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Effect of predation risk on the presence and persistence of yellow-bellied marmot (*Marmota flaviventris*) colonies

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Abstract

Habitat selection may have population level consequences and ultimately may influence a population's local persistence or extinction. We capitalized on a long-term study (1962–2004) of yellow-bellied marmots *Marmota flaviventris* in and around the Rocky Mountain Biological Laboratory, Gothic, Colorado, USA, and compared habitat characteristics associated with food availability and predation risk to explain variation in persistence of marmots at 27 sites, and their absence at 22 additional, randomly selected sites. We classified sites as persistent, intermittent or null based on whether there was a history of extinction; intermittent sites periodically went extinct and null sites never had marmots. Logistic regression analyses revealed that environmental variables associated with visibility and safety, rather than food, correctly classified sites as persistent or non-persistent as well as persistent or intermittent. Discriminant function analysis that included the null sites revealed that the same visibility-related characteristics predicted where marmots were found. These results highlight the importance of variation in safety among sites in predicting long-term population persistence, as well as a species' distribution.

Introduction

With sufficient time, populations ultimately go extinct. A variety of behavioral, ecological and life-history characteristics may predispose a population to extinction (e.g. Bessa-Gomes *et al*., 2003; Brashares, 2003; Cardillo, 2003; Morrow & Pitcher, 2003). Current metapopulation theory emphasizes how connectivity of a patch and local patch quality influence the likelihood of a patch persisting over time (Hanskii, 1999). Where connectivity of an extinct patch to surrounding patches determines its recolonization probability, local patch quality determines the probability of an occupied patch going extinct (Hanskii, 1994; Moilanen & Nieminen, 2002). In simplistic modeling approaches, local population size (or a proxy such as patch area) is generally preferred as a measure of patch quality. Such approaches, however, ignore important factors that influence the decisions that individuals make about where to settle: food availability and predation risk.

Studies have shown that predation alone can be responsible for local extinction (Schoener, Spiller & Losos, 2001). However, predation is often cryptic (Van Vuren, 2001), and the effect of predation is seldom included in studies of local extinction. By contrast, many studies have demonstrated links between variation in food resources and demography (e.g. Cockburn & Lidicker, 1983; Dobson & Kjelgaard, 1985; Armitage, 1988; Frey-Roos, Brodmann & Reyer, 1995; Byrom *et al*., 2000; Karels *et al*., 2000). However, we are left with the question, is this variation itself responsible for local persistence? We quantified variation in habitat characteristics associated with food availability and predation risk and found that for yellow-bellied marmots, variation in predation-related characteristics best predicted where marmots were found and where they persisted. Thus, predation risk may be a major determinant of patch persistence over time in our study system.

Habitat selection has important consequences for an individual's subsequent survival and reproduction (e.g. Morse, 1980). Habitats may vary with respect to their relative 'safety' (e.g. Prins & Iason, 1989; Brown & Kotler, in press). One way in which habitats vary is in the degree that prey can detect predators. Early detection of predators is essential for prey to have a chance of surviving an encounter with a predator. For instance, vigilant ungulates are less likely to be preyed upon than non-vigilant individuals (FitzGibbon, 1989). Vigilance is influenced by microhabitat characteristics, and prey often become wary when their ability to detect predators decreases (e.g. Leger, Owings & Coss, 1983; Arnez & Leger, 1997; Sharpe & Van Horne, 1998; Blumstein *et al*., 2004). Species are less vigilant when they have good peripheral visibility (Burger, 2001). If the ability to detect predators influences predation risk, then we would expect that animals would on average survive better in areas with relatively good visibility.

Yellow-bellied marmots *Marmota flaviventris* are semi-fossorial rodents (Frase & Hoffmann, 1980). Active for 4–5 months annually, marmots spend much of their lives hibernating (Armitage, 2003*a*). Obtaining sufficient food during the brief summer active season is essential for marmot over-winter survival. Marmots must also avoid a variety of terrestrial and aerial predators (Van Vuren, 2001), and they dig numerous burrows in their 0.13–1.02 ha home ranges that serve as refuges (Armitage, 1975). Because marmots are sensitive to forage abundance and predation, they are an ideal species to study the relative effects of food availability and predation risk on population persistence.

Methods

Location and data collection

Since 1962, marmots have been annually live-trapped and monitored at as many as 27 sites throughout Colorado's East River Valley surrounding the Rocky Mountain Biological Laboratory (RMBL) (38°57′N, 106°59′W). Marmots around RMBL have a patchy distribution and are found in sub-alpine meadows and in forest openings. Habitat varies within and between sites from rolling grassy meadows to steeper talus.

We conducted a valley-wide cross-sectional habitat analysis between 16 June and 26 July 2003 (the time period when the growth of the vegetation is at least 75% completed; Kilgore & Armitage, 1978; Frase & Armitage, 1989). We classified sites as null, intermittent or persistent (Fig. 1). Null sites are areas where marmots have never been detected during 43 years of study, and were selected at random from locations that we judged to be suitable habitat (sub-alpine meadows or forest openings associated with rocks) from a 7.5 min topographic map of the East River Valley. We initially defined persistent sites as those sites occupied $\geq$90% of the surveyed years between 1962 and 2004, and intermittent sites as those sites occupied $<$90% of the surveyed years. However, because all 27 sites were not monitored in all years (survey data range from 11 to 43 years among sites), we also employed a more conservative definition where we defined persistent and intermittent sites based on data collected in the most comprehensive 9 years of the study (1986, 1987, 1988, 1989, 1991, 1993, 2002, 2003, 2004), where $\geq$24 sites were simultaneously surveyed. With this definition, persistent sites were consistently occupied during these years whereas intermittent sites included at least 1 year of marmot vacancy. Analyses using these two criteria to classify persistent and intermittent sites generated virtually identical results. Given enough time, we would expect that all sites would experience the occasional extinction event (however, seven of our sites have not yet gone extinct in 43 years of study). The order in which we surveyed sites (null, persistent, intermittent), as well as the rough geographical location in the valley, was randomized to prevent systematic bias from vegetation growth that would arise if we first surveyed null and then marmot-occupied sites, or if we started at one end of the valley and surveyed toward the other end.

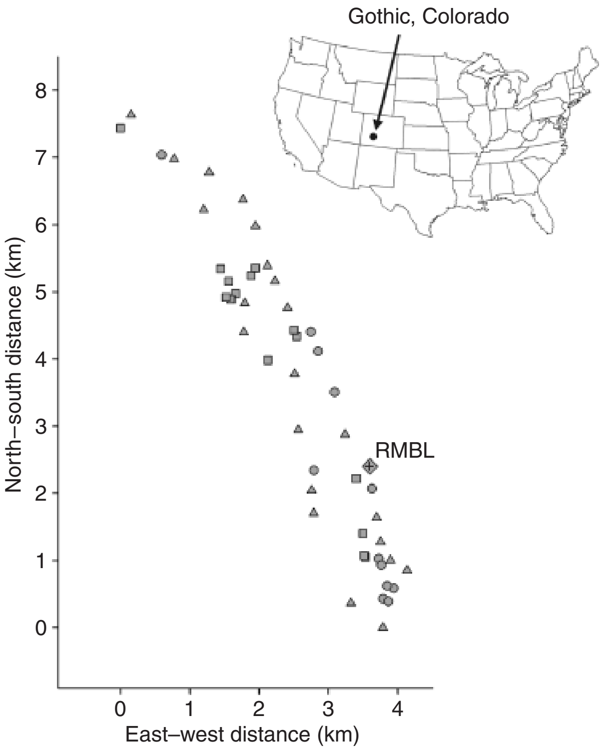

Figure 1 Distribution of study sites in relation to the Rocky Mountain Biological Laboratory, Gothic, Colorado, USA. Squares and diamonds indicate the location of persistent sites (diamonds indicate the seven sites that never went extinct between 1962 and 2004), circles indicate intermittent sites and triangles indicate null sites.

Sites varied in their size, so we focused on a randomly selected 1 ha plot within each site. Within each plot we established five, 50-m transects. Each transect was started from a randomly chosen point and was oriented along a randomly selected compass bearing. We quantified 'food-related' habitat characteristics and 'safety-related' habitat characteristics.

Food-related characteristics were associated with the type and amount of vegetation. Marmots are generalist herbivores (Frase & Armitage, 1989) that forage exclusively above ground and eat a variety of grasses and forbs. Ground cover of various types of vegetation is an adequate proxy for forage quality because marmots use different types of vegetation throughout the year. For instance, grasses are among the first things to begin growing following snowmelt and thus are an important early season food. However, various herbaceous plants which initiate growth later in the season are used throughout the remainder of the growing season. We estimated per cent ground cover by taking measurements every 10 m along the transect, starting at

0 m and using a 1-m^2 quadrat. The quadrats were placed along the tape measure in offset, paired plots at each 10-m mark. We visually estimated per cent cover of trees, shrubs, herbaceous plants, grass, bare ground, rock and water in each quadrat. Using the calibrated quadrat, we also estimated the average vegetation height for each plot along the transect and categorized it into five height classes: 0–10, 10–25, 25–50, 50–100 or >100 cm tall. The mid-point of these heights (or 100 cm for the category classified as >100 cm) was used in subsequent analyses.

Safety-related characteristics were associated with visibility and rocky cover. At each 10-m location along the transect, we measured the incline (in degrees) along the fall line. We also measured visibility from marmot height (a height of roughly 30 cm) for 0–10, 10–50, and >50 m annuli at each 10-m point along the transect. The surrounding 360° was divided into eight, 45° wedges. Each wedge was ranked as either open or obstructed. If there was an obvious place for a predator, such as a coyote *Canis latrans*, to hide, or the majority of the view was obstructed, the area was marked as obstructed. The largest continuous field of view was then tabulated for each distance annulus. Large rocks provide safety from fossorial predators such as badgers *Taxidea taxus* and bears *Ursus americana* that are less able to excavate marmot burrows beneath them. As we walked along a transect, we counted the number of rocks of various sizes in a 2-m belt centered on the tape. Rocks were divided into small, medium and large. Small rocks were 0.027–0.343 m^3 (i.e. 0.3–0.7 m diameter), medium rocks were 0.343 m^3–3.375 m^3 (0.7–1.5 m diameter) and large rocks were >3.375 m^3.

Statistical analyses

Our data set consisted of 2940 observations in 49 sites (five transects/site × six measurement stations/transect × two offset quadrats/measurement station × 49 sites). For each 1 ha site (described by 60 point observations) we averaged a variable's values to generate one set of values per site. We then compared the mean values of our dependent variables across persistent and intermittent sites. Variables that were significantly different were retained for further analysis. We calculated bivariate Pearson product moment correlation coefficients among these remaining variables, and, to avoid problems with multicollinearity, we removed one of the pair of additional variables that had substantial correlation coefficients ($r > 0.8$).

We used logistic regression to study environmental factors that discriminated between persistent and all other sites, persistent and intermittent sites, and between marmot-occupied sites and null sites. All variables were entered, and the models were interpreted. We report the per cent correct classification, the model's *P*-value, and each model's Nagelkerke R^2 values.

We used discriminant function analysis to identify how these variables simultaneously allowed discrimination among our 22 null, 12 intermittent and 15 persistent sites. We entered all variables simultaneously and interpreted the results. A forward stepwise procedure in SPSS 11 (SPSS Inc., Chicago, IL, USA) was used to compute discriminate functions. Variables were added based on the change in Wilk's lambda with the *F*-value to enter $=3.84$ and the *F*-value to remove $=2.71$.

We interpret *P*-values <0.05 as significant and $0.05 < P < 0.1$ as moderately significant. All analyses were conducted in SPSS 11 for Macintosh.

Results

Our final data set consisted of five variables that differed between persistent and intermittent sites (Table 1): average continuous visibility >50 m, average fall line, average per cent grass cover, average vegetation height category and the average number of large rocks counted along the transects.

A logistic regression model with these five variables correctly and significantly ($P < 0.0001$) classified sites as persistent or not persistent (intermittent and extinct) 87.8% of the time. Of these variables, only two – the average fall line and the average number of large rocks – had significant coefficients; continuous visibility had a moderately significant coefficient (Table 2). Persistent sites had less steep fall lines, more large rocks and greater continuous visibility (Table 2).

A logistic regression model with these five variables correctly and significantly ($P < 0.0001$) classified sites as intermittent or persistent 85.2% of the time. Of these variables, only one – average fall line – had a moderately significant coefficient. Persistent sites had less steep fall lines than intermittent sites (Table 2).

Table 1 Mean ± SD of independent variables across null ($n=22$), intermittent ($n=12$) and persistent sites ($n=15$)

	Mean	SD
Null sites		
Continuous visibility > 50 m (°)	0.07	0.32
Fall line (°)	−11.9	6.74
Grass cover (%)	12.3	8.16
Vegetation height (cm)	36.5	17.03
Number of large rocks	0.12	0.23
Intermittent sites		
Continuous visibility > 50 m (°)	2.3	3.91
Fall line (°)	−16.3	8.62
Grass cover (%)	9.9	10.19
Vegetation height (cm)	40.3	19.18
Number of large rocks	0.35	0.75
Persistent sites		
Continuous visibility > 50 m (°)	18.1	25.80
Fall line (°)	−7.5	5.45
Grass cover (%)	17.4	9.18
Vegetation height (cm)	24.2	11.27
Number of large rocks	0.89	1.57

Across sites, there were significant differences in continuous visibility ($P=0.001$), fall line ($P=0.007$) and vegetation height ($P=0.026$), and moderately significant differences in per cent grass cover ($P=0.092$) and the number of large rocks ($P=0.060$).

Table 2 Results (coefficient and *P*-value) from three binary logistic regression analyses predicting (1) whether a site was a persistent or not a persistent site, (2) whether a site was an intermittent or persistent site, and (3) whether a site was a marmot-occupied site or not

Model	(1) Persistent versus not persistent		(2) Intermittent versus persistent		(3) Occupied versus not occupied	
Variable	*B*	*P*-value	*B*	*P*-value	*B*	*P*-value
Constant	1.1016	0.557	4.155	0.142	1.191	0.515
Continuous visibility >50 m	0.234	0.089	0.008	0.907	1.694	0.223
Fall line	0.248	0.043	0.343	0.073	0.80	0.272
Per cent grass cover	−0.025	0.724	0.071	0.430	−0.128	0.091
Vegetation height	−0.030	0.564	−0.070	0.265	−0.006	0.819
Number of large rocks	2.514	0.031	2.339	0.170	3.332	0.045

Each model significantly explained 65.7, 71.8 and 60.0% of the variation in site type and correctly classified site to type 87.8, 85.2 and 79.6% of the time, respectively.

A logistic regression model with these five variables correctly and significantly ($P<0.0001$) classified sites as locations where marmots lived or not 79.6% of the time. Of these variables, only one – the number of large rocks – had a significant coefficient and per cent grass was moderately significant. Marmots occupied sites that had more large rocks and less grass than null sites (Table 2).

Discriminant analysis classified 65.3% of the observations correctly to type of site (null, intermittent and persistent) compared with a 33% random expected classification. The first function explained 88% of the variance whereas the second function explained 12% of the variance. The largest standardized canonical discriminant function coefficients for the first function were the number of large rocks (0.573) and continuous visibility >50 m (0.529); per cent grass was the smallest (0.160). Incline along the fall line (−0.730) and continuous visibility (0.681) were the largest coefficients for the second function. Stepwise discriminate analysis extracted only a single variable (continuous visibility >50 m) to correctly discriminate among sites 59.2% of the time.

Discussion

Our results are consistent with a radiotelemetry study of marmot mortality that identified certain locations in the East River Valley that acted as 'population sinks,' where predation on marmots was exceptionally high because of habitat features that obstructed predator detection (Van Vuren, 2001). Our study demonstrates that habitat features related to predator detection and avoidance are important determinants of both presence and persistence of yellow-bellied marmot colonies. Any way examined, locations where marmots thrived had good visibility. Continuous visibility, alone, was the best-measured variable that discriminated among null, intermittent or persistent sites. Visibility is essential for detecting approaching predators. Consequently, marmots spend 40–60% of their day aboveground sitting and looking (Armitage *et al.*, 1996), and specifically while foraging they spend 33% of their time vigilant (D. T. Blumstein, unpubl. data). The other consistently important variable was the number of large rocks, which is also a determinant of predation risk. Sites that contained large rocks provided safety from fossorial predators such as badgers, a major predator of marmots (Van Vuren, 2001). We have observed badgers pursuing marmots into their burrows and digging marmots out of burrows (Andersen & Johns, 1977; Armitage, 2004; D. T. Blumstein, unpubl. data). Badgers are not routinely observed near marmots, but when they are, the result is catastrophic. In the fall of 2000 and the summer of 2001, a badger foraged on marmots at the RMBL town-site. Most young of 2000 were eaten before hibernation, and all of the young of 2001 were killed while in their burrow one night. In 1999 adults were killed at a site 1 km away, and in 2001 yearlings and juveniles were killed at that site (Armitage, 2004). Because of the cryptic nature of predation, there are relatively few recorded cases of predation by badgers (out of 1423 monitored marmots, only 67 were known to be killed by badgers). Nonetheless, badger predation can have a large, localized impact (Armitage, 2004), thereby contributing to local extinctions. As a protection against such fossorial predators, marmots usually dig their burrows under large rocks and boulders (Svendsen, 1976). Thus, the presence of large rocks can significantly increase local persistence. Rocky burrows also provide refugia from coyotes, bears and foxes *Vulpes vulpes*, all of which may dig after marmots.

In a less comprehensive study, Svendsen (1974) reported substantial differences in the angle of vision from the burrows between satellite and colony sites; he defined satellite sites as smaller and non-persistent, whereas colony sites had more individuals and were persistent. Interestingly, satellite sites were situated on flatter slopes and had greater visibility from the burrow compared with colony sites. There were also no significant differences in the per cent ground cover and the mean vegetation height between satellite and colony sites. Other measured variables associated with food availability had little predictive power. In our larger study, we found that persistent sites are characterized by a slight incline. A moderate degree of incline would be expected to be associated with relatively good visibility; individuals on very steep slopes might be able to see well in one direction, but not in the other.

At our study area, overall vegetative biomass was plentiful (marmots consume less than 4% of aboveground primary production; Kilgore & Armitage, 1978). For instance, compared with golden marmots *M. caudata aurea*, yellow-bellied marmots had more than an order of magnitude more aboveground standing crop at the height of the growing season (Blumstein & Foggin, 1997). Thus, we might not expect variation in overall food availability to account for variation in long-term persistence. This should be viewed in context: from the marmots' perspective, vegetation may not be equally important. Certain key fatty acids (Hill & Florant, 1999; Arnold *et al*., 2003) might be essential to facilitate hibernation and ensure over-winter survival. Additionally, late summer droughts and delayed snowmelt were implicated in local extinction (Armitage, 2003*b*). Interestingly, recovery from local extinction was dependent on idiosyncratic local demographic and dispersal events.

The weather-related mechanism of extinction events remains to be clarified. It is possible that past weather-related extinctions resulted from insufficient food and hibernation-related mortality; heavier juveniles are more likely to survive hibernation and the termination of the growing season is associated with the termination of mass gain (Lenihan & Van Vuren, 1996). However, it is also possible that animals had to allocate more time to foraging and less to antipredator vigilance when food was scarce. Bachman (1993) found that body condition influenced antipredator vigilance in Belding's ground squirrels *Spermophilus beldingi*. Alternatively, individuals may have had to forage farther from refugia, and thus were more exposed to predation risk (*sensu* Blumstein, 1998). For example, in 2002, a drought led to a systematic increase in home range size as individuals sought green vegetation in the late summer (K. B. Armitage & D. T. Blumstein, unpubl. data). Future studies will need to examine directly examine the interaction between food and exposure to predation risk and its effects on population persistence.

For seasonally active species, we expect that the timing and abundance of food will be essential for reproduction as well as accumulating sufficient fat reserves to survive hibernation. Previous studies with the RMBL marmots have demonstrated that the onset and termination of a marmot's active season are affected by the date of 50% snowmelt, a metric of food availability (Van Vuren & Armitage, 1991), and that marmots given supplementary food gained mass faster (Woods & Armitage, 2003), but individuals were not more likely to survive hibernation or reproduce the next year. Studies of golden marmots demonstrated that food availability influenced weaning success in the subsequent year (Blumstein & Foggin, 1997). Our cross-sectional study, however, found that per cent ground cover had little predictive value in explaining variation in the presence or persistence of marmots.

Our results support the hypothesis that population persistence is not equal across habitats because certain habitat patches are more likely to go extinct than others. Marmots disperse widely (Van Vuren & Armitage, 1994*a*), and the failure to colonize null sites and to recolonize intermittent sites does not reflect a lack of connectivity. Recently, Oli & Armitage (2004) showed that population dynamic differences among marmot colonies were due primarily to colony- and spatial-specific variation in juvenile survival and age at maturity. Future analyses could examine individual fitness within these different patches to see if individuals are trading off a higher risk of extinction for a short-term gain in reproductive success. However, previous analyses of colonial and satellite females suggest that satellite females had lower fitness (Van Vuren & Armitage, 1994*b*).

In our study, we only considered food availability and predation risk as major determinants of local persistence. We recognize that these are not the only factors that are important. For instance, the area of sites and group size are often important predictors of extinction. However, site area was not a good determinant of group size because marmot densities varied substantially among sites and we believe that site-specific characteristics (considered in this study) other than the area are likely to be important determinants of group size. We elected to not include group size as a covariate because it alone is a strong determinant of persistence, but it does not allow us to identify the relative importance of predation-related and food-related factors.

For a hibernating mammal such as the yellow-bellied marmot, over-winter survival is also an important component of annual survival and, in turn, an important component of local persistence. Over-winter starvation is a major cause of winter mortality in Alpine marmots *M*. *marmota* (Arnold, 1993). We did not include determinants of hibernation suitability in our study for two reasons. First, yellow-bellied marmots are known to be very efficient hibernators (Armitage, Blumstein & Woods, 2003). Winter mortality may have a large impact for pups in some years (Lenihan & Van Vuren, 1996), but adults fare better (Van Vuren & Armitage, 1994*b*), and there are relatively small effects of winter weather on demographic parameters (Schwartz & Armitage, 2002). Second, environmental characteristics related to hibernation suitability are mostly related to the structure of the burrow and these were not easily quantified in our study. Moreover, null sites do not have hibernacula so they could not be included in our analyses. We also excluded landscape measures that determine patch connectivity from our analysis, because our aim was to investigate the relative importance of food availability and predation risk. Details on the effect of landscape metrics on patch occupancy dynamics of the yellow-bellied marmots around RMBL are given elsewhere (Ozgul *et al*., 2006). Nonetheless, it is important to note that unexplained variation in the persistence and presence of marmot colonies may result from variation in patch connectivity and hibernation suitability.

In general, we might expect that in systems where food is not a limiting factor, variation in predation risk might be vitally important in predicting presence and persistence. Predation itself need not be common to have such an effect. The risk of predation creates a 'landscape of fear' (Laundré, Hernández & Altendorf, 2001; Brown & Kotler, in press) and defines suitable habitat. Such trait-mediated indirect effects of predation are found in a variety of systems (Wootton, 1994) and are likely to be important predictors of presence. For marmots settling into sub-optimal habitat, uncommon predation events, acting either directly or through interactions with limited food, are likely to be responsible for periodic extinctions.

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