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Quantifying Predation Risk for Refuging Animals: A Case Study with Golden Marmots

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Abstract

Although a variety of behaviors expose animals to some risk of predation, there is no accepted way to compare their relative risk. For animals that retreat to refugia when alarmed by predators, the proportion of time devoted to each out-of-refuge behavior multiplied by the total time required to return to a refuge can be used to compare a behavior's relative predation risk. Total time to return to a refuge is a function of both response time – the time required to respond to an increased risk of predation — and travel time — the time required to flee to a refuge once alarmed. Quantifying these components can illustrate how animals minimize exposure to predators. Golden marmots (*Marmota caudata aurea*) were a refuging prey species used to examine the utility of this measure and to understand how marmots minimized their risk of exposure to predation. Golden marmots devoted different amounts of time to looking, foraging, self-grooming, and playing. To estimate the behavior-specific time required to return to refugia, the location of different activities was noted and a behavior-specific travel time was calculated. Alarm calls were played back to marmots engaged in different behaviors to determine, in a standardized manner, if there were behavior-specific response times. Marmots appeared to minimize their predation risk by performing most behaviors close to refugia. Results suggest that foraging was the riskiest behavior, largely because marmots foraged far from refugia and spent about 30% of their time foraging. While sample sizes were small, results also suggested that play, a rare adult behavior, exposed animals to predation because of a relatively long response time.

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Introduction

Behavior exposes animals to some risk of predation, but we know little about the relative riskiness of different behaviors. At least three lines of evidence suggest that behavior may differentially expose animals to an increased risk of predation: direct observations of animals engaged in certain behavior being preyed upon by predators (e.g. play, Harcourt 1991; begging, Redondo & Castro 1992), studies where behavior is influenced by the addition or removal of predators (e.g. mate choice, Godin & Briggs 1996; foraging, Stephens & Krebs 1986), and studies where animals engaged in a particular behavior have compromised vigilance (e.g. allogrooming, Maestripieri 1993; escalated fighting, Jakobsson et al. 1995; forag-

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ing, Krause & Godin 1996). To understand the relative importance predation may have played in selecting for current behavior, we need to go beyond simply documenting an effect of predation on a behavior – we need to study each behavior's 'relative' predation risk. Unfortunately, in lieu of directly observing predation, there is no accepted way to compare the predation risk of different activities. In this paper, I first develop an indirect way to conceptualize the relative riskiness of behavior for animals that escape pursuit predators by retreating to refugia. Then, I apply the method to the study of four behaviors exhibited by golden marmots (*Marmota caudata aurea*) to understand how marmots minimize these predation risks.

Exposure — A Metric of Relative Predation Risk

Predation risk, the probability of being killed by a predator over a specific time interval, is a function of three components: the encounter rate between the predator and the prey, the probability of death given an encounter, and the time spent vulnerable to attack (Lima & Dill 1990). Each of these can be subdivided into additional components, only some of which are under the prey's control. For instance, the encounter rate and the probability of death given an encounter may be more a function of a predator's behavior and hunting efficiency (e.g. Schaller 1972). Prey, however, can modify the time they spend vulnerable to an attack. The question is, how do we quantify the relative vulnerability of animals engaged in different behaviors?

For prey that use refugia to escape predators, the time required to reach a refuge is an important component of predation risk that influences the time spent vulnerable to attack (e.g. Barnard 1980; Caraco et al. 1980; Lima 1985, 1987; Dill & Houtman 1989; but also see Valone & Lima 1987). The time to reach a refuge has at least two components. First, an animal must respond to an increase in predation risk: I refer to this as 'response time' (see also Lazarus 1979). Operationally, I define response time as the time it takes to begin moving in response to a played-back alarm call. Response time thus includes detection time and orientation latency, but is only observable when an animal has an overt orienting response. Second, an alarmed animal must travel to a refuge: I refer to this as 'travel time'. The 'total time' to reach a refuge is the sum of response time and travel time.

Distance to a refuge generally is assumed to be related directly to the time to safety. This assumption implies that response times are of negligible importance and can be ignored. Ignoring response times would be appropriate if response times were constant, or if response times were very small in relation to travel times. While these assumptions have not specifically been tested, there is evidence that the first assumption is not supported. Jakobsson et al. (1995) recently reported that a willow warbler's (*Phylloscopus trochilus*) time to respond to the presence of a stuffed owl depends on the warbler's behavior. Moreover, the large literature on response/flight distance suggests that a variety of factors influence responsiveness and these factors may also influence response time (e.g. type of predator, Walther

1969; nutritional status of prey, Altmann 1958; reproductive status, Bauwens & Thoen 1981; prey group size, Siegfried & Underhill 1975; distance to a refuge, Dill & Houtman 1989). Finally, individuals engaged in certain behavior are less vigilant and may be less able to respond to predators (e.g. Maestripieri 1993; Cords 1995).

Predation risk, or exposure to predators, of different activities can be studied by quantifying the time animals are vulnerable to predation. For refuging animals, vulnerability is a function of the time spent away from their refugia, and the time required to return to a refuge. To calculate the relative risk of a behavior performed away from a refuge, exposure (E_i) is a function of the proportion of time allocated to that behavior (p_i), the time it takes an animal engaged in that behavior to respond to an increase in predation risk (t_{r_i}) and, once alarmed, the time it takes to travel back to its refuge (t_{e_i}). Formally,

$$E_i = p_i * (t_{r_i} + t_{e_i}). \tag{1}$$

Because velocity (v) = distance (d)/time (t), solving for travel time shows that

$$E_i = p_i * (t_{r_i} + d_i/v_i). \tag{2}$$

For any behavior performed away from a refuge (i.e. any behavior with a nonzero t_r or t_e), individuals could reduce their exposure to predators several ways; those ways not under a prey's control can be viewed as constraints on managing predation risk. First, if prey can decrease the time allocated to performing behaviors away from refugia (p_i), they can reduce their exposure while engaged in that behavior. This may not always be under an individual's control. For instance, hungry animals may need to forage more, not less, and by foraging more (Stephens & Krebs 1986) or more intensely (Godin & Smith 1988), they may increase their exposure to predators.

Second, if prey can decrease their response time (t_{r_i}), they can reduce their exposure. While there is a rich literature on factors that influence human response time dating back over a century (e.g. Obersteiner 1879; James 1890), which has most recently focused on principles of ergonomic design (e.g. Woodson 1981; McCormick 1982; Kroemer 1994), there is less information on factors influencing response times for nonhumans under natural conditions (but see Greig-Smith 1981; Jakobsson et al. 1995). Response time is influenced by the amount of attention devoted to performing a particular task. Neurophysiologists and psychologists who study attention view it as a fixed entity that can be divided but not increased (Roitblat 1987; Dukas & Ellner 1993; Laberge 1995). Thus, it is impossible to focus attention on one task while maintaining a previously high level of attention on another task. In humans, response time is also influenced by factors such as anticipation, practice, and the probability of a signal appearing (Woodson 1981). For nonhumans, it is likely that certain behaviors may be mutually incompatible with assessing predation risk. For instance, Southern fur seals (*Arctocephalus australis*) appear to have reduced vigilance, and a correlated increased predation rate, when playing (Harcourt 1991). Other social behavior, which by its nature requires the coordinated actions of at least two individuals, may similarly reduce the ability of an individual to attend to novel and potentially threatening stimuli simultaneously (e.g. Jakobsson et al. 1995). If individuals respond as soon as they can to the presence of a predator, and if response time is behavior-specific, then response time may be a constraint animals have to work around to minimize exposure.

Third, if individuals can either decrease the distance they perform a given behavior from the nearest refuge (d_i) and/or increase their escape velocity (v_i), they can reduce their exposure by reducing travel time (t_{e_i}). For some activities, the distance to the nearest refuge may be constrained. Animals may have to forage some distance away from a refuge because the area around the refuge may be trampled or otherwise be less productive (Hamilton & Watt 1970). Play may be restricted to certain suitable locations (Berger 1980). For those activities less tied to a specific location, performing them closer to a refuge should minimize risk. But distance to a refuge alone is not the appropriate way to estimate predation risk. Many extrinsic and intrinsic factors can influence escape velocity (e.g. Blumstein 1992; Clarke et al. 1993; Bonenfant & Kramer 1996). Theory predicts that animals should modify their escape behavior (Ydenberg & Dill 1986) and may modify their escape velocity (Dill 1990; Bonenfant & Kramer 1996) to reduce predation risk. Ultimately, the time it takes to reach a refuge is the appropriate way to estimate predation risk.

Other factors not under a prey's control may increase exposure associated with a particular behavior. Some of these are a function of the predator's behavior. For instance, predators may have preferences for attacking animals engaged in certain behaviors or living in certain aggregations (e.g. Fitzgibbon 1989; Krause & Godin 1995, 1996). Behavior, or a specific morphology associated with it, may also be differentially conspicuous to predators (e.g. nuptial coloration, Olsson 1993; clutch size, Svensson 1995). Finally, certain behavioral patterns may physically prevent animals from immediately responding to an increased predation risk (e.g. copulatory locks in canids, Beach & Lebouf 1967).

Exposure and Predation Risk Management by Golden Marmots

To study exposure and predation risk management, I asked the following five questions about four behaviors exhibited by adult golden marmots, standing-and-looking, foraging, self-grooming, and play. First, how much time do marmots allocate to each behavior? Second, are different activities performed at different distances from burrows? Third, does behavior differentially influence response time? Fourth, how long does it take marmots to return to a refuge if alarmed while engaged in a given behavior? Fifth, does behavior differentially influence exposure to predation risk? By addressing these questions, I demonstrate both that behavior may differentially contribute to predation risk and that marmots appear to minimize behavior-specific predation risk in different ways.

The golden marmot, a 3–5 kg Old World sciurid rodent, is an ideal species for the study of antipredator behavior and predation risk management. It is eaten by a variety of terrestrial and aerial predators including Tibetan red foxes (*Vulpes vulpes montana*), wolves (*Canis lupus*), snow leopards (*Panthera uncia*), golden eagles (*Aquila chrysaetos*), and possibly bearded vultures (*Gypaetos barbatus*) (Roberts 1977; Blumstein 1994, 1995a; Blumstein & Robertson 1995). All of these predators often pursue their prey, and in response to these predators, golden marmots, like all other marmot species (Blumstein & Armitage 1997b), emit alarm calls. Additionally, marmot burrows are easily identified refugia to which they generally run to escape predators. Marmots have two types of burrows. Escape burrows are shallow, single-entrance burrows scattered throughout their home range. Main burrows are deep, multiple entry burrows in which they sleep.

Methods

Study Site

Adult golden marmots were studied at Dhee Sar (36°81′N, 74°95′E; elevation 4100–4300 m) in Pakistan's Khunjerab National Park for 514 d from 1989 to 1993 during their 4—5 mo active season between late Apr. and late Sep. Marmots live in generally contiguous social groups containing two to seven adults along with younger individuals on home ranges averaging about 3 ha (Blumstein & Arnold 1998). Between 94 and 188 marmots ($\bar{X} = 120$) were studied annually. Some individuals were studied for more than one year. Marmots were trapped, individually marked with ear tags (for permanent identification) and fur dye (for temporary identification that lasted until the annual molt), and systematically observed from hides (100–500 m away) using a combination of scan and focal animal samples between 05.00 and 10.00 h. All experiments were conducted during the same time of day to control for time-dependent variation in responsiveness and/or predation risk.

How Much Time Do Marmots Allocate To Each Behavior?

To calculate time budgets I conducted 10-min. focal animal samples on selected adult marmots and recorded the initiation and termination of all bouts of looking, foraging, self-grooming, playing, and aggression. Observations were taken with a portable microcomputer (Tandy 102), and the duration of each behavior was calculated from the focal record. Results from all focal observations for the same individual were averaged by yr and then across yr to generate a single value for each individual. This value was then used in subsequent analyses of activity budgets. The total time focal marmots were in sight was used as the denominator when calculating proportions of time engaged in each behavior (Bekoff & Byers 1992).

Where Do Marmots Perform Each Behavior?

To determine where marmots performed different behaviors, assistants and I used a detailed ground area map and recorded the identity, activity, and exact location of individual marmots on an 17.2 ha flagged grid during 30-min scan samples during morning observation periods. Observer accuracy in locating marmots on the flagged grid was high (error = 1.27 m ± 0.61 SE, n = 3 observers, n = 25 test locations per observer). Marmots retreated to both types of burrows—

main and escape—when alarmed. In 1993, all focal marmots observed returning to a burrow following an alarm call given by other marmots, returned to a main burrow (n = 15), suggesting that main burrows were preferred refugia. However, marmots were occasionally observed fleeing initially to an escape burrow.

For each behavioral observation, I calculated the distance from the marmot to the nearest burrow and the nearest main burrow entrance. Using SuperAnova (Abacus Concepts Inc. 1991), I tested for differences between the distances at which each behavior was performed. To control for individual effects, I blocked by subject.

To place these observed results into proper perspective, I pooled all behavioral observations and compared the distances at which they were performed to 900 randomly selected locations on the grid.

Does Behavior Influence Response Time?

To study response time of marmots engaged in different behaviors, I played back '5-note' alarm calls to golden marmots engaged in different behaviors and videotaped their responses with a 8 mm camcorder (Sony SP-7) fitted with a telephoto lens (detailed description of golden marmot alarm calls, playback equipment, and procedures in Blumstein 1994, 1995b,c). Briefly, the number of notes per call covaried with degree of risk a caller experienced when it called; 5-note calls were elicited under relatively high-risk situations (Blumstein 1995b). All experimental calls were minimally degraded calls recorded in response to humans. Playbacks of these calls elicit alarm responses in marmots while playbacks of 'control' bird song tend to elicit nonalarm responses (Blumstein 1995c). I focused on four marmot behaviors: (1) quadrupedal standing-and-looking, (2) foraging, (3) sitting and self-grooming, and (4) playing – which included both locomotor play where one subject chased another, and rough-and-tumble play where one subject reared up on its hind legs and boxed and/or rolled around with another subject. Playing subjects frequently switched roles. Reciprocity and the outcome distinguished play from aggressive behavior.

The probability of habituation to experimental alarm calls was minimized by (1) using 10 different alarm call exemplars, (2) conducting no more than one playback per day, well below the 6–22 bouts of alarm calls/day marmots naturally heard (Blumstein 1995b), (3) conducting playbacks to different groups on successive days, (4) using camouflaged speakers, and (5) not using the same speaker placement on successive playbacks to a group. I tested for habituation by correlating the date of the experiment with the response time. There was no indication of habituation to the experimental alarm calls or the experimental set up, and the correlation between experiment date and response time was not significant ($r_s = -0.13$, $p = 0.549$, $n = 23$). Because marmots routinely responded to alarm calls from both social group members and from nongroup members, my use of random exemplars is justified.

Golden marmots naturally produced loud ($\geqslant 100$ dB) alarm calls, but the perceived intensity was a function of the distance between a caller and a perceiver.

Since response to alarm calls may vary as a function of call intensity (Leger et al. 1979; Hutson et al. 1993; Blumstein & Armitage 1997a), I adjusted line levels on the tape deck, line amplifier, and powered speaker until the sound pressure level 0.1 m in front of the speaker was between 100 and 104 dB (measured using a Realistic model 33–2050 sound level meter, ±5 dB accuracy), and I attempted to conduct playbacks to marmots who were $\approx$20 m from the camouflaged speaker. Despite my best attempts to control these variables, marmots generally did not perform a target behavior in the desired location and it was extremely difficult to conduct these experiments. The following variables were recorded and used in subsequent analyses: (1) the distance between a subject and the speaker, (2) the distance between a subject and the nearest main burrow, and (3) the actual sound pressure level at the speaker.

Response time was defined as the time from the beginning of the alarm call to a marmot's first head movement and was measured from single-frame analysis of the video record (temporal resolution = 33 ms). Playbacks to animals engaged in social play generated two nonindependent response times. I averaged these two response times and used the average in subsequent analyses. I randomly selected one observation per individual if there were repeated observations.

Using SuperAnova (Abacus Concepts Inc. 1991), I fitted a linear model (ANCOVA) to study variation in response time; the model contained the following five independent variables hypothesized to influence response time: (1) behavior, (2) the distance between the marmot and the speaker, (3) the distance between the marmot and the main burrow, (4) the sound pressure level at the speaker, and (5) the subject's sex. I used a backward stepwise algorithm to delete variables with the least significant Type III sum of squares having a $p > 0.1$. Planned comparisons compared the coefficient estimates for different behaviors against standing-and-looking. I chose standing-and-looking as a 'baseline' behavior because standing-and-looking animals are vigilant and appear alert and responsive. Response times were log-transformed prior to statistical analysis to meet distributional assumptions of linear models; residuals from linear models were examined visually.

How Long Does it Take Marmots to Return to a Refuge if Alarmed while Engaged in a Given Behavior?

To determine how long it took marmots engaged in different activities to return to burrows, I used the distribution of activity in space and an equation generated from a previous study to estimate travel time. I used the overall distribution of distances to burrows to estimate travel time rather than measuring travel time off the videotape for two reasons. First, if marmots were very close to a burrow they had no need to run back to it. Thus, not all playbacks elicited maximum bursts of running. Second, and more importantly, I wanted precise and accurate estimates of the distance to refugia, and therefore needed many more behavioral observations. Observing marmots throughout their active season generates very accurate annual estimates of the distance from burrows where behaviors are performed. By looking at annual averages, I am aware that marmot behavior varies seasonally (e.g. Barash 1976) and that marmots may seasonally vary where activities are performed. Golden marmots' maximum running speed (MRS) is influenced by substrate, distance, incline, and sex (Blumstein 1992). Marmots run faster across vegetated substrate, over longer distances, and when going down inclines. Females run slightly faster than males. To estimate the time it took adult male marmots to reach a burrow at a given distance across flat, stony surfaces, I used the following equation (from Blumstein 1992):

$$T = 0.3713 * d - 0.0030 * d^2 \tag{3}$$

where T = travel time in s, and d = distance run in m. It is important to point out that this method to calculate travel time assumes that animals immediately accelerate to maximum speed. While the assumption is unrealistic, marmots can accelerate quickly (pers. obs.), thus the magnitude of any acceleration effect is probably inconsequential. There may be situations when acceleration is known or thought to be an important component of travel time to reach a refuge. In these instances, acceleration should be studied in detail and included in the calculation of total time.

Does Behavior Differentially Influence Exposure to Predation Risk?

For each behavior, I estimated exposure, E_i, by summing the estimated travel time (t_{r_i}) and the response time (t_{e_i}) to generate a behavior-specific total time. This total time was then multiplied by Pi, the percentage time marmots allocated to each behavior.

Results

How Much Time do Marmots Allocate to Each Behavior?

Adults spent most of their time looking (43% of time), foraging (30%), or engaged in other behavior (primarily locomotion, 26.2%), and proportionally little time self-grooming (0.5%) or playing (0.3%). These results are based on a total of 45.6 h of focal animal samples made on 13 adult marmots (9 males, 4 females). Marmots were out of sight (behind objects or in their burrows) 9% of the time during focal samples.

Where do Marmots Perform These Behaviors?

All observations from 15 different marmots collected from 1989 to 1992 were averaged by yr and across yr to generate a distribution of distances to the nearest burrow and the nearest main burrow (Fig. 1). Fifty-percent of all marmot activity was within 4 m of the nearest burrow and 11 m of the nearest main burrow. Virtually all activity (99%) was within 50 m of the nearest burrow; 84% of all activity was within 50 m of the nearest main burrow.

The fact that marmots were typically not far from burrows was expected given the plethora of burrows (Fig. 2). However, marmots were significantly closer to burrows than expected by chance. The average (±SD) distance to the nearest

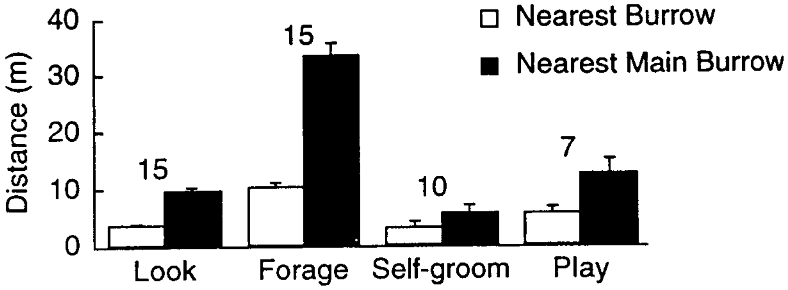

Fig. 1: Observed mean distances (± SE, n marmots) that different behaviors were performed from the nearest burrow or main burrow

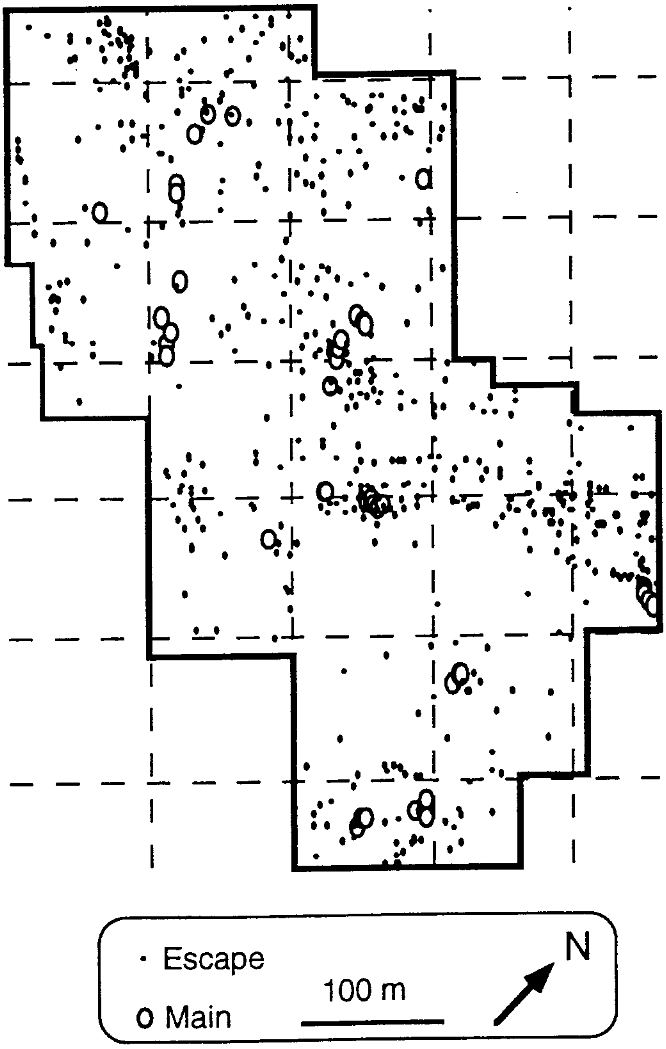

Fig. 2: Distribution of escape (dots) and main (circles) burrow entrances on the 17.2 ha flagged grid

burrow for all above-ground marmot behavior was 7.6 m (±6.7, n = 4350 observations); significantly less than the 12.6 m (±8.3) for 900 randomly selected points (Kolmogorov-Smirnov $\chi^2 = 281.9$, df = 2, $p < 0.0001$). I truncated all observations greater than 100 m from the nearest main burrow because there were other main burrows off the mapped area. For this smaller data set, the average (±SD) distance to the nearest main burrow for all above-ground marmot behavior was 20.2 m (±29.9, n = 4307 observations); significantly less than the 49.6 m (±23.9) for 844 randomly selected points (Kolmogorov-Smirnov $\chi^2 = 773.2$, df = 2, $p < 0.0001$).

Marmot identity and behavior explained 63% of the variation in the observed distance to the nearest burrow (adjusted $R^2 = 0.631$, identity $p = 0.013$, behavior $p = 0.0001$, model $p = 0.0001$), and 62% of the variation in the distance to the nearest main burrow (adjusted $R^2 = 0.619$, identity $p = 0.249$, behavior $p = 0.0001$, model $p = 0.0001$). In both cases, foraging was performed at a significantly greater distance than any of the other behaviors (p-values < 0.05). Behavior alone explained 46% of the variation in the distance to the nearest burrow (adjusted $R^2 = 0.455$, $p = 0.0001$), and 58% of the variation in distance to the nearest main burrow (adjusted $R^2 = 0.584$, $p = 0.0001$).

Does Behavior Influence Response Time?

Twenty-three playbacks from 16 different individuals were statistically analyzed (Fig. 3). The final data set consisted of observations made in 1991 and 1992 of marmots standing-and-looking (n = 8), foraging (n = 7), self-grooming (n = 5), playing (n = 3 pairs). Marmots averaged 18.2 m (±1.95 SE) from the speaker and 1.6 m (±0.54 SE) from the nearest main burrow. The sound pressure level of the playback averaged 101 dB (±0.80 SE). Overall, marmots took 0.83 s (±0.26 SE) to respond to the playback.

Behavior, the distance between the marmot and the closest main burrow

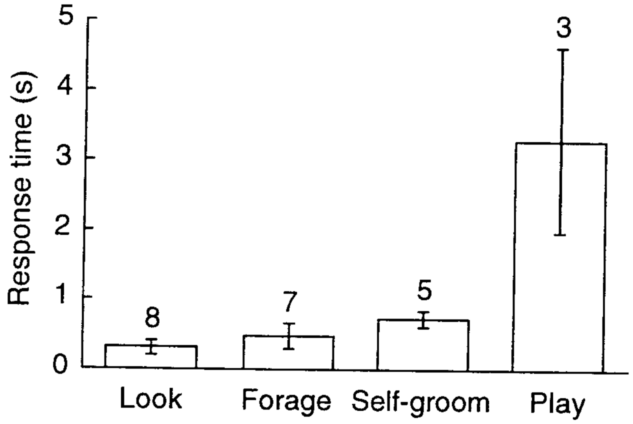

Fig. 3: Mean response times (s) (±SE, n marmots, n = pairs of playing marmots) for marmots engaged in different behaviors to respond to played back alarm calls. Statistical analyses conducted on log-transformed response times

(hereafter 'distance'), and the sound pressure level at the speaker (hereafter 'call volume') together significantly explained 63% of the variation in response time (adjusted $R^2 = 0.63$, $p = 0.0004$). Distance and call volume had significant negative coefficient estimates (distance = -0.068, $p = 0.028$; source dB = -0.063, $p = 0.012$), suggesting that marmots farther from main burrows responded faster than marmots closer to main burrows and that louder calls generated shorter response times than softer calls. Playing marmots took significantly longer to respond to alarm calls than standing-and-looking marmots ($p = 0.0001$). Response times for standing-and-looking were not significantly different from those for foraging ($p = 0.779$) or self-grooming ($p = 0.066$).

Partial correlation analysis revealed that behavior was most highly associated with response time (distance × response time $r_{partial} = 0.46$; call volume × response time $r_{partial} = 0.53$; behavior × response time $r_{partial} = 0.79$). Moreover, the addition of behavior to a model of call volume and distance explained considerably more variation (R^2-change = 0.63) than additions of call volume to a model of behavior and distance (R^2-change = 0.14), or than the addition of distance to a model of behavior and call volume (R^2-change = 0.10).

From these results I conclude that behavior, call volume, and the distance a subject is from a main burrow significantly influence response time. Anecdotal observations strengthen two of these conclusions. Vigilant, foraging, and self-grooming marmots appeared to respond quickly to natural alarm calls. I watched two playing marmots not respond to the first of several alarm calls. During a pause between play bouts, they immediately looked in response to a subsequent alarm call. Moreover, marmots appeared more likely to respond to the louder alarm calls emitted from callers in their social groups or neighboring social groups, and less likely to respond to the softer calls from callers in distant social groups.

How Long Does it Take Marmots to Return to a Refuge if Alarmed while Engaged in a Given Behavior?

By definition, the travel time to the nearest burrow mirrored the distance to the nearest burrow (Fig. 4). To these estimated travel times, I added response times

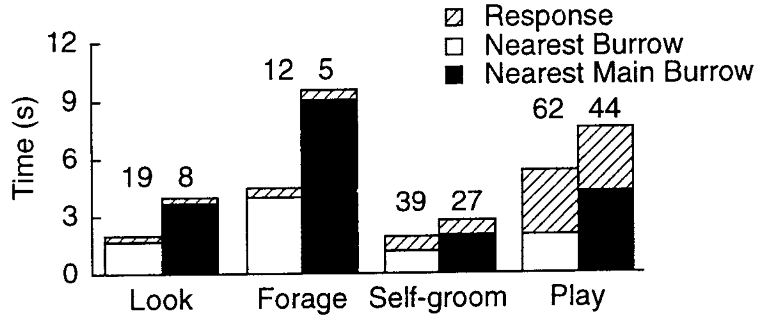

Fig. 4: Predicted total times to reach the nearest burrow and main burrow broken into its components: response time, estimated travel time to the nearest burrow, and estimated travel time to the nearest main burrow. Numbers above each histogram are the percentage of the total time that was response time. Travel times were predicted using eqn 3 (see text)

to generate the estimated total time (Fig. 4). Response times accounted for a variable, but often substantial, component of the total predicted time to reach a refuge. Response time was 12–62% ($\bar{X}$ = 36%) of the total predicted time to reach the nearest burrow, and 8–44% ($\bar{X}$ = 22%) of the total predicted time to reach the nearest main burrow.

Does Behavior Differentially Influence Exposure to Predation Risk?

When calculated with respect to the distance to either the nearest burrow or the nearest main burrow, exposure varied as a function of behavior (Table 1). Self-grooming and play behavior both exposed marmots to a relatively limited risk of predation while foraging exposed marmots to a relatively high predation risk.

Discussion

Marmots spent most time foraging and did not perform behaviors equidistant from refugia. While sample sizes are small, it appears that behavior influenced response time. Notably, playing marmots had significantly longer response times than looking marmots (whose response times did not differ from those for foraging marmots). Refuging animals are, by definition, safe inside refugia. Any and all time spent outside a refuge is risky. Thus, common 'outside' behaviors expose individuals to a greater risk of predation than rare 'outside' behaviors.

Behavior may, however, be risky for different reasons, and marmots may use different strategies to minimize exposure when engaged in risky behaviors. For example, marmots minimized exposure by performing most behaviors relatively close to refugia. That they did is consistent with a simple rule of thumb (Blumstein & Bouskila 1996; Bouskila & Blumstein 1992) to assess predation risk: risk increases with distance and/or time from a refuge.

Not all behavior can be performed at a burrow; foraging was risky because marmots foraged far from main burrows. One strategy to minimize foraging's risk is to dig numerous escape burrows (Fig. 2). Holmes (1984) reported 'strategic' burrow digging by hoary marmots (*Marmota caligata*) in response to an experimental treatment that increased forage availability in an area that previously had

Table 1: Estimated exposure to predation risk (E_i) for each of four marmot behaviors as a function of the distance to the nearest burrow and the nearest main burrow

Behavior	E_i to nearest burrow	E_i to nearest main burow
Look	0.697	1.565
Forage	1.197	2.715
Self-groom	0.006	0.010
Play	0.006	0.013

little forage. Compared to other species, golden marmot burrow densities (35.4 burrows/ha over the mapped area) were relatively high. For instance, yellow-bellied marmots (*M. flaviventris*) have about 4.3 burrows/ha (data from Svendsen 1974; Armitage 1988), woodchucks (*M. monax*) have 3.6–6.4 burrows/ha (Henderson & Gilbert 1978; Swihart 1991), hoary marmots have 32 escape burrows/ha (in one well-studied group – Holmes 1979), alpine marmots (*M. marmota*) have 36 burrows/ha (in two mapped groups – Sala et al. 1996), while steppe marmots (*M. bobac*) and Vancouver Island marmots (*M. vancouverensis*) may have densities of 100 burrows/ha in core areas of their home range (D. T. Blumstein unpubl. data).

Another strategy marmots may use to reduce exposure is to be vigilant while foraging. Foraging marmots responded almost immediately to the played-back alarm calls. Unlike playing, foraging appeared not to be incompatible with monitoring peripheral acoustic stimuli.

While previous studies revealed predation costs of juvenile play (Hausfater 1976; Harcourt 1991), the current study is the first to consider predation costs of adult play. The risk of play, however, was not a function of its relative frequency. Rather, the risk associated with playing stemmed from the relatively long response time of playing marmots. This result mirrors the Jakobsson et al. (1995) finding that birds engaged in a complex social behavior are relatively unresponsive to potentially threatening stimuli. Together the results are consistent with an underlying attentional mechanism (Roitblat 1987) whereby animals that focus their attention on conspecifics are less able to respond immediately to potentially threatening stimuli from elsewhere. Thus, social behavior may be risky because it requires a relatively large amount of attention.

Are exposure differences biologically significant? I suggest yes because marmot predators move faster than marmots. While marmots may sprint 3–4 m/s across flat stony substrate (Blumstein 1992), red foxes and wolves sprint as fast as 20 m/s (Terres 1941; Meinertzhagen 1955), and large raptors such as bearded vultures may fly from 35 to 49 m/s (Meinertzhagen 1955). Further, the effect of group size on vigilance behavior is relatively weak (Blumstein 1996) and not all marmots voice an alarm call when a predator or potential predator is present (Blumstein 1995b). Thus, animals in larger groups may not be able to rely on conspecifics to warn them of a sudden increase in risk, and each individual's ability to respond to a sudden increase in predation risk may be crucial. Every fraction of a second may be important for a fleeing marmot.

In conclusion, for refuging prey, both the relative frequency of behavior and how long it takes alarmed animals to return to their refuge influence an individual's exposure to predation. Golden marmots may have reduced their exposure to predators by performing most behavior relatively close to refugia and by increasing their attention devoted to monitoring external stimuli for behaviors performed relatively far from refugia. Future studies of predation hazard assessment and management in refuging species should quantify the time taken by individual animals, engaged in different behaviors, to return to refugia. Such data will advance our understanding of the relative riskiness of different behaviors and on how animals manage these risks.

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