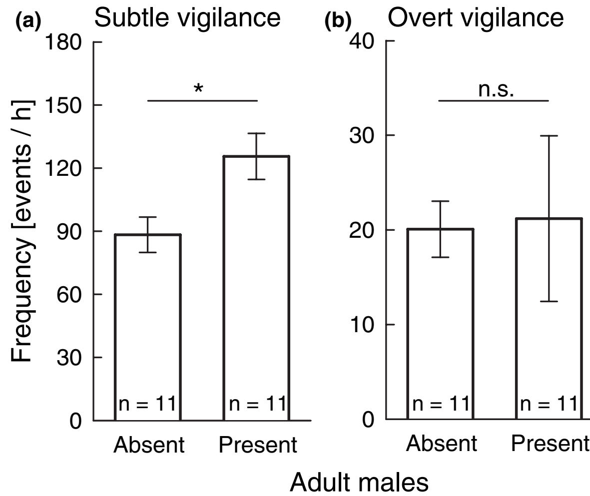

Fig. 5: Effects of the presence of male intruders in close proximity (<5 m) on the frequency of (a) subtle and (b) overt vigilance displayed by adult male European rabbits. Data (given as means ± SE) represent repeated measurements of the same individuals; sample sizes are shown in the bars. Statistically significant differences are indicated by asterisks; see text for statistics.

males were in proximity compared to situations when no other males were close (Fig. 5a). The stability of the males' social situation did not show any significant effect.

We did not find significant differences in the males' display of subtle vigilance when considering the presence/absence of adult conspecifics of both sexes (Table 1c).

Overt vigilance of females

Females did not show any differences in the frequency of overt vigilance between situations when other females (Table 1a) or females and males (Table 1b; see Fig. 4c,d) were in close proximity or not.

Overt vigilance of males

In males, we also did not find any significant effects of the presence/absence of other males (Table 1c; see Fig. 5b) or of adult conspecifics of both sexes (Table 1d) on the display of overt vigilance.

Discussion

Vigilance is usually considered as an anti-predator behaviour but can also have social functions (e.g. Renouf & Lawson 1986; Blumstein et al. 2001; Tchabovsky et al. 2001; Lung & Childress 2007). This was confirmed in our study on European rabbits: the animals increased their vigilance either when a predator was present or when conspecifics were in close proximity. However, we found that the animals showed two different types of vigilance (subtle and overt vigilance), which were mainly displayed in response to the proximity of conspecific competitors or to predator presence, respectively. The existence of two distinct patterns of vigilance for predators and for conspecifics has been shown in nutmeg mannikins (*Lonchura punctulata*) (Coolen & Giraldeau 2003).

The two types of vigilance in rabbits differed in the rate, the mean duration, and the distribution over time. Subtle vigilance, which was increased when conspecifics were close, consisted of frequent and short scans. Overt vigilance, which was increased when the predator was present, consisted of long and less frequent scans. Therefore, subtle vigilance followed the conditions for monitoring objects in close proximity, allowing an individual to assess small and subtle variations in the position of close-by individuals. Overt vigilance met the conditions for long distance surveillance, because longer scans are necessary to detect far away objects (Bertram 1980; Roberts 1988). Moreover, in most of the cases it was possible to assess that the subtle vigilance was directed to a member of the group, whereas we could not assign any specific direction to overt vigilance.

Both forms of vigilance did not correlate, pointing out that different cues may trigger their display. The further results of our study confirm the adaptive use of the two different behaviours in social and anti-predator contexts: we found clear differences in the rabbits' display of the two types of vigilance in situations with/without the presence of predators and with/without close proximity of conspecifics. When common buzzards were present, rabbits increased the frequency of overt vigilance. Generally, such an increase in scanning rates during situations of increased predation risk has been described in many other studies (e.g. Bertram 1980; Caine & Weldon 1989; Frid 1997; Monclús et al. 2006). However, our results clearly show that only the more overt form of vigilance was increased in response to predator presence. The adoption of an upright posture with the ears up could serve different purposes. Above all, the early detection of the spatial location of the predator, including an estimate of the distance, increases the chances of a successful escape (Bednekoff & Lima 1998; Kats & Dill 1998; Lima 1998). Moreover, the vigilance display itself could act as a cue for the predator about the wariness of the animal, and therefore act as a pursuit-deterrent signal (Woodland et al. 1980; Caro 2005). In rabbits, the upright postures highlight some physical features that make them very conspicuous to visual predators, such as the long and contrasting-coloured ears (Lockley 1964). This might act as a signal for the predator and might deter predatory attacks (see FitzGibbon 1989; Scannell et al. 2001).

Interestingly, we did not find a buffering effect of group size on the display of anti-predator vigilance as exemplified by the lack of a correlation between the number of conspecifics around the focal animal and the frequency of overt vigilance. One possible explanation could be that we only considered cases when the predator was present what constitutes a high-risk situation; under such conditions usually all animals of a group increase vigilance (Lima & Dill 1990).

We did not find sex-specific differences in the overt alert response to predator presence. In contrast, such differences have been reported in black-tailed prairie dogs (*Cynomys ludovicianus*), where males were more vigilant than females (Loughry 1993), and in elks (*Cervus elaphus*) where males were less vigilant (Winnie & Creel 2007).

Because of the observational and semi-natural character of our study, it was not possible to study the animals in situations with conspecifics present vs. situations of complete social isolation. Instead, we used the proximity of rabbits within a radius of 5 m around the focal animal. We found a clear increase in subtle vigilance when conspecifics were within this distance. However, this response was sex-specific. Male rabbits generally increased their scanning rates when potential competitors were nearby. A similar reaction has been found in other species (e.g. nine-banded armadillos *Dasypus novemcinctus*: McDonough & Loughry 1995; giraffe *Giraffa camelopardalis*: Cameron & du Toit 2005). In females, we also found increased vigilance to close conspecifics. However, the stability of the females' social situation was an important factor in modifying these responses. Females in unstable social situations increased the frequency of subtle vigilance when other rabbits of both sexes were close, whereas females with a stable social situation did not. This points out that not only the presence of potential same-sex competitors but also of potential mating partners are important cues for vigilance in females. Female rabbits share space with other females of their group, and agonistic interactions between them are frequent (Mykytowycz 1959; von Holst et al. 1999). The increased number of scan bouts could be due to the need to gather information about the group members (Fernández-Juricic et al. 2005), such as their relative spatial position. Based on this information, females might avoid attacks or start them, for example to chase away potential infanticidal females from the own breeding burrows (reviewed in: Agrell et al. 1998; European rabbits: Rödel et al. 2008). On the other hand, scanning for present males and gathering information about their movements might also be relevant: especially younger males are sometimes harassing females outside their oestrus by showing courtship behaviour (pers. obs.), and females are usually terminating these apparently unwanted approaches by chasing the young males away.

Apart from differing in the shape and in the eliciting context, both forms of vigilance might differ in the costs associated. Subtle vigilance could be considered a low cost behaviour as it did not affect other activities, such as feeding (Lima & Bednekoff 1999; Tchabovsky et al. 2001). In those herbivores, where the food resource is not limited, and their main limitation resides in food handling, the time while processing food could be used for other behaviours, such as vigilance (Illius & Fitzgibbon 1994; Cowlishaw et al. 2003; Fortin et al. 2004). In fact, the rabbits in our study handled food while looking for conspecifics, so subtle vigilance and foraging were not exclusive.

However, when the rabbits displayed overt vigilance, which apparently served for anti-predator purposes, they did stop their feeding activity. A study carried out in bison (*Bison bison*) and elk (*Cervus elaphus*) also showed that in some occasions the animals stopped chewing while scanning (Fortin et al. 2004). The authors suggested that this could be due to the perception of elevated risk. Nevertheless, we think that it is not likely that the skip of a few feeding opportunities could entail a notable cost for a grazer such as the European rabbit. A further hint comes from experimental studies on rabbits under laboratory conditions, where increased rates of vigilance did not affect the animals' daily food intake (Monclús et al. 2005). We believe that adult rabbits in healthy body condition are not limited in their daily time budget for feeding, at least during the vegetation period. Similar findings have been reported for golden marmots (*Marmota caudata aurea*: Blumstein 1996).

In conclusion, we recommend taking into account both, the form and the context of the behavioural displays when studying vigilance in group-living animals. Only summing up the animals' frequency of scans may lead to incorrect conclusions. Moreover, the social situation of an animal might strongly affect its perceived risk and therefore the display of its alert response.

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