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Alpine marmots (*Marmota marmota*) adjust vigilance behaviour according to environmental characteristics of their surrounding

C. FERRARI [1,3], G. BOGLIANI [1] and A. VON HARDENBERG [2]

[1] *Dipartimento di Biologia Animale, Università di Pavia, Piazza Botta 9, 27100 Pavia, Italy*
[2] *Centro Studi Fauna Alpina, Parco Nazionale del Gran Paradiso, Degioz 11, 11010 Valsavarenche (Aosta), Italy*

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Predation risk can strongly affect behaviour of preys, and natural selection should have favoured the evolution of behavioural plasticity in the strategies used to avoid predation. The level of predation risk can be affected by environmental characteristics and we expect individuals to adjust vigilance behaviour to the level of risk. In this study we investigate if Alpine marmots (*Marmota marmota*) living in an area delimited by the forest and with scarce visibility (Closed Site) differ in their vigilance behaviour from marmots inhabiting an open meadow further away from the forest edge and with greater visibility (Open Site). The rate of vigilance and the time spent vigilant in the Closed Site were higher than in the Open Site, while the mean duration of each vigilance bout did not differ between the two sites. Our results suggest that Alpine marmots adjust vigilance behaviour according to the environmental characteristics of their surroundings while there appears to exist an optimal duration of scan bouts which is independent of relative predation risk.

KEY WORDS: vigilance predation risk, environmental characteristics, Alpine marmot, vigilance bout, trade-off.

[3] Corresponding author: Caterina Ferrari, Département des Sciences Biologiques, Université du Québec à Montréal, Case Postale 8888, succursale centre-ville, Montréal H3C 3P8, Canada (E-mail: catferr@libero.it).

INTRODUCTION

An animal's behaviour is influenced by a number of factors among which predator avoidance and foraging efficiency are likely to be particularly important (LIMA 1985). In species subject to strong predation pressure natural selection favoured the evolution of strategies that allow both foraging and vigilance behaviour at the same time. A common anti-predator behaviour adopted by herbivorous species consists of a sequence of head-down/head-up movements, in order to visually scan the surroundings and detect potential predators while foraging (LIMA & DILL 1990). Scanning the surroundings for predators, however, is potentially a costly strategy, as it reduces the time available for foraging. Various studies show that individuals behave as a trade-off does exist between these costs, adjusting the rate and mean duration of vigilance events to the current predation risk (LIMA & BEDNEKOFF 1999, DEVEREUX et al. 2005). Environmental characteristics such as proximity to woods, slope, substrate or scarce visibility are likely to influence predation risk and, consequently, vigilance behaviour in prey species: individuals are more vigilant when they have scarce peripheral visibility (ELGAR 1989, BURGER 2001, FERNÀNDEZ-JURICIC & TRAN 2007, RÉALE et al. 2009).

Previous studies on North American marmot species, Hoary marmot *Marmota caligata* (HOLMES 1984) and Yellow bellied marmot (*Marmota flaviventris*) (CAREY & MOORE 1986, ARMITAGE 1991), have shown that scarce visibility of the surroundings due to proximity to forest or a steep slope increases individuals' vigilance rate. Furthermore, in a study on habitat selection of Yellow bellied marmot, BLUMSTEIN et al. (2008) shown that visibility-related characteristics, rather than food availability, explain correctly variation in persistence of this species in different site. In this study we investigate whether environmental characteristics of the habitat influence the vigilance behaviour in Alpine marmots (*Marmota marmota*).

Alpine marmots are large, diurnal, burrow-dwelling rodents inhabiting high alpine and subalpine meadows in Europe. This species lives in social groups of 2 up to 20 related individuals and spends half of the year hibernating underground (ARNOLD 1988, PERRIN et al. 1993). Marmots dig burrow systems with several entrances surrounding a core area. There are two principal types of burrows: the *main burrow* (sleeping or nest burrows), with multiple entrances, where marmots spend most of their time; *escape burrows* are shorter, not connected to each other, and spread out over the entire home-range of a family. Each escape burrow usually has only one entrance (BASSANO et al. 1991, BLUMSTEIN 1998). Marmots frequently scan their surroundings while they forage, groom or play, and they flee into a burrow as soon as they detect a potential danger. Marmots also use alarm calls when they perceive a threat (ARMITAGE 1962, BLUMSTEIN 1998).

In June-September 2006, we compared vigilance behaviour in 12 Alpine marmot families inhabiting two distinct habitats in the Gran Paradiso National Park, Italy: one habitat was open, located above the tree line with great visibility of the surroundings (Open area), and the other habitat was surrounded by the forest and allowed less visibility due to rocks, isolated trees and bushes (Closed area). These characteristics are likely to negatively influence marmot's chances of detecting on time an approaching terrestrial predator as found in other marmot species (HOLMES 1984, CAREY & MOORE 1986, ARMITAGE 1991) as well as in other animal species (RÉALE et al. 2009).

METHODS

Study area

The research was conducted in the Orvielles Study Area (Valsavarenche, Aosta, Gran Paradiso National Park, North-Western Italian Alps, 45°34'N/7°11'E). The study area contains a high density of Alpine marmots and of their main natural predators: golden eagles (*Aquila chrysaetos*) and red foxes (*Vulpes vulpes*). These conditions guarantee frequent predator-prey interactions.

We studied marmots in two sites with similar marmot densities but different environmental characteristics:

Closed Site: (1870-2000 m above sea level). Characterised by an alpine meadow (mainly *Festuca varia* and *Poa alpina*) surrounded by mixed conifer forest (European larch *Larix decidua,* pine *Pinus silvestris* and Norway spruce *Picea abies*).

Open Site: (2100-2500 m above sea level). Characterised by an open alpine meadow (mainly *Festuca varia* and *Poa alpina*).

The two sites differ significantly in their distance from forest edge: the main burrows inside the Closed Site have an average distance of 81.17 ± 7 m from forest edge, while in the Open Site the average distance of main burrows to forest edge is 239.56 ± 60 m (Mann-Whitney U Test: Nsite1 = 6, Nsite2 = 6, U = 0; $P < 0.05$). Thus, the two sites differ in proximity to the forest and degree of openness of the landscape, with the Closed Site characterised by a scarce visibility due to trees and bushes.

Field methods

We spent the week before the beginning of this research observing marmots at the two sites; these preliminary observations and all the observations during the study were made by the same observer. We identified, recorded with a handheld GPS and closely inspected all the burrow systems at the two study sites. This allowed us to distinguish between main and escape burrows and between different family groups. We observed 6 family groups per site. By sitting quietly on the edge of the colonies, we observed Alpine marmots with a scope (Swarosky 30 × 75) from a minimum distance of 200 m during their foraging activities at different times during the day (7.00-13.00; 14.30-18.00) and different days during the summer to collect a broad and homogenous dataset for different levels of analysis (site, month, age, etc.). We recorded vigilance behaviour of individual marmots on a voice recorder as described in BLUMSTEIN (1996); we decided to observe and record marmots exclusively during their foraging activity. As

we did not catch and mark each marmot, we did not record more than one individual of the same family during the same day to avoid pseudoreplication. Using main burrows and natural features of the site as references we were able to distinguish between families**.** We did not record any marmot in ambiguous locations. In addition, we never observed marmots from the same site both in the morning and in the afternoon during the same day. Once we located a foraging marmot, we waited for two minutes before starting an observation session to avoid recording behaviour during or straight after any particular situation or disturbance (e.g. predators passage, agonistic interaction with other marmots, tourist passage ...). We then recorded the beginning and the end of each vigilance event (head up) and foraging event (head down) during the following 2 min (120 sec) (HOLMES 1984, BLUMSTEIN 1996).

We used the software EthoLog 2.0 (OTTONI 2000) to digitalise all the records from the tape recorder. The following parameters were calculated for each observation session: percentage of total time spent vigilant and foraging, frequency of vigilance and foraging bouts (number of bouts/total observation time) and mean duration of vigilance and foraging bouts (MARTIN & BATESON 1993).

Data analysis

To account for repeated measurements of individuals belonging to the same family group and thus reduce the possible effects of pseudoreplication, we fitted linear mixed effects models (LME) with family group identity and Age class nested in family group as random grouping factors. Site type (Open or Closed) and Month were fitted as fixed effects. For fitting LMEs we used the nlme 3.1-85 package for R (PINHERO & BATES 2001). For all analyses we used the open source statistical environment R version 2.8.1 (R DEVELOPMENT CORE TEAM 2008). We followed the model building approach suggested by PINHERO & BATES (2001) for all fitted LME models. To meet the assumptions of normality vigilance rate and duration data were log transformed, while percentage of time spent vigilant was arcsin (square root) transformed. The significance of fixed terms was assessed using conditional F tests with an $\alpha = 0.05$ level of significance.

RESULTS

Rate of vigilance bouts

Marmots inhabiting the Closed Site showed a greater rate of vigilance than marmots living in the Open Site (Closed Site: mean rate 6.3 ± 0.4 bouts/min; Open Site: mean rate 2.8 ± 0.2 bouts/min) (Table 1, Fig. 1).

Percentage of time spent vigilant

In accordance with the previous result, marmots living in the Closed Site spent more time vigilant. The mean percentage of time spent vigilant in the Closed Site is 29% ± 0.02, more than twice the time marmots spent vigilant in the Open Site (12% ± 0.013; Table 2, Fig. 2).

Table 1.

Conditional F tests for the significance of terms included in the LME model with the rate of vigilance (events/min) as the dependent variable, Family group identity and Age class nested in Family group identity as grouping random factors, a general positive-definite within-group error structure, a random intercept and Site type and Month as fixed effects. Orvielles (Gran Paradiso National Park, Italy). Significant terms are tagged with an asterisk.

Model terms:	β	f	F	*P*
Site	0.96 (±0.18)	1,13	26.94	≤ 0.0002 *
Month	—	2,76	1.54	≤ 0.22

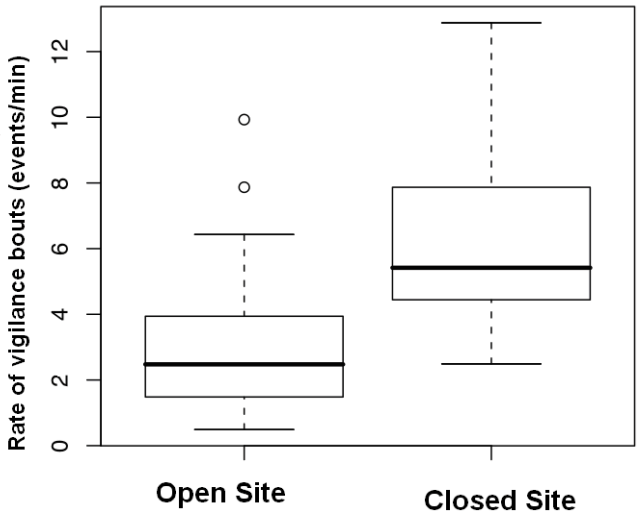

Fig. 1. — Difference in the rate of vigilance (events/min) of Alpine marmots in the Open and the Closed Site in Orvielle, Gran Paradiso National Park, North-Western Italian Alps. The thick line is the median, the box shows the first and the third qu artile. The notches extend to ± 1.58 Interquartile range/sqrt(n) giving roughly the 95% confidence intervals for the difference in the two medians.

Table 2.

Conditional F tests for the significance of terms included in the LME model with the percentage of time spent vigilant (%) as the dependent variable, Family group identity and Age class nested in Family group identity as grouping random factors, a general positive-definite within-group error structure, a random intercept and Site type and Month as fixed effects. Orvielles (Gran Paradiso National Park, Italy). Significant terms are tagged with an asterisk.

Model terms:	β	df	F	*P*
Site	0.24 (±0.04)	1,13	30.94	≤ 0.0001 *
Month	—	2,76	2.40	≤ 0.971

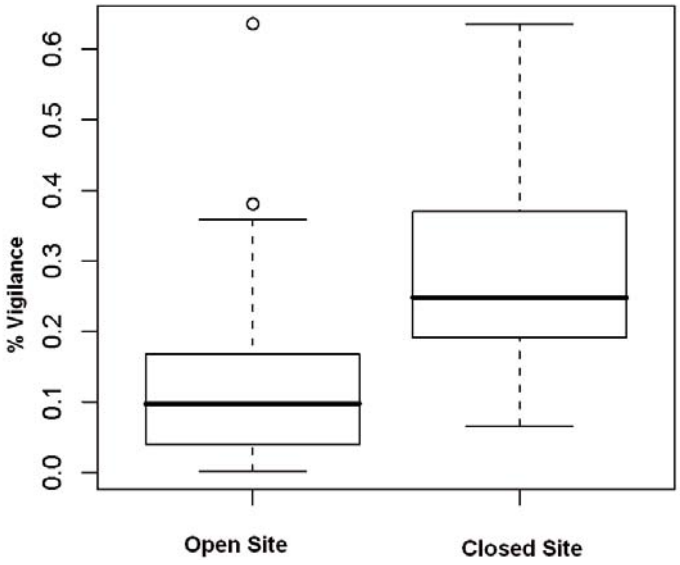

Fig. 2. — Difference in the percentage of time spent in vigilance in marmots inhabiting the Open and the Closed Site in Orvielle, Gran Paradiso National Park, North-Western Italian Alps. The thick line is the median, the box shows the first and the third quartile. The notches extend to ± 1.58 Interquartile range/sqrt(n) giving roughly the 95% confidence intervals for the difference in the two medians.

Table 3.

Conditional F tests for the significance of terms included in the LME model with the duration of vigilance bounts (sec) as the dependent variable, Family group identity and Age class nested in Family group identity as grouping random factors, a general positive-definite within-group error structure, a random intercept and Site type and Month as fixed effects. Orvielles (Gran Paradiso National Park, Italy). Significant terms are tagged with an asterisk.

Model terms:	β	df	F	*P*
Site	0.28 (±0.14)	1,13	3.76	≤ 0.07
Month	—	2,76	0.41	≤ 0.67

Difference in mean duration of vigilance bouts

We found no significant difference in the mean duration of vigilance bouts in marmots inhabiting the Open Site vs those inhabiting the Closed Site (mean value in the Open Site: 2.6 ± 0.2; mean value Closed Site: 2.9 ± 0.2 sec) (Table 3, Fig. 3).

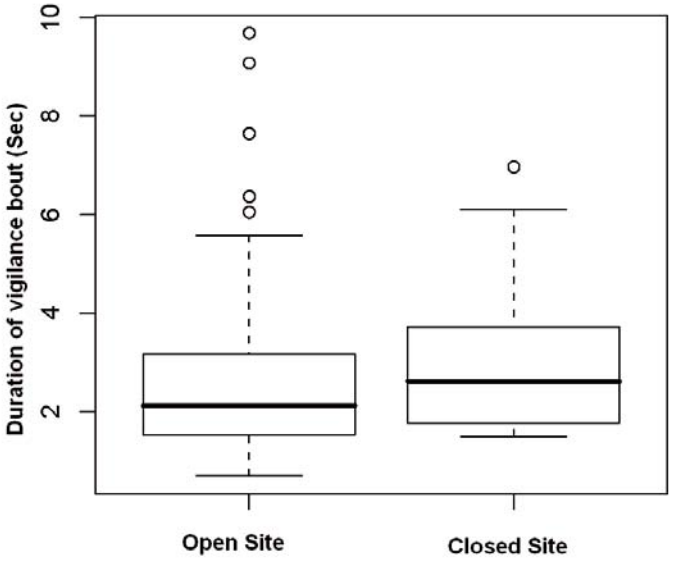

Fig. 3. — Difference in the duration of vigilance bouts of marmots inhabiting the Open and the Closed Site in Orvielle, Gran Paradiso National Park, North-Western Italian Alps. The thick line is the median, the box shows the first and the third quartile. The notches extend to ± 1.58 Interquartile range/sqrt(n) giving roughly the 95% confidence intervals for the difference in the two medians.

DISCUSSION

Marmots living in the area closer to the forest show a higher frequency of vigilance events. We suggest that the greater vigilance in the forest habitat improves the chances of marmots to detect a potential predator approaching which, due to the scarce visibility of the environment, would otherwise remain undetected.

These results are in accordance with those from previous studies both in mammals and birds. MATEO (2007) showed that Belding's ground squirrels (*Spermophilus beldingi)* living in visually closed sites, where burrows and predators are difficult to see, spend more time alert than those living in more open habitats. In birds, European starlings (*Sturnus vulgaris*) compensate their difficulties to scan surroundings due to habitat complexity by increasing their scan rate (DEVEREUX et al. 2005). Bighorn sheep (*Ovis canadensis*) have been shown to increase their vigilance rate with proximity to the forest due to an higher risk of being predated by an ambush predator (*Cougar cougar*) (RÉALE et al. 2009).

Red fox is the main terrestrial predator of the Alpine marmot in our study area (CAGNACCI et al. 2003) and we observed a higher frequency of visits by foxes in the Closed site than in the Open site (C. FERRARI pers. obs).

We suggest that proximity to the forest increases the possibility for foxes to approach marmots undetected, increasing predation risk for marmots, which, consequently, show a higher vigilance rate.

We found that in Alpine marmots the time spent scanning in the Closed Site is more than double than in the Open Site. Furthermore in this study, we found that the mean duration of vigilance bouts in the Closed Site is not different from the mean scan duration of marmots living in the Open Site while we expected a shorter duration. This result suggests the existence of an optimal duration of vigilance scan, independent of the environmental characteristics. A shorter bout could be inefficient and thus, even with a higher frequency of scans, marmots of the Closed Site cannot make their scans shorter. Thus they cannot trade off a higher rate of vigilance bouts with a shorter duration of each bout. In fact, a longer bout does not necessarily result in a greater probability of detecting a predator and would certainly decrease food intake with possible negative effects on summer weight gain and fat accumulation, essential for winter survival (Bednekoff & Lima 1998, 2002). We suggest that marmots inhabiting Closed site may reduce the cost of the higher amount of time spent vigilant by chewing the food while looking around; Armitage et al. (1996) divided behaviours of Yellow bellied marmot as foraging, vigilance and foraging-alert (when individuals chewing their food sitting upright and looking around) and they shown that, in this way, individuals are able to reduce the cost of being vigilant.

An increase in vigilance rate in Alpine marmots could be due also to a reduction in group size. Social species like the Alpine marmot, often benefit from group size effects to both increase chance of detecting a predator and decrease individual's vigilance rate (dilution effect and collective detection) (Elgar 1989, Lima 1995, Burger 2001). It has been shown, however, that visual and spatial separations between individuals in a group, decrease the benefits of group size effects and individuals have to increase their own vigilance rate (Devereux et al. 2005). We suggest that possibly, since the Closed site is a patchy environment characterized by several natural obstacles such as shrubs and rocks across the entire area, visual and spatial contacts between individuals are not optimal compared to the Open site. Thus the benefit from being in a group at the Closed site decreases.

As we predicted, Alpine marmots change their vigilance behaviour according to the environmental characteristics of their habitat, in accordance with the hypothesis that proximity to the forest and scarce visibility influence the level of risk for this species.

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