Behavioral Ecology
doi:10.1093/beheco/arp104
Advance Access publication 16 July 2009

Peripheral obstructions influence marmot vigilance: integrating observational and experimental results

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Animals generally allocate some time during foraging to detecting predators. We used a combination of observations and an experiment to examine how vegetation height and peripheral obstructions influence vigilance by foraging yellow-bellied marmots (*Marmota flaviventris*). First, we analyzed a large sample of observations of marmots foraging in nature. Marmots increased vigilance with vegetation height and reared on their hind legs when in tall vegetation. Second, we observed that marmots foraged in locations with lower vegetation than randomly selected sites in the same meadow. These observations suggest that marmots account for what they can see while foraging but do not rule out the influence of other factors correlated with vegetation height. Therefore, we experimentally blocked the view for 3 sides for marmots feeding on a controlled food source. When the apparatus blocked their vigilance, marmots were less vigilant when foraging, often moved outside the apparatus, and showed heightened vigilance while outside the apparatus. Peripheral obstructions explained more of the variance in our experimental than in our observational results. Together, our results demonstrate that marmots employ antipredator behavior to compensate for peripheral obstructions. Long-term studies show that marmots go locally extinct more often in areas with more obstructions to vigilance. Thus, marmots likely face greater predation risk in those areas, despite the behavioral responses documented in this study. *Key words:* antipredator vigilance, obstruction, predation risk, yellow-bellied marmot. *[Behav Ecol 20:1111–1117 (2009)]*

In general, vigilance involves pauses in foraging or other activity to monitor the environment. Such vigilance generally increases in situations with greater danger, such as when predators are nearby (Creel et al. 2008), when animals are in exposed positions (di Blanco and Hirsch 2006), and when they are in smaller groups (Elgar 1989; Roberts 1996; Beauchamp 2009). Despite a rich correlative literature consisting of hundreds of studies, relatively few experiments have directly tested for effects of each of these factors. Fewer studies yet have linked observational and experimental studies of the same organisms.

In previous studies, animals often changed their vigilance when their view is naturally or experimentally obstructed. Shorebirds were more vigilant where rocks blocked their view of flock mates and potential attacks (Metcalfe 1984). As vegetation grew through the year, degus (*Octodon degus*) increased their vigilance and switched from quadrupedal to bipedal postures while vigilant (Ebensperger and Hurtado 2005). Sparrows (*Passer domesticus*) were more vigilant when foraging among overturned flowerpots (Harkin et al. 2000), and dark-eyed juncos (*Junco hyemalis*) were more vigilant when feeding among a grid of small boards (Bednekoff and Lima 2005). When foraging in tallgrass, starlings (*Sturnus vulgaris*) were more vigilant and, when they had their heads down, were slower to react to a simulated predator (Devereux et al. 2006). When feeding in a large box that completely obstructed their view, gray squirrels (*Sciurus carolinensis*) carried large food items out before consuming them (Makowska and Kramer 2007). Finally, thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*) foraged for shorter periods inside experimental boxes that blocked their vision to the sides (Arenz and Leger 1997a, 1997b).

We studied the importance of natural and experimental obstructions to vigilance by yellow-bellied marmots (*Marmota flaviventris*). Marmots are also an ideal experimental system in which to study the relationship between predation risk and vigilance behavior. Marmots are prey to a variety of predators (Van Vuren 1991, 2001; Van Vuren and Armitage 1994; Armitage 2004), and vigilance is an important antipredator behavior for marmots; they increase it after detecting increased predation risk (e.g., Blumstein and Daniel 2004; Blumstein, Barrow, and Luterra 2008; Blumstein, Cooley, et al. 2008), and a variety of factors, including incline and group size, influence background levels of vigilance (Blumstein et al. 2004). Additionally, field surveys show that areas with more obstructions to vigilance are less likely to have marmot colonies, and those colonies are less likely to survive over years (Blumstein et al. 2006). Thus, understanding vigilance and related antipredator behavior is important as we seek to develop individual-based models that link behavioral decisions to population and community ecology.

To develop a more integrated view of vigilance, we tested 3 hypotheses. First, we asked specifically what habitat factors influenced marmot foraging and vigilance behavior. Analyses on subsets of our data suggested that marmots would change their vigilance with habitat variables, but for this analysis, we combined the results from 6 years of data to obtain the best possible estimate of obstructions to vigilance. Second, we asked if marmots preferred to forage in areas where vigilance was more likely to be effective. We studied this by comparing the vegetation height, substrate, and slope of locations where marmots were observed foraging with randomly selected

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Received 3 February 2009; revised 20 June 2009; accepted 20 June 2009.

locations where they could have foraged. Third, we experimentally blocked what foraging marmots could see in 3 directions. By conducting an experiment, we would determine, with certainty, whether peripheral obstructions directly influence vigilance.

MATERIALS AND METHODS

General methods

Free-living yellow-bellied marmots were studied at the Rocky Mountain Biological Laboratory in Gunnison, County, Colorado; a site where marmots have been studied since 1962 (Blumstein et al. 2006). Social groups and social group memberships are known at this site from ongoing trapping, marking, and observation of individuals. Marmots were baited with Omalene 100 horse food (Ralston Purina, Inc., St Louis, MO) into Tomahawk live traps. Once trapped, uniquely numbered ear tags were inserted or checked, and their dorsal pelage was uniquely marked with nontoxic Nyanzol fur dye (for full details, see Blumstein, Barrow, and Luterra 2008).

What habitat factors influence marmot foraging and vigilance behavior?

Focal methods

Following Blumstein et al. (2004), we conducted 2-min focal animal observations (Martin and Bateson 1993) on foraging subjects where we noted the onset of each bout of quadrupedal (i.e., standing) foraging, bipedal (i.e., rearing on hind legs) foraging, quadrupedal vigilance, bipedal vigilance, locomotion, and periods of time when animals were out of sight. Observers dictated observations into microcassette recorders and later scored them using JWatcher 1.0 (Blumstein and Daniel 2007). While conducting focal observations on identified subjects, observers categorized the incline (0–10°, 10–30°, >30°), substrate (stones or talus, dirt or short vegetation [<20 cm], and tall vegetation [≥20 cm]), and the number of individuals within 10 m of the focal subject. We chose these substrate categories because substrate influences maximum running speed (Blumstein et al. 2004). The difference between short and tall vegetation is based on the height of a quadrupedally standing marmot's eyes; while foraging in short vegetation, we assumed that marmots could forage and simply lift their heads to detect threats, but in taller vegetation, marmots had to rear up bipedally to detect threats. Observers were trained to identify behaviors, broad slope categories, and substrate with 100% accuracy and then trained to score behavior with JWatcher until all behaviors were scored consistently, and the correlation in time budgets between different sessions of the same focal was >0.9.

Analysis

We selected 1 observation per individual per year from focal samples taken during 2003 through 2008. When more than one focal was available for a given individual in a particular year, we first randomly selected from among possible vegetation heights and then randomly selected within the chosen vegetation type. In some cases, animals moved between vegetation types while foraging, and these multiple vegetation types were recorded. Marmots most often foraged in areas of low vegetation. Where no observations were available in which an individual used just bare ground or high vegetation, mixed ones were used and counted as either high or bare, rather than the more common low vegetation. This increased our sample size for foraging on bare ground or in high vegetation but would be conservative otherwise. Observations on talus were excluded because animals on talus may have very good view when on top of large rocks or very poor one if between large rocks. Our final sample size was 389 bouts.

We analyzed the data by fitting a general linear model with 5 fixed effects—vegetation height, angle of substrate, sex, age (adult vs. yearling), and the logarithm of feeding group size, which was defined as the focal marmot plus any marmots within 10 m of it (see also Blumstein et al. 2004). Because some 3-way combinations of factors were rare in the data set, we analyzed all 2-way interactions but none of the higher order interactions. We combined foraging while rearing with foraging while standing on 4 feet into total time spent foraging. We arcsine square root transformed the proportion of time spent foraging and looking. The percentage of time rearing to look contained many zeroes, and its distribution was skewed even after transformation. We performed a parallel analysis of rearing to look as a binary variable. Because the analyses yielded similar results, we only report the analysis of percentage of time.

We present partial eta-squared (η^2) values rather than the more familiar F values. Partial eta-squared values can be converted to F values because $F_{x,y} = y\eta^2/(x(1 - \eta^2))$, where x and y are the numerator and denominator degrees of freedom. Partial η^2 gives a measure of effect size analogous to R^2 in regression that estimates the variation explained by a factor separate from the effects of other factors. We used these values to compare both within studies and across the observational and experimental studies, which differ markedly in degrees of freedom.

Do marmots prefer to forage where vigilance is more likely to be effective?

Methods and analysis

Preliminary analyses in Blumstein et al. (2004) suggested an effect of habitat structure on time allocated to foraging and vigilance, but there was no attempt to determine if marmots elected to forage in areas where vigilance was relatively effective. To do so, we observed marmots foraging at our Picnic colony from 23 to 30 June 2008 with binoculars and a 10–45× spotting scope. We observed this colony because it was topographically particularly diverse and included shallow, moderate, and steep slopes and different heights of vegetation in close proximity to burrows.

Each time an individual was spotted foraging, we scored the vegetation height, substrate angle, and substrate type at that spot, at a spot 10 m away on 1 of the 4 diagonals (selected according to a structured random procedure), and finally at a randomly selected spot in the general area. These random points in the general area were generated by dividing a photograph of the study site (from the same perspective) into 32 cells in a 4 × 8 grid. We selected one of these cells at random, pointed the spotting scope to the middle of it, and then pointed the scope to an area 10 m away along a randomly selected diagonal. At these randomly selected points, we recorded the vegetation height, slope, and substrate. At each observation point, vegetation height and substrate angle were categorized as above, whereas substrate type was categorized as dirt, small rocks, or talus.

We scanned the slope at least every 30 min and took 1 observation per individual per day. When several individuals were visible at once, we selected the individual that had been observed least in previous sessions. Twenty-one individuals were observed an average of 3.05 times each. We converted the ordinal categories to numerical scores (1, 2, or 3), then averaged the scores for each individual, and compared observed, 10 m away, and random points using repeated measures analysis of variance (ANOVA).

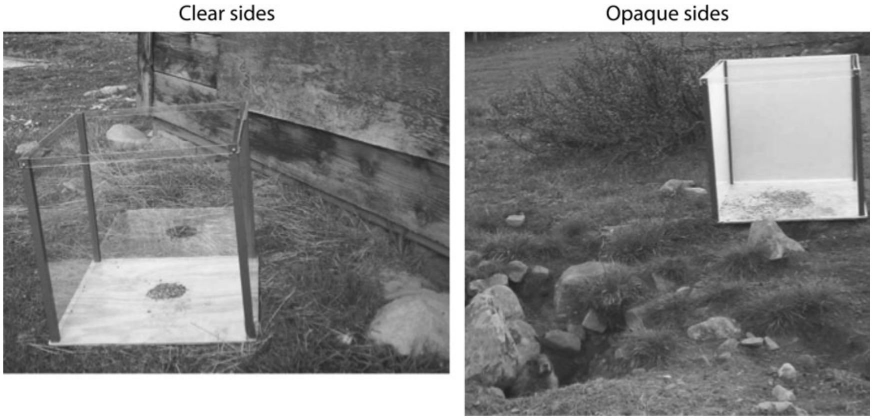

Figure 1
The experimental apparatus used to obstruct vision. The left photograph illustrates the clear side panels, whereas the right photograph illustrates the opaque side panels. A marmot has emerged from an adjacent burrow in the right photograph.

Does manipulating peripheral vigilance influence marmot foraging and vigilance?

Methods and analysis

We generally assume that vigilance involves visual monitoring, though sounds and smells are often important to animals (Caro 2005), and yellow-bellied marmots are able to detect predators using these modalities (Blumstein 2007; Blumstein, Barrow, and Luterra 2008; Blumstein, Cooley, et al. 2008). We tested for the importance of peripheral vision by testing the effects of obstructions that block an animal's line of sight compared with a transparent control. To do so, we built a 3-sided 0.61-m^3 box (Figure 1). The bottom was urethane-coated 1/4″ plywood. The 3 sides were removable and either consisted of 1/16″ thick clear polyethylene terephthalate glycol copolyester sheets or 1/16″ thick opaque white polypropylene plastic sheets. By baiting a marmot into the box and quantifying its vigilance behavior, we could study the effect of peripheral obstruction on vigilance behavior.

We conducted the experiment from 6 to 19 June 2008. Twenty-five marmots completed both treatments with 13 individuals experiencing the blocked treatment first and 12 individuals the clear treatment first. We conducted the experiment at similar times of day for each location (mean difference = 4.48 ± 13.6 min earlier in the day). Other marmots joined the focal marmot in the feeding apparatus during 13 blocked trials and 11 clear ones. The resulting number of dining companions (0.598 vs. 0.483) did not differ between treatments ($t_{24} = 0.810$, $P = 0.426$). All age and sex classes of marmots completed the experiment in roughly equal numbers: 7 adult females, 6 yearling females, 5 adult males, and 7 yearling males. Results were analyzed with repeated measures ANOVA.

RESULTS

What habitat factors influence marmot foraging and vigilance behavior?

Marmots foraged for a lower percentage of the time when in taller vegetation and tended to forage more when more marmots were nearby (Table 1, Figure 2). Marmots also foraged for a higher percentage of the time when on steep slopes, though males and females reacted somewhat differently to intermediate and low slopes (Table 1, Figure 3).

Marmots changed how they looked with vegetation height. They looked more while standing on 4 feet in low vegetation than on bare ground or in high vegetation but looked while

Table 1

Results from general linear models explaining variation in the proportion of total time in sight yellow-bellied marmots allocated to foraging, standing and looking, or rearing and looking as a function of vegetation type, angle, sex, age, and the natural log of group size along with 2-way interactions

		Total foraging		Stand look		Rear look	
Factor	Degrees of freedom	Partial η^2	P	Partial η^2	P	Partial η^2	P
Vegetation	2	0.017	0.045	0.019	0.029	0.018	0.039
Angle	2	0.015	0.060	0.013	0.094	0.005	0.439
Sex	1	0.000	0.931	0.001	0.560	0.001	0.493
Age	1	0.000	0.688	0.000	0.916	0.000	0.868
ln Group size	1	0.010	0.053	0.003	0.272	0.011	0.045
Angle × vegetation	4	0.009	0.536	0.020	0.117	0.022	0.091
Sex × vegetation	2	0.000	0.961	0.007	0.302	0.007	0.297
Age × vegetation	2	0.000	0.935	0.000	0.954	0.002	0.667
Vegetation × ln group size	2	0.010	0.156	0.013	0.095	0.009	0.185
Sex × angle	2	0.030	0.004	0.031	0.003	0.009	0.184
Age × angle	2	0.003	0.618	0.000	0.930	0.001	0.793
Angle × ln group size	2	0.002	0.738	0.002	0.741	0.001	0.879
Sex × age	1	0.002	0.397	0.004	0.249	0.023	0.004
Sex × ln group size	1	0.005	0.195	0.006	0.131	0.000	0.749
Age × ln group size	1	0.000	0.744	0.001	0.604	0.000	0.876
Error	362						

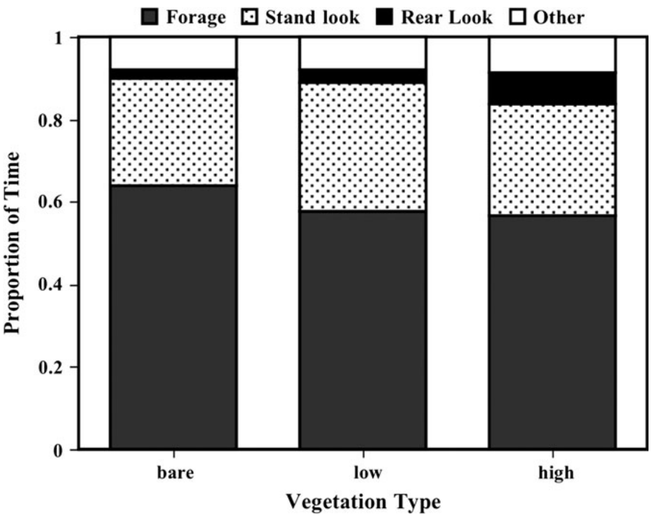

Figure 2
Proportion of time marmots allocated to foraging, standing and looking, rearing and looking, and "other" as a function of the vegetation height (bare, low, or high vegetation height) during 2-min focal observations.

rearing most in tall vegetation (Table 1, Figure 2). Also, more rearing occurred with more marmots around. Sex and age interacted with yearling females rearing more than adult females but yearling males rearing less than adult males. Finally, marmots looked less on steep slopes, and (mirroring the results for foraging) males differentiated more between low and intermediate slopes than did females (Table 1, Figure 3).

Do marmots prefer to forage where vigilance is more likely to be effective?

Marmots mostly foraged on slopes between 10 and 30 degrees. Foraging sites were similar in average slope to random points 10 m away and at random across the site ($F_{2,40} = 0.808$, $P = 0.453$), though perhaps a bit less variable (Figure 4). Marmots did not consistently choose or avoid rocky areas for foraging ($F_{2,40} = 0.398$, $P = 0.675$; Figure 4). Marmots foraged on areas that had lower vegetation than found at randomly selected points 10 m away or randomly selected points across the entire site ($F_{2,40} = 8.835$, $P = 0.001$; Figure 4).

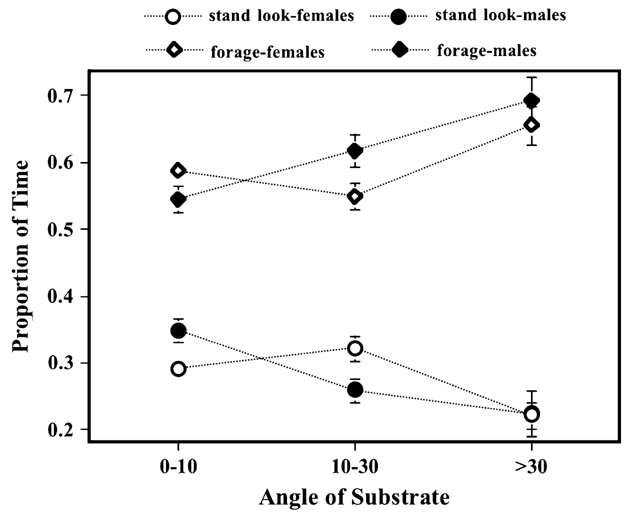

Figure 3
Proportion of time male and female marmots allocated to foraging and standing and looking as a function of the substrate angle on which they foraged during 2-min focal observations.

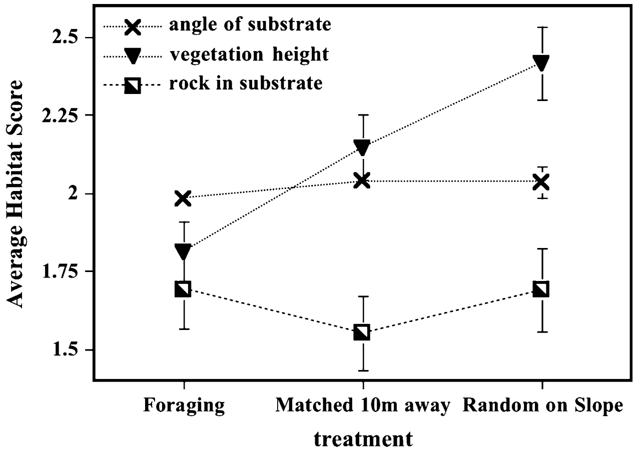

Figure 4
The average habitat score (angle of substrate categories, vegetation height categories, and rock in substrate categories—see text for description) for where marmots elected to forage (foraging) compared with 2 randomly selected locations (a location 10 m away from the focal or a randomly selected location).

Does manipulating peripheral vigilance influence marmot foraging and vigilance?

When their views were blocked, marmots spent less total time on the feeding platform (Table 2). This effect was consistent across all sorts of marmots but tended to be stronger for males than for females (Figure 5a). Marmots often shuttled in and out of the feeding box when their view was blocked, versus staying inside it when the sides were clear. Thus, they spent more overall time walking in trials with the blocked view than with the clear view (0.039 ± 0.007 vs. 0.022 ± 0.007, respectively, see Table 2). As predicted, the treatment changed how marmots paused during feeding to scan their surroundings. When their view was blocked, marmots were less vigilant while inside the feeding box but more vigilant when outside it (Table 2, Figure 5b,c). This compensation in vigilance was very strong for adults and moderate for juveniles. Foraging showed a weaker but generally inverse pattern. Juveniles foraged more in the box than adults (Table 2). While in the box, marmots tended to rear and look more when their view was blocked and forage less (Table 2). These effects, however, depended on the sex of the marmots. Males reared and looked considerably more often when their view was blocked (0.0152 ± 0.0044 vs. 0.0018 ± 0.0012), whereas females reared slightly less often (0.0032 ± 0.0019 vs. 0.0076 ± 0.0051, Table 2). Males ate less of the time when their view was blocked (0.376 ± 0.062 vs. 0.537 ± 0.071), whereas females ate more (0.450 ± 0.055 vs. 0.405 ± 0.059, see Table 2).

DISCUSSION

Taken together, our correlative and experimental studies demonstrate that marmots value unobstructed views while foraging. As vegetation grows, marmots change their amount and kind of vigilance. Like degus (Ebensperger and Hurtado 2005), marmots switched to bipedal vigilance as vegetation became too tall to see over while quadrupedal. Furthermore, we observed marmots foraging in areas of lower vegetation than expected

Table 2
The effect of peripheral visual obstruction on marmot foraging and vigilance behavior

		Time in apparatus		Walk		Rear look		Stand look out		Stand look in		Forage in	
Factor	Degrees of freedom	Partial η^2	P	Partial η^2	P	Partial η^2	P	Partial η^2	P	Partial η^2	P	Partial η^2	P
View	1	0.394	0.001	0.176	0.046	0.163	0.056	0.369	0.002	0.379	0.002	0.128	0.093
View × age	1	0.114	0.115	0.05	0.307	0.103	0.135	0.141	0.078	0.341	0.003	0.000	0.990
View × sex	1	0.144	0.074	0.087	0.173	0.237	0.019	0.016	0.570	0.007	0.712	0.316	0.005
View × age × sex	1	0.000	0.940	0.038	0.370	0.001	0.866	0.095	0.152	0.001	0.890	0.024	0.483
Age	1	0.036	0.384	0.031	0.421	0.004	0.772	0.079	0.195	0.103	0.135	0.197	0.034
Sex	1	0.017	0.559	0.007	0.707	0.063	0.248	0.003	0.816	0.041	0.356	0.000	0.990
Age × sex	1	0.014	0.590	0.013	0.603	0.079	0.195	0.006	0.728	0.020	0.520	0.008	0.690
Error	21												

on local or broader scales. Finally, the experiment isolated the effect of obstructions and produced parallel results: when their view was experimentally blocked, marmots foraged for less time in the box and shuttled out of the feeding box regularly to look. They were less vigilant inside but more vigilant outside of the box. The mix of long-term correlative results combined with focused experimental studies in a single species is novel and allows us to make causal inferences about behavior in nature.

Marmots on steep slopes were less vigilant than marmots on moderate or negligible slopes, an effect also seen in Blumstein et al. (2004). It is not clear if vigilance is more or less effective on steep slopes. Marmots may be able to see downslope without raising their heads but may have a limited view upslope even if they lift their heads. Incline had no notable effect on rearing to look, so we hesitate to interpret the effect to low effectiveness of regular vigilance. Other work indicates that marmots escape at similar speeds on slopes and flat areas, but it is exceedingly difficult to encourage a marmot to run up a steep slope (Blumstein et al. 2004). If their predators are affected more severely by slopes, it could be that yellow-bellied marmots are relatively safe when escaping on steep slopes.

Different age and sex classes showed somewhat different responses. Adults reacted more strongly to the experimental treatment than did juveniles. Juveniles were less vigilant overall and responded less to lateral obstructions (Arenz and Leger 1997b). Juveniles are still growing and may generally value foraging more than adults do. Males seem more affected by obstructed views. Perhaps, this illustrates monitoring conspecifics rather than antipredator vigilance. Marmots are polygynous, and males may battle to establish and maintain territories (Armitage 1986). Thus, males may need to monitor conspecifics, especially potential competitors.

Blumstein et al. (2004) suggested that marmots sometimes adopt a "dine and dash" strategy that minimizes the time they spend in areas with relatively high predation risk. In the experiment, marmots mixed bouts of low vigilance in the box with bouts of increased vigilance outside the box. At least on this scale, marmots put off vigilance when it was ineffective and compensated during times when it was more effective. Vigilance involves fundamental trade-offs between feeding and avoiding predation. Different aspects of seeking, securing, and processing food may more and less be compatible with antipredator vigilance. In our case, marmots often masticated their food while vigilant. When their view was blocked, they did a good deal of their chewing while outside the box. Their reaction to blocked views was actually stronger than indicated in the data because some marmots turned in the box while chewing to look out the one open side when their view was blocked on the other 3 sides. Thus, animals may allocate foraging and vigilance across several temporal scales as they move through their varied landscapes. Our results are compatible with episodes of dine and dash interspersed with periods of "stop and check."

Behavioral ecology has a strong history of integrating field observations with experiments. Experiments are always useful in that they isolate and manipulate the variable of interest. Thus, experiments support inferences of causation that cannot be made from observations. In our case, the experiment confirmed that marmots change their behavior directly in response to what they can see to the sides while foraging. This is a strong finding, and we would like to quantitatively probe deeper in comparing the observational and experimental results. For all measures, the effect sizes from the experiment were larger than those from the observational studies. Although experiments can potentially expand the range of variation to be explained, our results show little scope for such an effect. The standard deviation in standing to look was 0.154 in the observational data, 0.191 while inside the experimental device, and 0.180 outside the experimental device. Thus, we examine why the experiment might have better explained a similar amount of variance.

Several factors might explain why effect sizes were larger in the experiment. First, the experiment manipulated the key variable. By contrast, the natural observations categorized a range of vegetation heights into 3 categories. Because marmots sometimes moved between these categories (and we categorized mixed observations into the rare class), natural observations had variation in the independent variable, whereas the experiments did not. Second, there were some differences in the way data were collected. The observations scored behavior for 2 min, whereas the experiment used 5 min, though this was split between time inside and outside of the feeding box. Also, the experiments used a single observer, although the focals were collected over a number of years by multiple observers. However, these sources of variation (and thus reduced effect size for the observations) are unlikely to be the entire explanation because both sex and age had bigger effects when estimated during the experiment than when estimated during the observations. Sex and age were scored without error in both situations. Third, the experiment controlled for slope and balanced group size effects (and their interactions) and took place in a portion of one season, whereas the natural observations were conducted through much of the active season. The difference between studies suggests that the difference between the sexes shifts over time, particularly across the season.

All our results indicate that marmots value unobstructed views and compensate for obstructions they cannot avoid. Similarly, their flight initiation distance is greater in tall vegetation

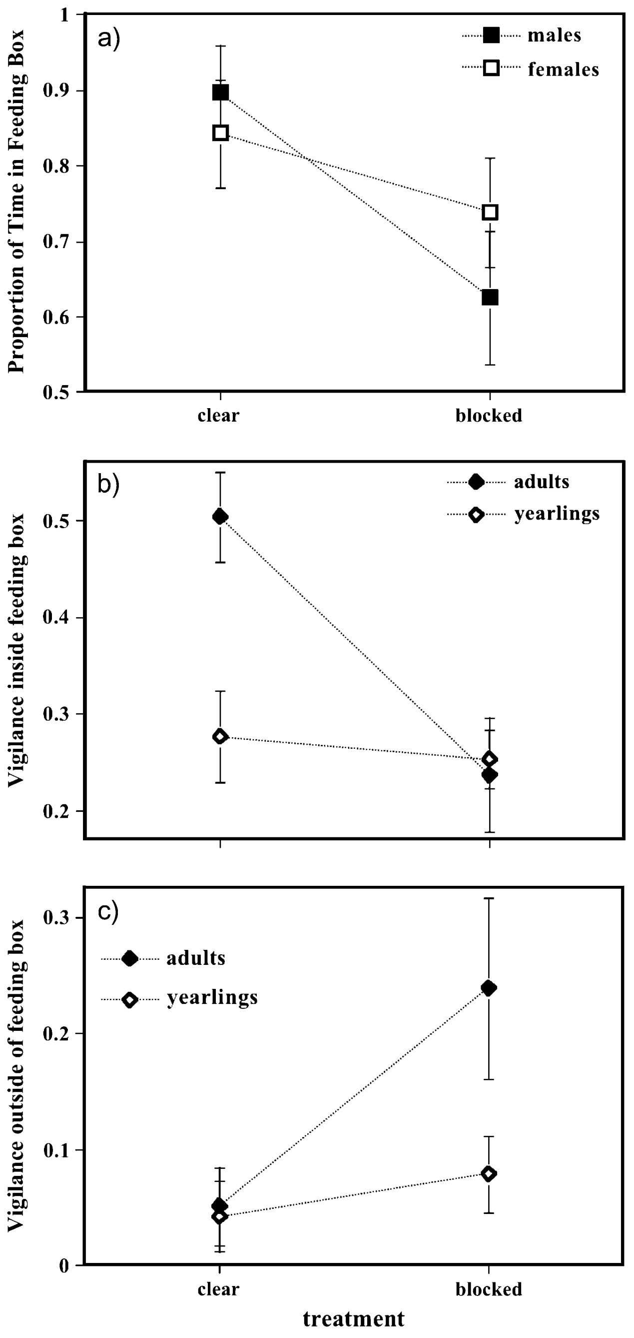

Figure 5
The effect of the artificial peripheral visual obstruction treatment on the proportion of time: (a) feeding in the box, (b) vigilance while in the box, (c) vigilance while outside the box.

(Blumstein et al. 2004). Nonetheless, colonies with more obstructions nearby are more likely to go locally extinct (Blumstein et al. 2006). It seems that the behavioral compensation of marmots is not enough to offset natural differences in risk that go with obstructed views.

More broadly, humans often manipulate vegetation height, which can have profound impacts on the habitat choice and survival of animals. British birds wintering in agricultural fields need good seed supplies among sparse or short stubble (Whittingham et al. 2006). Declines may be due to the structure of stubble rather than simply a shortage of food. Conversely, vegetation management to keep birds away is an important way to reduce bird strikes at airfields. Since 1998, US Air Force policy has maintained vegetation on airfields at 18–36 cm tall when possible, although the data for prescribing height alone are limited (Seamans et al. 2007).

FUNDING

National Science Foundation (DBI-0731346 to the Rocky Mountain Biological Laboratory); National Science Foundation (DBI-0754247 to D.T.B.).

We thank the 2008 marmoteers—especially Tina Wey, Helen Chmura, Eleonora Ferando, Patricia Jones, Lucretia Olson, and Aditya Singh for help keeping the marmots marked and the Rocky Mountain Biological Laboratory for logistical support. Don Kramer and an anonymous reviewer made constructive and astute comments that helped us improve our presentation.

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