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Locomotor Ability and Wariness in Yellow-Bellied Marmots

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Abstract

Animals employ a variety of behaviors to reduce or manage predation risk. Often, these are studied in isolation, but selection may act on packages of behavior that are referred to as behavioral syndromes. We focused on yellow-bellied marmots (*Marmota flaviventris*) and examined three commonly studied antipredator behaviors. We fitted general linear models to explain variation in maximum running speed, time allocated to vigilance and foraging during bouts of foraging, and flight initiation distance (FID). Marmot maximum running speed was influenced by the substrate run across; marmots ran fastest across dirt or low vegetation and slowest across stones or talus. Incline and several other variables shown to affect running speed in other marmot species failed to explain significant variation in yellow-bellied marmots. From these results we expected marmots to be sensitive to substrate while foraging, but insensitive to incline. However, time allocated to foraging was affected by incline but not by substrate. In bouts of foraging observed in different habitats, and on different inclines, more time was allocated to foraging and less to vigilance on steep slopes and less on level ground. Substrate influenced FID. Marmots in tall vegetation were less tolerant of an approaching person than were those in shorter vegetation. Finally, we found significant correlations between the residuals from the maximum running speed model and the residuals from the time allocated to vigilance and foraging models. We found a tendency for marmots that ran slower than predicted to be less vigilant while foraging. We also found that relatively slow marmots engaged in more active foraging and less vigilance during foraging bouts. This finding suggests a 'locomotor ability-wariness while foraging' syndrome. It also suggests that vulnerable individuals minimize their exposure while foraging.

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Introduction

Animals employ a variety of behaviors to avoid predation (Edmunds 1974; Lima & Dill 1990). Many behaviors, including antipredator behaviors, are typically studied in isolation and the relationship between them is often not explored (Sih et al. in press). This is unfortunate because survival is a function of many behaviors working together (Coss 1999) and, by adopting a more holistic view (Sih et al. in press), we may obtain novel insights not possible when behavior is 'atomized' (Gould & Lewontin 1979; Sih et al. in press).

For instance, crickets (*Gryllus integer*) with comparatively long sexually selected calls, compensated for increased exposure by ceasing calling for a longer period of time when their calls were interrupted by a predator, and they remained in their shelter longer when placed in a novel environment (Hedrick 2000). In one of the best-studied natural systems, a number of guppy traits covary with predation risk (Endler 1995), and such covariation with predation risk is expected on theoretical grounds (D. T. Blumstein, unpubl. data)

We might generally expect (and may see) natural selection acting on packages of antipredator behavior (Byers 1997; Coss 1999; D. T. Blumstein et al., unpubl. data). These correlated packages of behaviors are referred to as behavioral syndromes (Sih et al. in press). Antipredator behavioral syndromes have been identified in both invertebrates (Riechert & Hedrick 1993) and vertebrates (Sih et al. 2003). Identifying these syndromes is important because correlations among traits can cause trade-offs and conflicting selection pressures, whereas uncorrelated traits need not create conflict (e.g. Sih 1987; Sih et al. in press).

Sih et al. (in press) suggested that examination of correlations among behaviors (ideally measured in different contexts) is a key method for identifying behavioral syndromes. There are, however, a number of methods that can be used to identify correlated traits and thus could be potentially useful to identify behavioral syndromes. For instance, documenting traits that covary with a particular factor in nature (Endler 1995), or with each other (Magurran & Seghers 1994) can suggest traits that may not vary independently, and quantitative genetic techniques can formally identify genetic correlations (Brodie 1989; Boake 1994). QTL mapping can identify traits under common genetic control (Colosimo et al. 2004). Genetic knock-outs can identify the effect of a single gene on multiple behaviors (Dulawa et al. 1999; Malleret et al. 1999), but such techniques are of little use in field studies, unless genetically modified animals are released. Similarly, pharmacological manipulations (Blanchard 1997; Blanchard et al. 2001) and ablations (Blanchard & Blanchard 1972) can be used to identify packages of traits that are under common neural control. Given time budget or survey data, factor analysis (Capitanio 1999; Gosling 2001) and discriminate function analysis (Loughry & Lazari 1994) have been used to identify distinctive ‘packages’ of behavior. Such packages are, by definition, not independent.

A key characteristic of a behavioral syndrome is that behaviors in different contexts are in some way correlated or linked (Sih et al. in press). While not explicitly designed to identify ‘behavioral syndromes’, there is a growing literature in which researchers measure locomotor performance under laboratory conditions and then determine the degree to which performance in the lab is associated with habitat preferences measured in the field. Studies that link performance to fitness (Losos & Irschick 1996; Irschick & Losos 1999; Melville & Swain 2003) are important for several reasons. First, performance can constrain habitat selection or use, but this needs to be properly documented (Irschick & Losos 1999; Melville & Swain 2003). Secondly, there could be habitat-specific antipredator strategies (Cuadrado et al. 2001; Mandelik et al. 2003) that, in some way, depend on, or interact with, individual performance. Moreover, all species may not respond similarly to variation in risk. For instance, species that may be able to outrun predators, if warned with sufficient time, may perceive cover as obstructive compared with species that require cover for protection (e.g. Blumstein & Daniel 2002). Finally, by studying different behaviors across contexts, it is possible to identify potential ‘locomotor performance-wariness’ or ‘locomotor performance-habitat selection’ syndromes.

Consider a small mammal foraging in a meadow. It could avoid predation by carefully selecting the safest places to forage. However, if it had to leave safe areas to forage, it could increase its vigilance while foraging in exposed areas, or it could minimize its time in exposed areas by foraging more efficiently. It could also rely on flight to avoid predators once detected. Time allocation and escape behavior are often studied independently, but we should generally expect that they should be linked to habitat selection. More importantly, we should expect that locomotor behavior might be useful in defining, from the animal’s perspective, which habitats are particularly risky.

In this paper, we develop a strategy for analyzing such data to identify the relationship between variation in locomotor behavior and other behavior studied in field conditions. In doing so, we conduct and then synthesize the results of three independent studies of antipredator behavior. We first studied factors that influenced the speed with which yellow-bellied marmots (*Marmota flaviventris*) could escape predators. We used the results from this study to help identify potentially risky parts of their habitat. We then asked whether the marmots were able to compensate for reduced locomotor ability by being more vigilant while foraging or, by increasing the distance at which they fled an approaching human in certain microhabitats both while foraging or simply while in them. Finally, we studied the associations between these three antipredator behaviors [maximum running speed, time allocation, and flight initiation distance (FID)] within individuals to identify correlations, and thus potential behavioral syndromes. For instance, are relatively fast individuals less vigilant while foraging, or do relatively slow individuals flee an approaching human at a relatively greater distance? The habitat may influence each of these variables (e.g. animals might run faster downhill and be warier in tall vegetation). Thus, rather than studying correlations directly, we correlated residuals from linear models fitted to explain variation in each of the behaviors. In doing so, we develop and justify a novel approach to identifying correlated traits and behavioral syndromes in natural conditions.

Methods

General Methods

Adult and yearling yellow-bellied marmots were studied in Colorado's East River Valley in and around the Rocky Mountain Biological Laboratory (RMBL) (38°57′N, 106°59′W) during the summers of 2002 and 2003. Marmots at RMBL are preyed on by a variety of avian and terrestrial predators (Van Vuren 1991, 2001), and thus should be expected to have a sophisticated suite of antipredator behavior. Marmots at RMBL are found in subalpine meadows and in forest clearings. Habitat varied within and between sites from rolling grassy meadows to steeper talus slopes. Substrate varied seasonally within (i.e. as the vegetation grew and senesced) and across sites. Marmots were routinely live-trapped and marked with ear-tags for permanent identification and, for observation from afar, were marked with fur dye (Armitage 1982). When trapped, marmots were transferred to a canvas handling-bag and their weights and reproductive status were noted. Subjects were observed with 15–45× spotting scopes from locations that did not obviously affect their behavior during times of peak activity (sunrise to 10:00 h, and 16:00 h to sunset) on days without rain or excessive wind.

Statistical analyses were conducted using SPSS-10 (SPSS, Inc. 2000). To preserve independence, we selected randomly a single observation per individual for analysis. To study repeatability, we used the entire data set and calculated the intra-class correlation coefficient (Sokal & Rohlf 1981) from individuals who were observed three or more times. Transformations were used to normalize residuals from linear models and thus to meet model assumptions. Throughout, we report adjusted R^2 values, and we interpret p-values < 0.05 as significant and $0.05 < p < 0.1$ as marginally significant. We report partial eta squares as a measure of effect size (Cohen 1988) for variables in the general linear models, and adjusted R^2 values when reporting total variation explained by a model.

Studying Variation in Maximum Running Speed

We studied maximum running speed as a way to objectively define risky microhabitats for marmots. We assumed that variation in locomotor performance has fitness consequences (Losos 1990). Specifically, we assumed that marmots that ran faster on average would be better able to escape pursuit predators. At our study site, marmots are preyed upon by bears (*Ursus americanus*), coyotes (*Canis latrans*), martens (*Martes americana*), badgers (*Taxidea taxus*), golden eagles (*Aquila chrysaetos*), and possibly by red-tailed hawks (*Buteo jamaicensis*: Andersen & Johns 1977; Blumstein 1989; Van Vuren 1991, 2001). All of these predators may pursue individuals, and marmots flee to burrows to escape these predators (Blumstein 1998). Even badgers may chase marmots (D. T. Blumstein, pers. obs.) before beginning to dig them out of their burrows; thus, we assumed that rapid flight should generally be valuable. Successful flight is not only a function of 'innate' performance ability, but is also influenced by habitat selection and overall wariness. Therefore, studying the interactions between these behaviors is essential if we are to identify possible tradeoffs and obtain a deeper understanding of antipredator strategies.

Many animals optimize antipredator behaviors, including maximum running speed (Ydenberg & Dill 1986; Dill 1990). Specifically, individuals can reduce their escape speed to reduce costs associated with escape. Thus, at some level, the term maximum running speed may be a misnomer. We use it to measure the maximum speed a subject was able and willing to travel in a certain context. Previous studies of maximum running speed in marmots and other taxa have identified several factors that influence escape velocity (body mass: Trombulak 1989; substrate: Djawdan & Garland 1988; incline: Taylor et al. 1972; distance run: Blumstein 1992). Therefore, to identify the relative risk of substrate and incline, we needed to control for body mass, distance run, and the distance the marmot was from a burrow when it was timed. Unlike captive studies that control for microhabitat variation experimentally (e.g. Irschick & Losos 1999) to study locomotor performance, we wished to statistically control for this variation and by doing so, identify significant factors influencing running speed in nature (Blumstein 1992; also see Irschick 2003). We assumed that if particular angles or particular substrates significantly decreased escape speed, then marmots would be exposed to greater risks of predation while in those habitats (Blumstein 1992, 1998).

We followed the methods described in Blumstein (1992) to study maximum running speed in golden marmots (*M. caudata aurea*). Following capture, marmots were released from the handling bag and encouraged, by shouting and arm waving, to run to a burrow. Humans represented a standardized alarming stimulus with which we evaluated running speed. Using digital stopwatches, observers timed animals that were running across a homogeneous substrate and incline through an interval of approximately 5, 10, 15 or 20 m (the exact distance was subsequently measured). Many observations were excluded. Marmots often turned or began running across a different substrate or incline while escaping, or veered into a different burrow, thus truncating many runs. Observations were also excluded where animals were obviously not running at their maximum speed (e.g. they suddenly slowed or stopped running) across the interval that they were timed. Following a run, we noted the time it took a subject (run time) to cross the distance over which it was timed (distance run), the direct distance to the burrow (distance to burrow), the incline, measured in degrees, over which the subject ran (incline), and the substrate (classified as primarily 'stones or talus', 'dirt or short vegetation' which was lower than a foraging marmot's ears, and 'tall vegetation' which was above a foraging marmot's ears).

Analysis focused on modeling the variation in run time to avoid the ratio-correlation problem (Atchley et al. 1976; Schoener 1988) that would be expected in analyses of velocity that included independent variables such as distance run (Blumstein 1992). To reduce measurement error, we eliminated runs that were < 1.5 s because of the enhanced effect of any error on estimating velocity from a short run (Blumstein 1992). From the remaining dataset of timed runs, we selected randomly a single run from each yearling or adult. The final data set contained a total of 48 yearling and adult subjects.

We fitted a linear model to explain variation in run time (our dependent variable) that included the following independent variables: distance run, direct distance to burrow, substrate, body mass, incline, and, as a measure of vertical displacement, the interaction of incline × distance run. The linear model was forced through the origin because a marmot running no distance should not take any time. Residuals from this linear model were examined for normality and the residuals were saved for subsequent analysis.

The data set used to calculate the intra-class correlation coefficient consisted of 120 runs on 28 individuals timed ≥ 3 times.

Studying Variation in Time Allocation

Time allocation is often influenced by microhabitat characteristics (Leger et al. 1983; Arnez & Leger 1997; Sharpe & Van Horne 1998; Boinski et al. 2003) but the effect of an individual's performance on time allocation in different habitats is unknown. The results of the maximum running speed study suggested that marmots would be exposed to a greater risk of predation when foraging in microhabitats consisting of stones or talus. This is especially a problem when trying to escape avian predators, where substrate has no effect on the predator's locomotor efficiency. We studied time allocation to understand if in fact marmots modified their foraging behavior in these microhabitats. Group size typically has a large influence on the time allocated to foraging and vigilance either through its effects on reducing predation risk (Vine 1971; Pulliam 1973), or by increasing foraging competition (Clark & Mangel 1986; Elgar 1989), or both. Marmots are herbivores and forage on a variety of plants (Frase & Hoffmann 1980) that are typically abundant in their 0.02–7.2 ha home ranges (Armitage 1988). It is unlikely that variation in time allocated to foraging or vigilance is influenced by scramble competition, but it is very likely that group size influences actual or perceived predation risk (Carey & Moore 1986; but see Blumstein 1996). Thus, while observing marmots forage, we counted the number of conspecifics within 10 m as a measure of foraging group size. We focused on yearlings and adults throughout the study. Fifty percent of females and most males disperse as yearlings (Armitage 1987). Because yearling dispersal is often preceded by aggression from resident adults (Armitage 1975), and animals in the process of being evicted might be particularly wary of dominant conspecifics, we therefore included age and sex in our general linear model. Finally, because vegetation varied as the growing season progressed, and because time allocation may vary as a function of vegetation, we incorporated Julian date into models to explain time allocation.

We conducted 2-min focal animal observations on foraging subjects where we noted the onset of each bout of quadrupedal foraging, bipedal foraging (later combined into a total foraging variable), quadrupedal looking, bipedal looking (later combined into a total looking variable), locomotion, and periods of time when animals were out-of-sight. Observers dictated observations into microcassette recorders and later scored them using JWatcher 0.9 (Blumstein et al. 2000). While conducting a focal observation on an identified subject, observers categorized the incline (0–10°, 10–30°, > 30°), substrate (stones or talus, dirt or short vegetation, tall vegetation), and the number of individuals within 10 m of the focal subject. Observers were trained to identify these broad slope categories and substrate with 100% accuracy. Observers were also trained to identify each behavior with 100% accuracy, and then trained with JWatcher until intra-observer reliability was ≥0.95.

Analyses focused on the proportion of time a subject was in sight that was allocated to each behavior. We eliminated focal observations where subjects did not forage for more than 20 s during the 2-min observation because we wished to study time allocation in obviously foraging animals. We randomly selected one observation from each subject and fitted a general linear model to explain time allocated to angularly transformed total foraging and angularly transformed total vigilance (our dependent variables). Independent variables included: substrate category, incline category, the age and sex of the focal subject (yearling male, yearling female, adult male, and adult female), the number of conspecifics within 10 m, and the Julian date. Residuals from these linear models were examined for normality and saved for subsequent analyses.

The data set used calculate the intra-class correlation coefficient consisted of 290 focal samples on 50 subjects observed ≥3 times.

Studying Variation in FID

The results from studies of performance and time allocation suggest that foraging marmots do not allocate more time to vigilance while in potentially risky microhabitats. However, marmots could still increase their general wariness. We studied marmot FID, the distance from an approaching threat at which an animal flees (Ydenberg & Dill 1986), in different microhabitats to determine whether the microhabitat influenced FID.

Many species have been observed to optimize FID (Blumstein 2003). Thus, to study the effects of microhabitat on FID, we included several variables that have been demonstrated to influence FID in other species. Because group size may influence predation risk (Lima & Dill 1990), we kept track of the number of conspecifics within 10 m of our focal subject. Other studies have demonstrated that animals react at a greater distance when farther from refugia (Dill & Houtman 1989; Dill 1990; Bonenfant & Kramer 1996). Thus, we included the distance a focal subject was from a burrow in our models. Incline and initial activity might influence either detection (Lima & Bednekoff 1999; Dukas & Kamil 2000), or predation risk (Blumstein 1998); therefore, we focused on marmots that were either foraging or standing and looking in a 'relaxed' way. We nevertheless included initial activity and incline as variables in our model to explain variation in FID. Finally, the distance one initiates an approach (starting distance) is often positively correlated with FID and has been shown to explain significant variation in many species (Blumstein 2003; Ikuta & Blumstein 2003). Thus, starting distance was included in our models to explain variation in FID.

Individually identified foraging or standing and looking marmots were approached after no fewer than 5 min of observation by a single observer wearing similar clothes throughout the season. Once habituated to the observer's presence, subjects were approached by directly walking toward the focal individual at a speed of 0.5 m/s. To ensure constant approach speed, the observer trained with a stopwatch and a meter tape until she could walk at a constant pace in the different habitats. The distance (in paces, later converted to meters) where the following events occurred was noted: detection distance (the distance the marmot first oriented itself toward the person), FID (the distance the marmot first moved away). In addition, we recorded the starting distance (the distance between the marmot and the observer when the experimental flush began), the direct line distance the marmot was from the nearest burrow when the experimental approach began, the incline the marmot escaped across, and the substrate the marmot escaped across. To minimize the effects of habituation, no more than one trial at a site was conducted during a morning or afternoon observation period. Individuals were typically flushed no more than once each week.

We fitted a general linear model to explain variation in the square root of FID (our dependent variable). The model included starting distance, as an independent variable, and was forced through the origin because a marmot for which the approach started at 0 m would, by definition, have a 0 m FID. Additional independent variables included: escape incline, distance to burrow, initial activity, and substrate.

The data set used calculate the intra-class correlation coefficient consisted of 46 measurements of FID on nine subjects observed ≥3 times.

Correlations Between Residuals

To identify correlated traits, and thus behavioral syndromes, we calculated correlations between the residuals from the linear models described above. By doing so, we focused on individual variation that was not explained by the measured variables. We expect such 'innate' differences in performance and behavior. Our statistical approach allowed us to eliminate the effects of measured environmental variation that accounted for trait variation. We believe that this is essential specifically because these dependent variables are influenced by environmental heterogeneity.

The different sites in which we studied marmots were not identical and this could have created some potential confounds. For instance, it would be troublesome if all the relatively fast subjects were found in the habitat with the steepest slope. Thus, for each set of residuals, we tested for site-specific effects in explaining residual variation by using ANOVA to compare mean residual scores across sites.

We then calculated correlation coefficients between those individuals that appeared in pairs of data sets. The overall data set was not balanced: 21 individuals were observed foraging and were flushed in the FID study; 28 were observed foraging and were run in the maximum running speed study, and 12 were run in the maximum running speed study and flushed in the FID study.

A Preliminary Study of Microhabitat Selection

As a preliminary to conducting a proper and detailed study of microhabitat selection, we used contingency table analyses to compare the expected distribution of the location of 330 observed focal observations across incline and habitat type. We acknowledge an unavoidable bias of being less able to detect marmots foraging in dense, tall vegetation. We also realize that while each focal observation was unique, some dependency exists between observations insofar as individuals appeared more than a single time in this data set. We view results from these analyses as preliminary and suggestive, not conclusive.

Results

Variation in Maximum Running Speed

From a total of 200 observations, our model included data from 21 adult females, two adult males, 16 yearling females, and nine yearling males. Animals were timed running across all substrate types and a range of distances to their burrows. The general linear model explained 96.4% of the variation in run time. As expected, distance run explained a significant amount of the variation in run time, and had the largest effect size ($p < 0.0001$; partial eta square = 0.618; Table 1). After accounting for this variation, substrate was the only other variable that explained significant variation in run time ($p < 0.0001$; partial eta square = 0.460). Marmots ran the fastest on dirt or short vegetation, and the slowest on stones or talus (Table 1; Fig. 1a). Given the large amount of variation explained by the linear model, and hence by external environmental effects, the intra-class correlation coefficient, which indicates the relative importance of individual effects, was expectedly small ($r_I = 0.03$).

Variation in Time Allocation

From a total of 336 focal samples, our model included data from 21 adult females, seven adult males, 21 yearling females, and 15 yearling males. General linear models significantly explained 20.6% of the variation in time allocated to foraging, and 25.9% of time allocated to vigilance while foraging. Only two

Table 1: Results of general linear model explaining variation in run time (n = 48 subjects). On this and following tables, B's are model coefficients, p-values and partial eta squared values report the significance of a factor or a coefficient estimate

Factor	B	p-value	Partial eta squared
Substrate		0.000	0.460
Stones and talus	1.469	0.000	0.452
Dirt and short vegetation	0.828	0.013	0.146
Tall vegetation	0.981	0.003	0.202
Incline (°)	0.0006	0.945	0.000
Distance run (m)	0.217	0.000	0.618
Distance run × incline	0.0012	0.183	0.044
Body mass (g)	0.00002	0.849	0.001
Distance to burrow (m)	0.0209	0.209	0.039

The model significantly explained 96.4% of the variation.

variables, incline and group size, explained significant variation in either model (Tables 2 and 3; Fig. 2). Marmots allocated the most time to foraging during bouts of foraging on slopes $>30°$, and least on the slopes 0–10°. There was a non-significant tendency for marmots to forage more when in larger groups. In contrast, marmots allocated the most time to looking when on relatively flat slopes (0–10°), and the least time to looking when on steep slopes ($>30°$). There was a significant effect of group size on time allocated to total vigilance, such that as group size increased, vigilance decreased. The intra-class correlation coefficients were moderately large (foraging $r_I = 0.26$; vigilance $r_I = 0.29$).

Variation in FID

From a total of 103 experimental flushes, our model included data from 12 adult females, five adult males, 13 yearling females, and seven yearling males. The general linear model explained 96% of the variation in FID. After explaining significant variation accounted for by starting distance, there was a tendency for initial activity, group size, and substrate (Fig. 1b) to explain variation in FID (Table 4). Foraging animals tended to tolerate closer approaches before fleeing ($p = 0.07$) than those that were standing and looking. Animals with more conspecifics within 10 m tended to tolerate closer approaches ($p = 0.059$) before fleeing. Furthermore, substrate tended to influence tolerance to approach ($p = 0.097$). Marmots in tall vegetation were the wariest; they fled at greater distances than those on stones or talus, or those on dirt or short vegetation. However, while coefficient estimates were significantly different from 0, they overlapped each other to varying degrees. As expected from a variable that had so much variation explained by environmental factors, the intra-class correlation coefficient was small ($r_I = 0.09$).

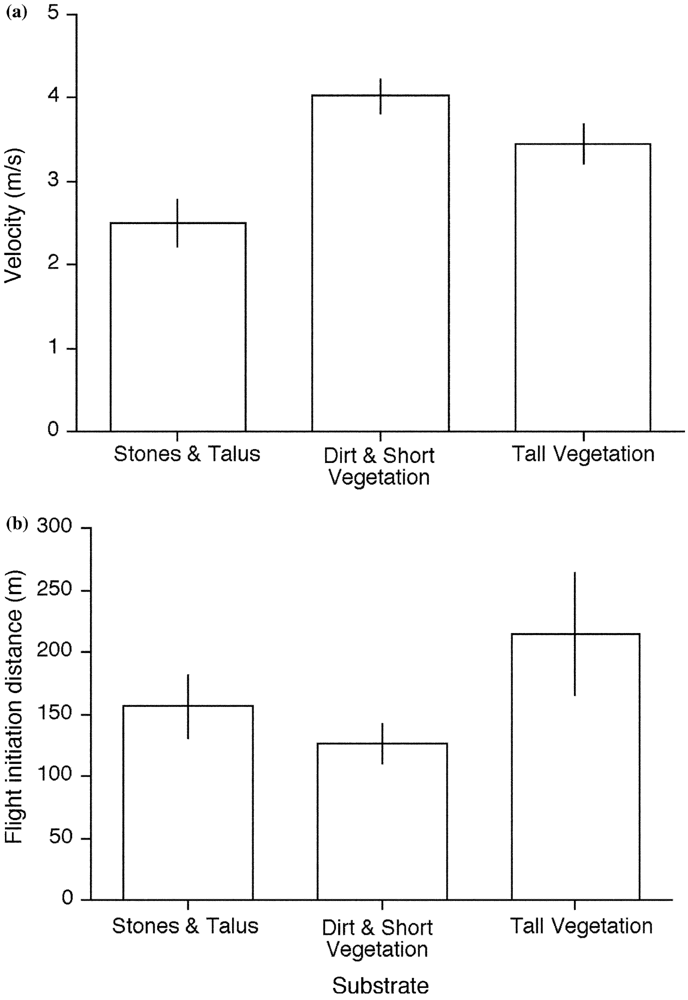

Fig. 1: Plots illustrating raw data for (a) mean velocity (± SE) and (b) mean flight initiation distance (± SE) as a function of substrate type

Correlations Between Residuals

There was no significant effect of study site on any of the residuals (all p-values > 0.56; Fig. 3). Thus, we assumed that the following correlative analysis of residuals was not confounded by site-specific effects.

The main result from the analysis of residuals was that individuals that tended to be slower than predicted from the maximum running speed study, foraged more ($r = 0.37$, $p = 0.051$, $n = 28$), and were less vigilant ($r = -0.35$, $p = 0.069$, $n = 28$) while engaged in bouts of foraging than predicted from the time allocation study. There was no significant relationship between time

Table 2: Results of general linear model explaining variation in the angularly transformed proportion of time in sight allocated to foraging (n = 64 subjects)

Factor	B	p-value	Partial eta squared
Intercept	0.772	0.007	0.126
Age-sex		0.107	0.106
Adult female	−0.058	0.406	0.013
Adult male	−0.230	0.021	0.095
Yearling female	−0.092	0.166	0.035
Yearling male	0		
Incline (°)		0.002	0.202
0–10	−0.210	0.001	0.202
10–30	−0.079	0.212	0.029
> 30	0		
No. conspecifics within 10 m	0.029	0.067	0.061
Julian date	0.0009	0.594	0.005
Substrate		0.101	0.081
Stones and talus	0.0099	0.915	0.000
Dirt and short vegetation	0.124	0.046	0.072
Tall vegetation	0		

The model significantly explained 20.6% of the variation.

Table 3: Results of general linear model explaining variation in the angularly transformed proportion of time in sight allocated to vigilance (n = 64 subjects)

Factor	B	p-value	Partial eta squared
Intercept	0.680	0.002	0.162
Age-sex		0.121	0.101
Adult female	0.069	0.190	0.032
Adult male	0.181	0.017	0.101
Yearling female	0.060	0.235	0.026
Yearling male	0		
Incline (°)		0.001	0.235
0–10	0.176	0.000	0.234
10–30	0.072	0.138	0.040
> 30	0		
No. conspecifics within 10 m	−0.025	0.033	0.082
Julian date	−0.0013	0.307	0.019
Substrate		0.235	0.052
Stones and talus	0.049	0.495	0.009
Dirt and short vegetation	−0.054	0.248	0.025
Tall vegetation	0		

The model significantly explained 25.9% of the variation.

allocation and FID (foraging r = −0.19, p = 0.413, n = 21; vigilance r = 0.11, p = 0.63, n = 21), or between maximum running speed and FID (r = 0.04, p = 0.910, n = 12).

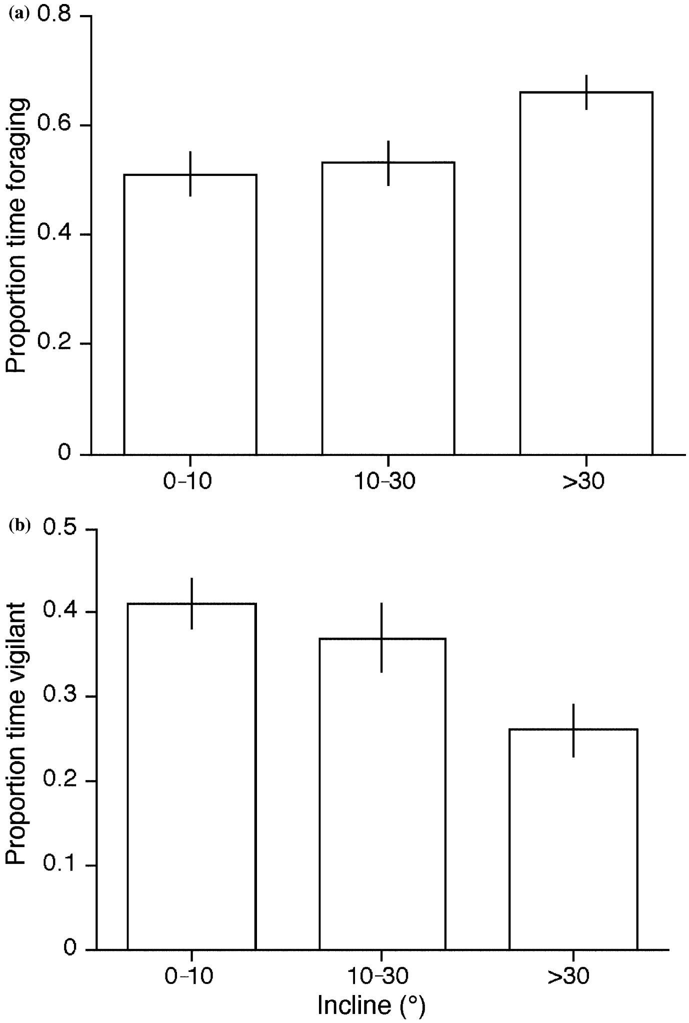

Fig. 2: Plots illustrating raw data for (a) mean time allocated to foraging (± SE) and (b) vigilance (± SE) as a function of incline category

Microhabitat Selection

Focal data suggests that marmots preferentially selected safer microhabitats in which to forage. While there was no difference between the observed and expected distribution of the 330 foraging bouts as a function of incline ($\chi^2 = 1.15$, 3 df, $p > 0.1$, $n = 330$ bouts of foraging), there was a significant deviation from random with respect to the substrate on which they foraged ($\chi^2 = 187.22$, 3 df, $p < 0.0001$, $n = 330$ bouts of foraging). Specifically, marmots were more likely to be observed foraging in short vegetation or on dirt (227 focals), than on stones or talus (48 focals), or in tall vegetation (57

Table 4: Results of general linear model explaining variation in the square root of the flight initiation distance (n = 37 subjects)

Factor	B	p-value	Partial eta squared
Starting distance (m)	0.027	0.000	0.521
Substrate		0.097	0.149
Stones and talus	5.348	0.000	0.491
Dirt and short vegetation	5.448	0.000	0.618
Tall vegetation	8.254	0.000	0.522
Initial activity		0.070	0.109
Foraging	−2.497	0.070	0.109
Standing and looking	0		
No. conspecifics within 10 m	−0.544	0.059	0.118
Escape incline (°)	0.025	0.301	0.037
Distance to burrow (m)	0.036	0.330	0.033

The model significantly explained 96% of the variation.

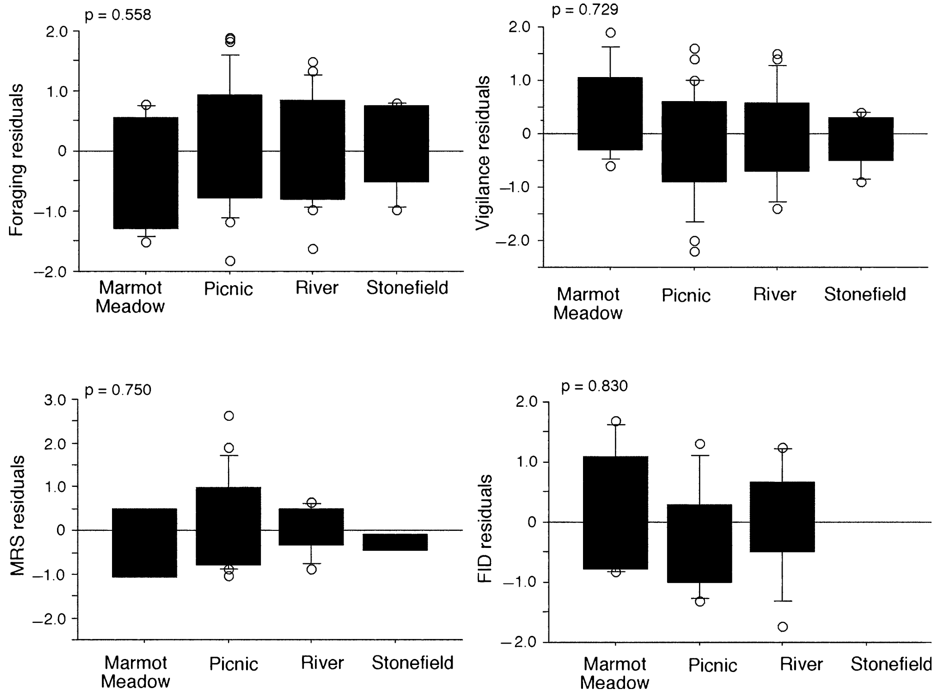

Fig. 3: Box plots illustrating the standardized residuals from the general linear models (time allocated to foraging and vigilance, maximum running speed and flight initiation distance) used in the subsequent correlative analyses. There were no significant differences in the standardized residuals from the linear models across sites. p-values are from Kruskal–Wallis non-parametric ANOVA

focals). Because observers aimed to conduct focals on any animal seen foraging, this result suggests microhabitat selection; a detailed study of which remains to be conducted.

Discussion

Examining the link between locomotor performance and both FID and time allocation demonstrates one way in which studying multiple behaviors, and designing studies to identify behavioral syndromes, enriches our understanding of antipredator behavior. Our results suggest that yellow-bellied marmots have a 'locomotor ability-wariness while foraging' syndrome. We found that yellow-bellied marmots modified their behavior in ways that suggested that they were sensitive to predation risk, and seemingly attempted to minimize their risk while foraging. Marmots minimized their time in exposed locations and animals that ran slower than expected, foraged more intently.

Marmot maximum running speed was influenced by the substrate they ran across, but surprisingly not much by incline or the distance they were from the burrow when experimentally timed. Substrate has been demonstrated to influence maximum running speed in other species. Incline has no effect on locomotor performance for very small mammals (Taylor et al. 1972), but does for slightly larger body-sized marmots (Blumstein 1992). It is possible that yellow-bellied marmots are below the body-size threshold where incline influences locomotor costs, or that our data may be insufficient to properly address the question. While our data included a range of inclines (−50°, +35°), the average incline was negative ($\bar{x} = -3° \pm 18.4$). More importantly, marmots appeared reluctant to run uphill. On many occasions, when we tried to encourage a marmot to escape uphill to an adjacent burrow, it ran between our legs to a more distant burrow located downhill or along flatter areas. Thus, we expect that marmots do perceive running uphill as a potentially risky mode of escape, and we expect that individuals should be aware of their relative location while engaged in other activities (*sensu* Blumstein 1998).

Furthermore, marmots foraged more intensely – by looking less and foraging more during bouts of foraging – when on steep slopes and when in larger groups. Therefore, despite our maximum running speed results, marmots may in fact perceive steep slopes as a potentially risky place to forage and seek to minimize time on slopes. An alternative explanation for this pattern is that visibility, and therefore the ease of detecting predators is greater on slopes and thus, despite the potential locomotor cost, marmots perceive slopes as a relatively safe location. Aggregating with others may reduce the risk of predation in several ways (dilution: Hamilton 1971; detection: Pulliam 1973; security: Dehn 1990). Foraging group size has been previously demonstrated to affect time allocation in yellow-bellied marmots (Carey & Moore 1986), while there is a limited effect of social group size on time allocation in golden marmots (Blumstein 1996). External environmental variables, however, explained much less variation in time allocation than for FID and maximum running speed, and the relatively large intra-class correlation coefficient suggests that there are intrinsic individual factors that explain additional variation. Armitage et al. (1996) found significant age and sex effects on overall patterns of time allocation, and it is likely that animals of different social status, size, or age may employ different strategies to manage predation risk (e.g. Werner & Gilliam 1984; Longland & Jenkins 1987; Cooper et al. 1990; Hanson & Coss 1997).

Group size, initial activity, and substrate explained variation in FID. The fact that animals with more conspecifics within 10 m tolerated closer approaches, suggests they perceived 'safety in numbers'. These findings could be interpreted in two ways, and await experimental manipulation to properly interpret. On the one hand, the relative cost of fleeing a foraging patch might be relatively great. In support of this interpretation, once a marmot flees to a burrow it may take many minutes for it to emerge and resume foraging. Alternatively, foraging marmots may have been less able to detect an approaching person. Such attentional costs of foraging have been reported in other species (Dukas 1998; Dukas & Kamil 2000). However, in contrast to this finding, while foraging, golden marmots responded almost immediately to played back alarm calls (Blumstein 1998). More importantly, yellow-bellied marmots allocated time to vigilance when foraging in tall vegetation and thus attention, per se, may not be the factor that explains the difference in FID with respect to initial activity. It is possible that the yellow-bellied marmots habituated to our experimental approaches. While we selected only a single flush to use in these analyses, subjects inevitably were exposed to people during trapping and while other individuals were flushed. A detailed study of habituation with these marmots (Runyan & Blumstein in press) found that some subjects seemingly habituated (i.e. with subsequent human visits FID decreased), while other individuals did not. Regardless, each subject contributed only a single observation to our data set and any effects of habituation would be obscuring, not confounding. In lieu of experimental evidence to the contrary, it seems likely that the relative cost of flight (Ydenberg & Dill 1986; Blumstein 2003) explains why foraging marmots tolerate close approaches.

Interestingly, and in contrast to previous studies of a congener (Bonenfant & Kramer 1996), yellow-bellied marmots were not sensitive to the distance they were from their burrow when escaping (also see Runyan & Blumstein in press). Yellow-bellied marmots are more social (Blumstein & Armitage 1998; Armitage & Blumstein 2002) than the mostly solitary woodchucks (*M. monax*) studied by Bonenfant and Kramer, and marmots are thus able to reduce risk by associating with others. Woodchucks may have to be more sensitive to the distance they are from their burrows because they cannot rely on conspecifics warning them or diluting predation risk.

Yellow-bellied marmot running speed, time allocation while foraging, and FID were systematically influenced by factors that influence predation risk in marmots and other species. Marmots appeared to minimize exposure while foraging as relatively slow animals foraged more intensively. Yellow-bellied marmots reduce overall exposure to predators (Blumstein 1998) by reducing the time they must allocate to bouts of foraging in potentially risky microhabitats, and they do so by foraging intensely when away from cover. This is unlike fox squirrels (*Sciuris niger*), and gray squirrels (*S. carolinensis*), which are generally wary when far from cover (Newman et al. 1988; Brown et al. 1992; Bowers et al. 1993), but similar to guinea pigs (*Cavia aperea*), which forage more when away from cover (Cassini 1991).

While marmots fled at greater distances in microhabitats that had limited visibility, there was no relationship between FID and other studied variables. Initially, this finding seems counter-intuitive because theory predicts that packages of antipredator behavior should co-evolve and, at a genetic level, be linked (e.g. Sih et al. in press; D. T. Blumstein et al., unpubl. data).

Repeatability, however, sets an upper limit on heritability (Falconer 1981; Boake 1989), and when it is low, we expect that extrinsic factors, such as substrate, group size, incline, etc. will have a large effect on behavior. The low intra-class correlation coefficients argue against a large heritable component to these activities. In golden marmots, repeatability for maximum running speed was similarly low (Blumstein 1992), but we have no comparable data from other species with which to assess repeatability for time allocation or FID.

In conclusion, we have identified a 'locomotor ability-wariness while foraging' syndrome. Future research will be required to identify the proximate causation and fitness consequences of this syndrome. In general, we believe our use of residuals to identify behavioral syndromes will be useful in future studies.

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