ethology international journal of behavioural biology

Ethology

RESEARCH PAPER

Do Yellow-Bellied Marmots Perceive Enhanced Predation Risk When they are Farther from safety? An experimental study

Raquel Monclús*†‡, Alexandra M. Anderson*† & Daniel T. Blumstein*†

* Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA, USA
† The Rocky Mountain Biological Laboratory, Crested Butte, CO, USA
‡ Laboratoire d'Ethologie Expérimentale et Comparée, Université Paris 13, Sorbonne-Paris Cité, Villetaneuse, France

Correspondence
Raquel Monclús, Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA, USA.
E-mail: raquel.monclus@uam.es

Received: January 12, 2015
Initial acceptance: April 1, 2015
Final acceptance: April 22, 2015
(L. Fusani)

doi: 10.1111/eth.12397

Keywords: antipredator behavior, flight initiation distance, risk assessment, vigilance

Abstract

Whereas there are many studies of the time allocated to antipredator vigilance while animals forage, the vast majority of these studies remain correlative. This is potentially problematic because a variety of factors other than variation in perceived risk might influence putative antipredator behaviors such as time allocated to vigilance and foraging. We conducted an experimental study of yellow-bellied marmot (*Marmota flaviventris*) antipredator behavior while marmots foraged at a replicated set of feeding stations established 1, 5, 10, and 20 m from their main burrows. Marmots appeared to perceive a reduced risk of predation when they foraged in the presence of other marmots; they allocated more time to foraging and decreased the time allocated to vigilance. When they foraged farther from their burrows, marmots initiated foraging after a substantially greater amount of time, tended to increase the frequency of their bouts of vigilance, and decreased the duration of each bout. Yearling marmots took less time to begin foraging than adults. Marmot flight initiation distance at our feeding trays was independent of the distance they foraged away from the burrow. Taken together, these experimental results demonstrate that marmots' perceptions of risk increased with distance to the burrow and decreased when other individuals were within 10 m of them while they foraged.

Introduction

Predation is a strong selective force that has triggered the evolution of different antipredator strategies in prey species (Kats & Dill 1998). One of the most common tactics involves early detection of predators because this might allow prey sufficient time and distance to react and successfully escape (Lima 1987a). However, antipredator behaviors may be costly and may be traded-off with some self-maintenance behaviors, such as foraging, searching for mates (Preisser et al. 2005). Therefore, prey should assess accurately their actual risk of predation and modulate their responses accordingly (Horat & Semlitsch 1994; Kesavaraju et al. 2007).

Vigilance is a frequently displayed antipredator behavior in species that visually detect their predators. It is effective at the early stages of the predatory sequence (Lima & Dill 1990), and it is typically assumed that vigilance trades off with activities that require a head down posture, such as foraging or drinking (but see Favreau et al. 2015). Thus, animals optimize their time budgets depending on their perception of the risk of predation (Ydenberg & Dill 1986). In turn, risk perception is modified by the presence and the composition of the predator guild (Périquet et al. 2010) and also by state-dependent factors such as body condition, sex, or age (Pays & Jarman 2008; Monclús & Rödel 2009), and environmental factors, such as the social group or habitat structure (Moreno et al. 1996; Laundré et al. 2001; Kotler et al. 2002; Cameron & du Toit 2005).

In addition to individually based factors, environmental factors are known to affect the perception of predation risk. The presence of conspecifics is a strong modulator of the antipredator response elicited. Most species studied decrease individual vigilance as group size increases, a phenomenon known as the group size effect (Elgar 1989). However, in other cases, conspecifics become competitors, and vigilance rates increase as group size increases, serving mainly a social function (Monclús & Rödel 2008; Favreau et al. 2009; Dupuch et al. 2014). Apart from social cues, other indirect cues are essential to understand the perception that an animal might have of its environment (Laundré et al. 2001; Morrison 2011).

The distance to cover is often an important modulator of risk perception. Cover can be safe or represent a threat, as predators may conceal in dense vegetation (Newberry & Shackleton 1997; Devereux et al. 2006; Beauchamp 2010; Dupuch et al. 2014). When cover constitutes a refuge, animals must balance the use of the refuge with the foraging needs, and as distance to refuge increases, the probability of a successful attack increases (Dill 1990; Morrison et al. 2004; Cresswell et al. 2010). However, animals may forage away from the refuge to fulfill the energetic demands, and thus, they might follow two different strategies: (i) increase the vigilance rates to increase the detection of a potential attack or (ii) minimize the exposure time, increasing the foraging effort (Lima 1987b; Crosmary et al. 2012). For instance, Dall's sheep (*Ovis dalli dalli*), increased vigilance as they increased the distance to the nearest cliff, a location where they are safe from predators (Frid 1997). Chacma baboons (*Papio cynocephalus ursinus*) used the alternative strategy when refuge abundance was low; they minimized the exposure time at risky environments (Cowlishaw 1997). A mixture of both strategies was followed by white-browed sparrow-weavers (*Plocepasser mahali*), which increased the foraging rate further from cover as well as the vigilance rate (Fong et al. 2009).

Although there are many studies dealing with different aspects of the perception of the risk of predation, the strategies followed by a particular individual might depend on factors such as energetic requirements and thus, individually based studies are essential. Additionally, experimental studies are also required to tease apart competing hypotheses that may generate similar patterns of vigilance (Elgar 1989).

We conducted a study on individually marked yellow-bellied marmots (*Marmota flaviventris*), in a well-studied population living in and around the Rocky Mountain Biological Laboratory, in Colorado (Armitage 2014). Marmots are ground-dwelling, sciurid rodents, where the burrow constitutes a safe place against most predators. We designed an experiment to test whether marmots modified their vigilance at varying distances from the burrow. We took into account the sex and the age of the focal animal (which influences energetic requirements) and the presence of other group members within 10 m (which should influence risk perception).

We expected to find that marmots foraging further from the burrow with higher energetic requirements (i.e., younger individuals) would increase the time spent foraging, at the cost of reducing the time allocated to vigilance, because they might favor food over safety, whereas older marmots would show the opposite pattern. Following this line of reasoning, we would also expect to find a sex-effect because male marmots are larger than females. This might also hold true for non-reproductive animals (subadults). However, in adults we might expect to find the opposite pattern; our study took place while females were lactating, and their energetic demands were higher. Moreover, we expected to find that marmots further from the burrow might be more wary, and that wariness would be apparent by individuals initiating flight at greater distances to an approaching human. The presence of other group members might also modulate the wariness, and thus, we expected to find that marmots foraging with conspecifics might decrease their allocation to vigilance, as would be expected from the group size effect hypothesis.

Methods

Animals and Study Site

The study was conducted in and around the Rocky Mountain Biological Laboratory (Colorado, USA). These marmots have been the subjects of a long-term study for more than 50 yrs (Armitage 2014), and group identity, family identity as well as individual identity are known for all the group members (Blumstein 2013). All the animals are individually marked with ear-tags and with a mark drawn on their dorsal pelage with Nyanzol fur dye (Albanil Dyestuff, New Jersey, USA), so they could be individually recognized from afar.

Experimental Setting

The experiment was conducted from early May to early July 2010 at three marmot colonies that were located in flat areas (slope <10°). From each colony, we chose those burrows that were currently used and that had no other entrances within a 20 m radius.

From the entrance of the burrow, we set an imaginary line, and we nailed to the ground four feeding stations consisting of a plastic box (12.7 × 12.7 × 2.54 cm) at 1, 5, 10, and 20 m. In total, we established 10 transects, each with the four feeding stations. Marmots were left to habituate to the novel objects for 1 wk, until they ignored the empty feeding stations.

Data Collection

The order of presentation of the food at the different feeding stations from each transect was randomly assigned. We only tested one feeding station at a time. The experiments took place in the morning (from 06:30 to 11:30 h). We placed 30 g of horse fed (Omolene 100, Purina, Missouri, USA) in the chosen station and observed the marmots with spotting scopes from a distance that was determined to not influence their behavior (from 20 to 150 m, depending on the colony). We noted whether marmots foraged or not from that particular feeding station and, if so, the time from when we first detected the marmot above ground to reach the station (*latency to feed*). Following Bednekoff & Blumstein (2009), when a marmot started feeding at the station, we conducted a continuous focal animal sample for 2 min. We used a voice recorder to record the following foraging focal marmots' behavioral transitions: vigilance (the marmot raised the head and looked around, either in a quadrupedal or bipedal position); foraging (head down, ingesting food); engagement in social interactions with other marmots (see Blumstein et al. 2009 for detailed ethogram of social behaviors); locomotion (walking or running); and other (any other activity that did not fall within those categories). We scored our audio recordings with JWatcher 1.0 (Blumstein & Daniel 2007). The single observer who conducted focal samples (A.M.A.) was trained to identify all behaviors with certainty and then was trained to have 95% scoring accuracy with JWatcher before we further analyzed data. We calculated the proportion of time marmots allocated to the different behaviors.

Flight Initiation Distance

Once the focal sample was completed, we approached the focal subject at a constant speed (0.5 m/s) and recorded the distance the marmot responded to our approach by looking up at us (alert distance) and the distance the marmot fled from the observer (flight initiation distance, FID). We also measured the starting distance, the distance from the observer to the marmot at the start of the experimental approach.

Statistical Analysis

We fitted linear mixed models with the library *lme4* (Bates et al. 2014) from software R, version 3.1.0 (R Core Team 2014). We ensured the residuals of all the models followed a normal distribution by visually checking normality plots. We also checked for the homogeneity of the variances by plotting residuals versus fitted values (Faraway 2006). The latency to feed at a given feeding station was log-transformed to reach normality criteria. We included in all the models the experimental feeding station (1, 5, 10, or 20 m), the order at which it was presented, the age (whether it was an adult or a yearling), the sex of the focal marmot, and whether there were other marmots within 10 m, as fixed factors. We incorporated the marmot identity as a random factor to control for repeated measurements. We included the interaction between the feeding station and the presence of other marmots and, when non-significant, it was removed from the final model (Engqvist 2005). We calculated p-values with Wald chi-square tests. We removed any observations in which marmots alarm called to alert the presence of a natural predator.

Results

We conducted 156 feeding experiments. On nine occasions (5.7% of the cases), marmots failed to visit the station; 78% of these failures were when marmots elected to not forage at the furthest station from the burrow (i.e., 20 m). From the 156 attempts, we successfully recorded 87 focal observations on 22 unique individuals (8 adults and 14 yearlings) and collected 72 FID measurements on 21 unique individuals.

Latency to Forage from the Feeding Stations

Marmots started foraging significantly sooner at the stations located closer to the burrow (latency at 1 m = 5.9 s; latency at 5 m = 21.9 s; latency at 10 m = 16.6 s; latency at 20 m = 39 s; $\beta = 0.759$, n = 22, $p < 0.001$; Fig. 1). On average, it took longer for adult marmots (32.42 s ± 50.70 SD) than for yearlings (10.70 s ± 26.89 S.D.) to visit the feeding stations ($\beta = 0.728$, n = 22, p = 0.056). The order of presentation of the foraging stations and the marmot's sex did not influence the latency to forage at the stations (order: $\beta = 0.056$, p = 0.403; sex: $\beta = 0.928$, p = 0.669). All interactions were non-significant and were removed from the final model.

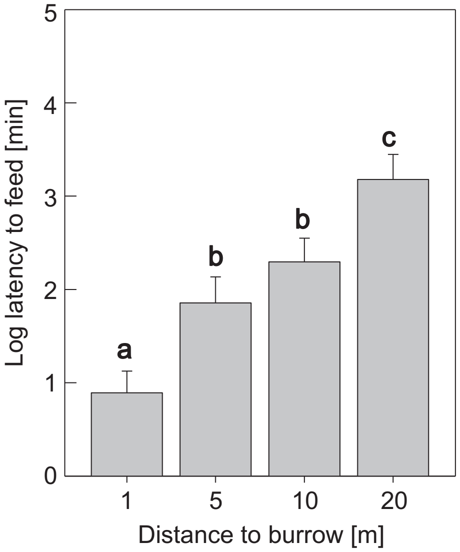

Fig. 1: It took yellow-bellied marmots significantly more time to visit the feeding stations located further away from the burrow. Different letters denote significant *post hoc* comparisons.

Time Allocation While Foraging

Once at the feeding stations, the marmots that foraged in close proximity with other marmots decreased the proportion of time spent vigilant (alone: 53.75% ± 19.98 SD; with other marmots: 43.06% ± 20.19 SD; β = 9.630, p = 0.019). The time vigilant was independent of the distance to the burrow (β = −0.892, p = 0.572) and of the interaction between distance and presence of conspecifics (β = 1.840, p = 0.630). The order of the food presentation at the different feeding stations, as well as age and sex, did not modify the time the marmots were vigilant (order: β = 0.911, p = 0.358; age: β = 1.514, p = 0.878; sex: β = 2.790, p = 0.861).

Similarly, the presence of other marmots modified the time allocated to foraging; marmots spent significantly more time foraging when other marmots were around than when they were alone (alone: 45.7% ± 20.3 SD; with other marmots: 55.8% ± 21.1 SD; β = 9.838, p = 0.017). This was independent of the feeding station they were foraging at (β = 0.179, p = 0.456), the interaction between feeding station and presence of marmots (β = 1.952, p = 0.609), the order the stations were presented (β = 0.861, p = 0.387), and marmot age or sex (β = 1.854, p = 0.857; β = 3.280, p = 0.920, respectively).

However, the distance to the burrow did affect the way the marmots performed vigilance. In the furthest stations from the burrow, marmots tended to increase the frequency of scans (β = 0.305, p = 0.058, Fig. 2a) and significantly decreased the duration of their scans (β = −0.429, p = 0.045; Fig. 2b). The presence of other marmots within 10 m decreased the frequency of vigilance scans (β = 13.464, p < 0.001), but not the average duration of the scans (β = 0.187, p = 0.729). All other measured factors did not significantly affect the frequency of vigilance (all p-values >0.4; Table 1).

Whereas distance to cover affected the type of vigilance displayed, it did not affect the characteristics of foraging behavior (frequency: β = 0.192, p = 0.186; average duration of a bout: β = −0.008, p = 0.868). However, foraging was affected by the presence of other marmots (frequency: β = 1.010, p = 0.007; average duration of a bout: β = 0.462, p < 0.001): Marmots foraging with other marmots within 10 m engaged in longer, but less frequent, feeding bouts

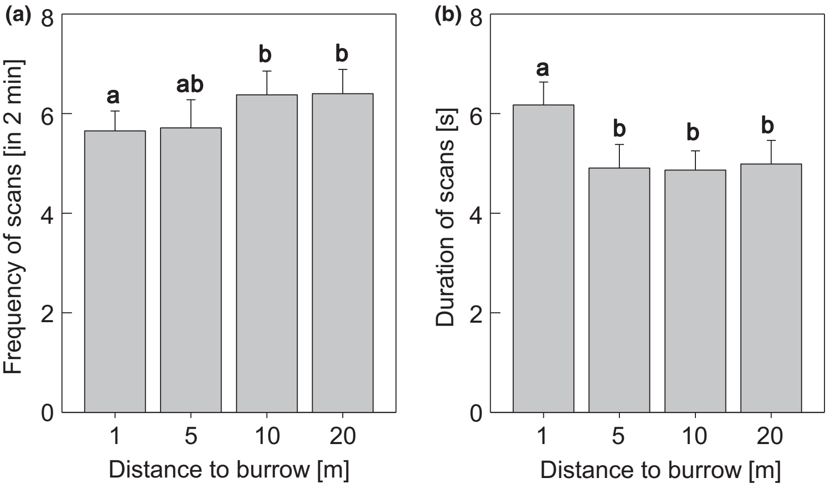

Fig. 2: Frequency (a) and average duration (b) of scans in relation to the distance to the burrow. Different letters denote significant *post hoc* comparisons.

Table 1: The effect of starting distance, feeding station, the presence of other marmots within 10 m, age, and sex on frequency and average duration of yellow-bellied marmot vigilance and foraging behavior

	Vigilance				Foraging			
	Frequency		Duration		Frequency		Duration	
Variable	β	p	β	p	β	p	β	p
Feeding station	0.305	0.058	**−0.429**	**0.045**	0.192	0.186	−0.008	0.868
Marmots within 10 m	**1.532**	**<0.001**	0.187	0.729	**1.010**	**0.007**	**0.462**	**<0.001**
Age	0.806	0.416	0.315	0.692	0.722	0.356	0.313	0.355
Sex	1.335	0.651	1.834	0.603	0.193	0.688	0.159	0.789
Order	0.009	0.923	0.020	0.874	0.0430	0.634	0.020	0.504

Significant values p < 0.05 are bolded.

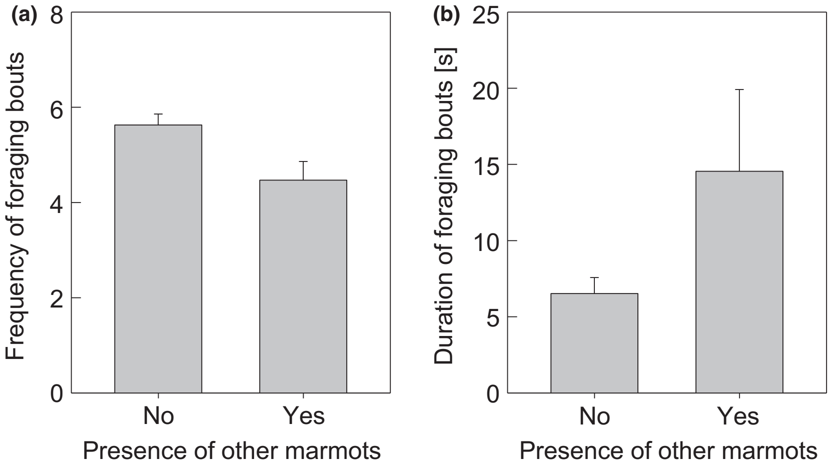

Fig. 3: The presence of other marmots affected the (a) frequency and (b) duration of foraging bouts. See text for statistics.

(Fig. 3). No other variables affected the way marmots foraged (all p-values >0.35; Table 1).

Flight Initiation Distance

Alert distance was independent of the feeding station, as well as age and sex (Table 2). The starting distance of the approach (21–75 m, average = 45.4 ± 11.4 m), however, was positively related to alert distance (β = 0.332, p = 0.002) and to the presence of other marmots (β = 15.065, p = 0.029). Marmots foraging alone were more wary, showing signs of alertness at a larger distance from the observer than marmots foraging with conspecifics. Flight initiation distance was significantly associated only with starting distance (β = 0.279, p = 0. 038; Table 2).

Discussion

Animals must make constant decisions about when and where to fulfill their energetic requirements. In theory, an individual's decisions are based on evaluating both internal and external cues, including the risk of predation. Our experimental results showed that yellow-bellied marmots followed different strategies depending on the distance to their burrow and the presence of conspecifics. Marmots perceived burrows as affording safety (Holmes 1984; Rhoades & Blumstein 2007), and their perceptions of risk increased with distance to the burrow and decreased when other marmots were within 10 m of them while they foraged. Marmots were more prone to forage near the burrow, and as they foraged further away, they increased vigilance. However, when other marmots were in close proximity, they were less wary, decreasing their alertness, as well as allocating less time to vigilance, while increasing the time allocated to foraging.

Marmots were more reluctant to visit the stations that were located further away from the burrow. Indeed, most of the stations marmots failed to visit were the ones located 20 m away. When marmots fed at those stations, it took them >6 times longer to visit them than the ones located next to the entra-

Table 2: The effect of starting distance, feeding station, the presence of other marmots within 10 m, age, and sex on yellow-bellied marmot alert distance and flight initiation distance

	Alert distance		Flight initiation distance	
Variable	β	p	β	p
Start distance	**0.346**	**<0.001**	**0.323**	**0.012**
Feeding station	0.891	0.417	0.001	0.999
Marmots within 10 m	**15.065**	**0.029**	8.738	0.344
Age	1.047	0.680	0.739	0.819
Sex	1.001	0.682	1.308	0.674

Significant values $p < 0.05$ are bolded.

nce to the burrow. Although it is not unusual to see marmots foraging 20 m from the burrow, it is a risky location given the average running speed of a marmot is approximately 4 m/s (Blumstein et al. 2004). Our experimental results demonstrate that they are aware of the risk and modify their behavior accordingly. At that distance, marmots should increase their time allocated to vigilance or reduce their exposure time (Dill 1990; Dupuch et al. 2014). Other studies have found that animals are reluctant to forage far from safety (e.g., Hochman & Kotler 2007; Fong et al. 2009), and many studies have shown that animals foraging in riskier areas, such as far away from the burrow or closer to obstructive cover, increase vigilance (Roberts 1988; Hochman & Kotler 2007; Liley & Creel 2008; Beauchamp 2010). For example, starlings (*Sturnus vulgaris*) increased the scanning rate when in high predator risk (Devereux et al. 2006). However, vigilance can be increased in different ways. For instance, animals might allocate a larger proportion of time to scanning their surroundings, or they could modify the rate and the average duration of their scans. Indeed, marmots further away from the burrow followed the latter strategy; they displayed shorter but more frequent scans than in locations closer to the burrow. It has been suggested that more frequent scans might improve the detection of nearby predators (Bertram 1980).

On the other hand, other animals are known to follow the opposite strategy (Crosmary et al. 2012). For example, common wombats (*Vombatus ursinus*) decreased the vigilance time with increasing distance to cover, maximizing food intake during that time (Favreau et al. 2009). The strategy followed might depend on the actual risk of predation, the foraging costs, and the vulnerability of the species or of the group, among other potential reasons (Griesser & Nystrand 2009; Périquet et al. 2010; Crosmary et al. 2012; Powolny et al. 2014). A formal meta-analysis might be able to determine how these factors influence the strategy adopted.

In our study, the perception of vulnerability was age dependent. It took longer for adult marmots than for subadults (yearlings) to visit the foraging stations. Several studies have shown that age plays an important role in antipredator behavior. On the one hand, juveniles are normally subjected to a higher predator pressure (Chase 1999), and they might be more responsive to new stimuli, which could lead to stronger responses to predators than adults (Inglis 1979). On the other hand, young animals normally have higher energetic requirements than older ones, and thus, they might accept a higher predation risk to fulfill their requirements, leading to reduced antipredator behavior (Avilés & Bednekoff 2007; Monclús & Rödel 2009). This study took place shortly before subadults dispersed (Van Vuren & Armitage 1994), so subadults not only had higher energetic demands, but also they were more exploratory at that time of the season. This might explain the fact that they had shorter latencies to use the different feeding stations.

The presence of other marmots affected the activity budgets. Marmots foraging with conspecifics decreased the time allocated to vigilance, whereas they increased the foraging time. The presence of conspecifics nearby might play an important role reducing the individual risk of predation (Hamilton 1971). Conspecifics dilute the risk of predation because the larger the group, the smaller the probability for each individual to become the prey (dilution effect, Turner & Pitcher 1986). Moreover, more individuals increase the probability that at least one of them detects a predator (many eyes hypothesis, Lima 1995). However, other studies have suggested the opposite effect; conspecifics might constitute a threat if there is a clumped resource, such as the high-quality food offered at the feeding stations. In a resource competition scenario, animals might choose to increase their feeding effort to maximize the intake of high-quality food (Bednekoff & Lima 2004). Thus, our results could be driven by our focal animals trying to prevent other marmots from using a high-quality patch. We think this unlikely for two reasons. First, there was typically only one other individual present. Second, in 74% of the cases, the conspecific was a subadult. Both of these might reduce the likelihood that the other animal was perceived as a potential competitor. Moreover, the reduced vigilance, apparent both by a decrease in the time allocated to vigilance, as well as the decrease in the frequency of bouts of vigilance, are consistent with the idea that other marmots were regarded more as allies than as competitors. Further evidence comes from the fact that when other marmots were in close proximity, the focal animals were less wary and permitted closer approach before alerting.

Contrary to our expectations, marmots did not increase their flight initiation distance as the distance to the burrow increased, at least on the scale of this manipulation. Other species of marmots, such as the woodchuck (*Marmota monax*) showed a positive relationship between distance to safety and FID (Bonenfant & Kramer 1996). There are several potential explanations for our results. Apart from modifying the alert and flight initiation distance, marmots could modify their running speed while fleeing, adjusting it to the distance to a safe place and to the speed of the approaching predator (Dill & Houtman 1989). Although we could not test this hypothesis, we could infer that marmots were within their margin of safety. In our study, marmots fled at an average distance of 24.3 m ± 4.0 SD independently of their feeding station. That distance must be perceived as a safe distance because it might allow them to escape from a (pedestrian) predator approaching at a constant pace of 0.5 m/s, without maximizing their running speed (Dill 1990) and, thus, without increasing the costs of escape (Bonenfant & Kramer 1996).

In conclusion, with our study we showed how the trade-off between vigilance and foraging is modulated by both internal and external cues. The integration of the social and the physical environment in individually based systems provides a good scenario to understand how animals perceive their environment and the consequent decision-making process. We have experimentally demonstrated that distance to a safe place and the presence of conspecifics affect yellow-bellied marmot escape strategy when they are within their margin of safety. A question worth further investigation might be whether the same strategies are consistently displayed once the animals are outside their margin of safety.

Acknowledgements

We are grateful to Heiko G. Rödel for his thoughtful comments on earlier versions of the manuscript. We would like to thank two anonymous reviewers for their constructive suggestions that greatly improved the manuscript. R.M. was supported by postdoctoral fellowships from the Spanish Ministerio de Innovación y Ciencia and from the Fulbright program. A.M.A. was a NSF REU Fellow. D.T.B was supported by the National Geographic Society, UCLA (Faculty Senate and the Division of Life Sciences), a Rocky Mountain Biological Laboratory research fellowship, and by the NSF (IDBR-0754247, DEB-1119660 to D.T.B., as well as DBI 0242960 and 0731346 to the Rocky Mountain Biological Laboratory).

Literature Cited

Armitage, K. B. 2014: Marmot Biology: Sociality, Individual Fitness, and Population Dynamics. Cambridge University Press, Cambridge.

Avilés, J. M. & Bednekoff, P. A. 2007: How do vigilance and feeding by common cranes *Grus grus* depend on age, habitat, and flock size? J. Avian Biol. **38**, 690—697.

Bates, D., Maechler, M., Bolker, B. & Walker, S. 2014: lme4: Linear mixed-effects models using Eigen and S4.

Beauchamp, G. 2010: Relationship between distance to cover, vigilance and group size in staging flocks of semipalmated sandpipers. Ethology **116**, 645—652.

Bednekoff, P. A. & Blumstein, D. T. 2009: Peripheral visibility influences marmot vigilance: integrating observational and experimental results. Behav. Ecol. **20**, 1111—1117.

Bednekoff, P. A. & Lima, S. L. 2004: Risk allocation and competition in foraging groups: reversed effects of competition if group size varies under risk of predation. Proc. R. Soc. B **271**, 1797—1496.

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

Blumstein, D. T. 2013: Yellow-bellied marmots: insights from an emergent view of sociality. Philos. Trans. R. Soc. Lond. B Biol. Sci. **368**, 20120349.

Blumstein, D. T. & Daniel, J. C. 2007: Quantifying behavior the JWatcher way. Sinauer Associates Inc, Massachusets.

Blumstein, D. T., Runyan, A., Seymour, M., Nicodemus, A., Ozgul, A., Ransler, F., Im, S., Stark, T., Zugmeyer, C. & Daniel, J. C. 2004: Locomotor ability and wariness in yellow-bellied marmots. Ethology **110**, 615—634.

Blumstein, D. T., Wey, T. W. & Tang, K. 2009: A test of the social cohesion hypothesis: interactive female marmots remain at home. Proc. R. Soc. B **276**, 3007—3012.

Bonenfant, M. & Kramer, D. L. 1996: The influence of distance to burrow on flight initiation distance in the woodchuck, *Marmota monax*. Behav. Ecol. **7**, 299—303.

Cameron, E. Z. & du Toit, J. T. 2005: Social influences on vigilance behaviour in giraffes, *Giraffa camelopardalis*. Anim. Behav. **69**, 1337—1344.

Cowlishaw, G. 1997: Refuge use and predation risk in a desert baboon population. Anim. Behav. **54**, 241—253.

Cresswell, W., Lind, J. & Quinn, J. L. 2010: Predator-hunting success and prey vulnerability: quantifying the spatial scale over which lethal and non-lethal effects of predation occur. J. Anim. Ecol. **79**, 556—562.

Crosmary, W.-G., Makumbe, P., Cote, S. D. & Fritz, H. 2012: Vulnerability to predation and water constraints limit behavioural adjustments of ungulates in response to hunting risk. Anim. Behav. **83**, 1367—1376.

Chase, J. M. 1999: To grow or to reproduce? The role of life-history plasticity in food web dynamics. Am. Nat. **154**, 571—586.

Devereux, C. L., Whittingham, M. J., Fernandez-Juricic, E., Vickery, J. A. & Krebs, J. R. 2006: Predator detection and avoidance by starlings under differing scenarios of predation risk. Behav. Ecol. **17**, 303—309.

Dill, L. M. 1990: Distance-to-cover and the escape decisions of an African cichlid fish, Menalochromis chipokae. Environ. Biol. Fish **27**, 147—152.

Dill, L. M. & Houtman, R. 1989: The influence of distance to refuge on flight initiation distance in the gray squirrel (*Sciurus carolinensis*). Can. J. Zool. **67**, 233—235.

Dupuch, A., Morris, D. W. & Halliday, W. D. 2014: Patch use and vigilance by sympatric lemmings in predator and competitor-driven landscapes of fear. Behav. Ecol. Sociobiol. **68**, 299—308.

Elgar, M. A. 1989: Predator vigilance and group size in mammals and birds: a critical review of the empirical vigilance. Biol. Rev. **64**, 13—33.

Engqvist, L. 2005: The mistreatment of covariate interaction terms in linear model analyses of behavioural and evolutionary ecology studies. Anim. Behav. **70**, 967—971.

Faraway, J. J. 2006: Extending the Linear Model with R. Generalized Linear, Mixed Effects and Nonparametric Regression Models. Chapman & Hall, New York, USA.

Favreau, F. R., Jarman, P. J., Goldizen, A. W., Dubot, A. L., Sourice, S. & Pays, O. 2009: Vigilance in a solitary marsupial, the common wombat (*Vombatus ursinus*). Aust. J. Zool. **57**, 363—371.

Favreau, F. R., Pays, O., Fritz, H., Goulard, M., Best, E. C. & Goldizen, A. W. 2015: Predators, food and social context shape the types of vigilance exhibited by kangaroos. Anim. Behav. **99**, 109—121.

Fong, T. E., DeLong, T. W., Hogan, S. B. & Blumstein, D. T. 2009: The importance of indirect cues for white-browed sparrow-weaver (*Plocepasser mahali*) risk assessment. Acta Ethol. **12**, 79—85.

Frid, A. 1997: Vigilance by female Dall's sheep: interactions between predation risk factors. Anim. Behav. **53**, 799—808.

Griesser, M. & Nystrand, M. 2009: Vigilance and predation of a forest-living bird species depend on large-scale habitat structure. Behav. Ecol. **20**, 709—715.

Hamilton, W. D. 1971: The geometry of the selfish herd. J. Theor. Biol. **31**, 295—311.

Hochman, V. & Kotler, B. P. 2007: Patch use, apprehension, and vigilance behavior of Nubian Ibex under perceived risk of predation. Behav. Ecol. **18**, 368—374.

Holmes, W. G. 1984: Predation risk and foraging behavior of the hoary marmot in Alaska. Behav. Ecol. Sociobiol. **15**, 293—301.

Horat, P. & Semlitsch, R. D. 1994: Effects of predation risk and hunger on the behaviour of two species of tadpoles. Behav. Ecol. Sociobiol. **34**, 393—401.

Inglis, I. R.. 1979: Visual bird scarers an ethological approach. In: Bird Problems in Agriculture. (Wright, E. N., Inglis, I. R. & Feare, C. J., eds). MAFF Publishers, London, pp. 121—143.

Kats, L. B. & Dill, L. M. 1998: The scent of death: chemosensory assessment of predation risk by prey animal. Ecoscience **5**, 361—394.

Kesavaraju, B., Damal, K. & Juliano, S. A. 2007: Threat-sensitive behavioral responses to concentrations of water-borne cues from predation. Ethology **113**, 199—206.

Kotler, B. P., Brown, J. S., Dall, S. R. X., Gresser, S., Ganey, D. & Bouskila, A. 2002: Foraging games between gerbils and their predators: temporal dynamics of resource depletion and apprehension in gerbils. Evol. Ecol. Res. **4**, 495—518.

Laundré, J. W., Hernández, L. & Altendorf, K. B. 2001: Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, USA. Can. J. Zool. **79**, 1401—1409.

Liley, S. & Creel, S. 2008: What best explains vigilance in elk: characteristics of prey, predators, or the environment? Behav. Ecol. **19**, 245—254.

Lima, S. L. 1987a: Vigilance while feeding and its relation to the risk of predation. J. Theor. Biol. **124**, 303—316.

Lima, S. L. 1987b: Distance to cover, visual obstructions, and vigilance in house sparrows. Behaviour **102**, 231—238.

Lima, S. L. 1995: Back to the basics of anti-predatory vigilance: the group-size effect. Anim. Behav. **49**, 11—20.

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

Monclús, R. & Rödel, H. G. 2008: Different forms of vigilance in response to the presence of predators and conspecifics in a group-living mammal, the European rabbit. Ethology **114**, 287—297.

Monclús, R. & Rödel, H. G. 2009: Influence of different individual traits on vigilance behaviour in European rabbits. Ethology **115**, 758—766.

Moreno, S., Villafuerte, R. & Delibes, M. 1996: Cover is safe during the day but dangerous at night: the use of vegetation by European wild rabbits. Can. J. Zool. **74**, 1656—1660.

Morrison, E. B. 2011: Vigilance behavior of a tropical bird in response to indirect and direct cues of predation risk. Behaviour **148**, 1067—1085.

Morrison, S., Barton, L., Caputa, P. & Hik, D. S. 2004: Forage selection by collared pikas, *Ochotona collaris*, under varying degrees of predation risk. Can. J. Zool. **82**, 533—540.

Newberry, R. C. & Shackleton, D. M. 1997: Use of visual cover by domestic fowl: a Venetian blind effect? Anim. Behav. **54**, 387—395.

Pays, O. & Jarman, P. J. 2008: Does sex affect both individual and collective vigilance in social mammalian herbivores: the case of the eastern grey kangaroo? Behav. Ecol. Sociobiol. **62**, 757—767.

Périquet, S., Valeix, M., Loveridge, A. J., Madzikanda, H., Macdonald, D. W. & Fritz, H. 2010: Individual vigilance of African herbivores while drinking: the role of immediate predation risk and context. Anim. Behav. **79**, 665—671.

Powolny, T., Bretagnolle, V., Aguilar, A. & Eraud, C. 2014: Sex-related differences in the trade-off between foraging and vigilance in a granivorous forager. PLoS ONE **9**, e101598.

Preisser, E. L., Bolnick, D. I. & Benard, M. F. 2005: Scared to death? The effects of intimidation in predator–prey interactions. Ecology **86**, 501—509.

R Core Team. 2014: R: A language and environment for statistical computing. R Foundation for Statistical Computing, http://www.R-project.org, Vienna, Austria.

Rhoades, E. & Blumstein, D. T. 2007: Predicted fitness consequences of threat-sensitive hiding behavior. Behav. Ecol. **18**, 937—943.

Roberts, S. C. 1988: Social influences on vigilance in rabbits. Anim. Behav. **36**, 905—912.

Turner, G. & Pitcher, T. 1986: Attack abatement: a model for group protection by combined avoidance and dilution. Am. Nat. **128**, 228—240.

Van Vuren, D. & Armitage, K. B. 1994: Survival of dispersing and philopatric yellow-bellied marmots: what is the cost of dispersal? Oikos **69**, 179—181.

Ydenberg, R. C. & Dill, L. M. 1986: The economics of fleeing from predators. Adv. Stud. Behav. **16**, 229—249.