

**Effects of Burrow Distance on Anti-Predator Vigilance in Foraging Yellow-Bellied
Marmots, *Marmota flaviventris***

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Abstract

The risk of predation influences the behavior of individuals and can determine how an animal allocates its time when searching for and obtaining food. To reduce predation risk, many animals use refuges and protective cover to increase their chances of survival, but it is unclear how these safe areas affect anti-predator vigilance behaviors (scanning and looking for predators) when the animal is no longer covered. We experimentally tested the effects of burrow distance on anti-predator vigilance in foraging yellow-bellied marmots (*Marmota flaviventris*) by placing food at increasing distances (1, 5, 10, and 20m) from designated marmot burrows. We measured (1) time latency to forage at feeding stations, (2) reluctance to forage at stations, (3) proportion of time allocated to anti-predator vigilance and foraging, and (4) alert and flight initiation distances in response to an approaching threat. Marmots were reluctant to forage far from the burrow, and time latency to forage increased linearly as distance from the burrow increased. When individuals foraged alone, distance from burrow did not affect the proportion of time allocated to foraging or anti-predator vigilance. However, individuals increased foraging and decreased anti-predator vigilance when 5m from the burrow in the presence of conspecifics. There was no effect of distance from burrow on alert and flight initiation distance. These findings suggest that marmots are equally alert at any distance from burrow, and there may be a distance limit to which social animals rely on others to alert them to predators.

Keywords

Anti-predator vigilance, foraging, distance to cover, burrow distance, refuge, flight initiation distance, predation.

Introduction

Animals must allocate a proportion of their time to anti-predator behavior including looking and scanning for threats. In birds and mammals, such anti-predator vigilance has a direct impact on fitness (Lima and Dill 1990) and can determine the survival of individuals (Bednekoff and Blumstein 2009; Lima and Dill 1990). Because the cost of predation (death) is greater than the lost opportunity to mate or forage, individuals must trade-off the time allocated to maintenance and other activities with anti-predator vigilance (Nonacs and Blumstein 2010). This balance between anti-predator vigilance and searching for food becomes increasingly important for two reasons: first, if it is too wary, it may starve (Inger et al. 2006), and second, foraging requires attention to be diverted away from scanning for threats and often results in a body posture that makes an individual more vulnerable to attack (Krause and Godin 1995). Ultimately, the fitness of an animal depends on its ability to properly assess predation risk and respond accordingly.

An animal's anti-predator vigilance has been shown to be impacted by many factors including food quality and availability (Krivan and Vrkoc 2000), presence of conspecifics (Beauchamp 2009), and patterns of habitat risk (Lima and Bednekoff 1998). In addition to increasing anti-predator vigilance in times of risk, it is common for animals to use refuges as a form of anti-predator behavior (Blumstein and Pelletier 2005; Rhoades and Blumstein 2007). As distance to cover and refuges increases, some organisms increase their anti-predator vigilance (Creel et al. 2008), resulting in a decrease in time allocated to other activities such as foraging. This has been documented in collared pikas (*Ochotona collaris*) that decrease food consumption at greater distances from talus slope refuges (Morrison et al. 2004). The same pattern has been observed in Nubian Ibex (*Capra ibex*, Hochman and Kolter 2007), Dall's sheep (*Ovis dalli dalli*,

Frid 1996), elk (*Cervus elaphus*, Liley and Creel 2007), white throated sparrows (*Zonotrichia albicollis*, Schneider 1984), white-browed sparrow-weavers (*Plocepasser mahal*, Fong et al. 2009), and semipalmated sandpipers (*Calidris pusilla*, Beauchamp 2010). Cape ground squirrels (*Xerus inauris*, Unck et al. 2009) and hoary marmots (*Marmota caligata*, Holmes 1984) also tend to increase anti-predator vigilance and decrease foraging as the distance from their burrows increases.

Alternatively, some animals choose to maximize food intake at the expense of decreased anti-predator vigilance when distance to cover increases. When using this strategy, the animal consumes large amounts of food in a short time period minimizing their exposed feeding time. This strategy has been observed in common wombat (*Vombatus ursinus*, Favreau et al. 2009), quokka (*Setonix brachyurus*, Blumstein et al. 2001), and red-necked pademelon (*Thylogale thetis*, Pays et al. 2009) individuals as well as springboks (*Antidorcas marsupialis*, Burger et al. 2000) and white-crowned sparrows (*Zonotrichia leucophrys gambelii*, Slowtow and Rothstein 1995). While many of these studies have found links between distance foraging from burrow and anti-predator vigilance, there is little understanding of what explains interspecific variation in the anti-predator vigilance strategy used.

We tested the effect of burrow distance on anti-predator vigilance in foraging animals using yellow-bellied marmots, *Marmota flaviventris*, as a model species. Yellow-bellied marmots are social, sciurid rodents that constitute a good study species because they must double their mass during the short vegetation period before entering 7-8 months of hibernation (Armitage et al. 2003). This means that the energetic demand required to ensure a marmot's survival through the winter can only be met while foraging under the threat of predators such as coyote, *Canis latrans*; red fox, *Vulpes vulpes*; American marten, *Martes americana*; badger,

Taxidea taxus; black bear, *Ursus americanus*; red-tailed hawk, *Buteo jamaicensis*; and golden eagle, *Aquila chrysaetos* (Blumstein et al. 2009; Van Vuren 2001). Predation on yellow-bellied marmots is high, with up to 98% of mortality during the summer months attributed to predation (Van Vuren 2001). Yellow-bellied marmots often take refuge in burrows to evade this high predation risk (Rhoades et al. 2007).

We compared the behavior of individually marked adult and yearling marmots foraging at different distances from their burrows and expected to see a reluctance to forage far from the burrow as well as an increase in time latency for the individual to forage at greater distances from refuge due to the increased predation risk. In addition, we expected to see a decrease in the percentage of time individuals allocated to foraging and an increase in the time allocated to anti-predator vigilance as individuals traveled farther from the burrow to forage. A change in the length and number of vigilance and foraging bouts was also expected as the animal foraged in areas of higher risk. When additional marmots were observed within 10m of the foraging marmot, we expected to see differences in its anti-predator vigilance because conspecifics can compete for resources and mates, or they can be beneficial in helping detect predators (Blumstein and Armitage 1998; Burger and Gochfield 1988). We also predicted that there would be age effects on anti-predator vigilance with increased distance from refuge since young individuals are more vulnerable to predation. Finally, we predicted that the high risk of predation far from the burrow would result in increased weariness in marmots which would be made apparent in increased alert and flight initiation distances in response to an approaching threat.

Methods

General Methods

Yellow-bellied marmots were studied at three marmot colonies and along 10 transects in and around the Rocky Mountain Biological Laboratory (38°57'N, 106°59'W), Gunnison County, Colorado, USA, where marmots have been studied since 1962 (Blumstein et al. 2006, Ozgul et al. 2010). Data were collected from late May through early July 2010. Each transect consisted of 4 feeding stations (each a 12.7 x 12.7 x 2.54 centimeter plastic container nailed to the ground) located 1m, 5m, 10m, and 20m from a targeted yellow-bellied marmot burrow. All transects were positioned on flat ground with slopes ranging from 0°-10° and were designed so that no additional burrows came within the designated feeding station distances. Marmots naturally forage at this range of distances from the burrow (personal observations).

Individual yellow-bellied marmots were routinely trapped in Tomahawk Live Traps (Tomahawk Live Trap Co., Tomahawk, WI), handled in cloth bags, ear tagged, and marked using black, nontoxic Nyanzol dye (Albanil Dyestuff Co., Jersey City, NJ) in order to identify the individual while observing from a distance that did not disrupt normal behavior (30-400m depending on the individual and colony site). Individuals were observed and identified using a 15-45x spotting scope. To ensure that marmots fed at specific distances from the burrow, we placed 30g of Omolene 100 horse food (Ralston Purina, Inc., St. Louis, MO) at one feeding station in a random order and began focal recordings as soon as an individual foraged at the station. If only one individual consumed food at the station during the 2 minute focal period, the food was collected and weighed to determine total food consumption. The presence of conspecifics within 10m and 50m of the foraging animal was noted in addition to any alarm calls vocalized during the foraging period. All focal observations were collected before pups emerged

in the social group to ensure that the focal animal's behavior was not affected by the presence of young.

Methods for Measuring Anti-predator Vigilance

Marmots were allowed to forage for 2 minutes at a station while focal observations were recorded. Following Bednekoff and Blumstein (2009), we recorded the onset of an individual marmot's foraging behaviors using a microcassette recorder. Foraging behaviors observed included quadrupedal (stand) foraging, bipedal (rear) foraging, quadrupedal anti-predator vigilance (looking while standing), bipedal anti-predator vigilance (looking while rear standing), walking, running, and miscellaneous behaviors. An animal chewing while looking was considered to be vigilant and not foraging. Recorded focal observations were scored using JWatcher 1.0 (Blumstein and Daniel 2007) to quantify the percentage of time allocated to anti-predator vigilance behaviors and foraging behaviors.

Following Runyan and Blumstein (2004), we measured alert distance and flight initiation distance (FID) as further measurements of risk assessment. After the 2 minute foraging focal, marmots were approached at the feeding station at a constant rate of one 0.5m-step/sec to simulate an approaching threat, and we recorded the distance from the marmot to the approaching person when it first looked in response to the approach (alert distance) and the distance at which it first fled (FID).

In addition to these metrics, we measured perceived risk by noting the marmot's latency to forage (the time between the first sighting of the marmot at the burrow and the moment the marmot began foraging at the station). We also measured the marmot's reluctance to forage at

certain distances from the burrow as measured by the proportion of set feeding stations at 1m, 5m, 10m, and 20m from the burrow that were not visited.

Data Analysis

To assess the reluctance to feed at specific distances from the burrow, we fitted linear and logarithmic models (in SPSS 18.0) to determine the best relationship between feeding station distance, the total number of set stations, and the total number of times stations were set but not visited.

To study time allocation as a function of distance from burrows, we first checked that the results followed a normal distribution by visually checking normal probability plots and by using a Shapiro-Wilk test. We also checked that the variances across treatments were homogeneous by visual inspection of the residuals plots. The latency to forage was $[\log+1]$ transformed in order to improve normality. Then, we fitted linear mixed effects models using the software package R version 2.10.1 (R Development Core Team 2009) to compare: (1) the time latency for an individual to begin foraging at a particular station, (2) the proportion of time each individual spent vigilant, (3) the proportion of time each individual spent foraging, and (4) the flight initiation distance in each of the 4 different treatments. For models 1-3 we considered age class (yearling or adult), sex (male or female), feeding station distance (1, 5, 10, or 20m), and the presence or absence of other marmots within 10m as fixed factors. In all cases, we included the individual identity as a random factor to account for the repeated measurements. We also included the interaction between feeding station distance and the order in which food was presented as well as the interaction between feeding station and presence of other marmots. Whenever the interactions were not significant, they were removed from the final model

(Engqvist 2005). For model 4 (flight initiation distance), we considered alert distance as a covariate and presence of other marmots, age and feeding station as fixed factors. Individual was included as a random factor. The significance of model parameters was estimated by comparisons to a probability distribution obtained by 10,000 Markov-Chain Monte Carlo simulations with the function `pvals.fnc` from package `languageR` (for further details see Baayen et al. 2008).

Results

In 146 hours, we observed 120 foraging bouts at our feeding stations and conducted 90 experimental approaches. Our final data set consisted of focal observations on 25 different foraging yellow-bellied marmot individuals. Twenty different individuals were observed at the 1m station, twenty at the 5m, sixteen at the 10m, and fourteen at the 20m station.

Marmots showed reluctance to forage as distance from burrow increased (log $R^2 = 0.465$, $p = 0.318$ vs. linear $R^2 = 0.582$, $p = 0.237$) with the linear model having the best fit (Figure 1). When alone, the latency for individual marmots to forage at feeding stations increased as the distance from burrow increased (Table 1(a), Figure 2). Here, significant differences were observed between all feeding stations except the second and third (post-hoc tests: Station1m-5m: $\beta = 1.174$; $n = 49$; $p_{\text{MCMC}} < 0.001$; Station1m-10m: $\beta = 1.177$; $n = 53$; $p_{\text{MCMC}} < 0.001$; Station1m-20m: $\beta = 2.047$; $n = 44$; $p_{\text{MCMC}} < 0.001$; Station5m-10m: $\beta = -0.009$; $n = 44$; $p_{\text{MCMC}} = 0.976$; Station2m-20m: $\beta = 1.072$; $n = 39$; $p_{\text{MCMC}} = 0.01$; Station10m-20m: $\beta = 0.771$; $n = 35$; $p_{\text{MCMC}} = 0.018$).

There were social effects on risk assessment. Distance from the burrow had no effect on time allocated to vigilance and foraging when animals foraged alone (Table 1(b,c)). However,

when other marmots foraged within 10m of the focal individual, the individual increased the proportion of time they spent foraging and decreased the proportion of time they spent vigilant at the feeding station 5m from burrow (Figure 3 and Table 1(b,c)).

There was no detectable effect of distance to the burrow on alert distances or flight initiation distance. As expected, alert distance explained a substantial amount of variation in flight initiation distance (Table 2). None of the other variables, covariates (age, sex, or the order in which food was placed at stations), or interactive effects significantly explained variation in any measured dependent variable (Table 1).

Discussion

The purpose of this study was to assess the effects of burrow distance on individuals' anti-predator vigilance strategies using yellow-bellied marmots as a model species. While we predicted that foraging far from the protective cover of a burrow would result in an increase in time allocated to vigilance and a decrease in time allocated to foraging, the experiment found no effect. As predicted, the presence of conspecifics within 10m of a foraging marmot had an effect on the proportion of time allocated to anti-predator vigilance and foraging. This finding is consistent with Frid's (1997) study of Dall's sheep as well as Martella et al.'s (1995) experiment on group vigilance in Greater Rheas (*Rhea americana*). Interestingly, our prediction that an individual's alertness of predation as measured by alert and flight initiation distance would increase as they traveled farther from the burrow to forage was not supported by the data. This suggests that an individual's awareness of predation is constant no matter the distance from refuge.

The relationship seen in an individual marmot's reluctance to forage farther from the burrow and the increased time latency for an individual to forage at greater distances is consistent with the idea that the burrow is protective (Holmes 1984; Rhoades and Blumstein 2007) and viewed as a low-risk area compared to locations farther from a burrow. Also, the individual marmot's reluctance to travel to the stations farthest from protective cover coincides well with many studies including those of Fong et al. (2009) on white-browed sparrow-weavers and Hochman and Kotler's (2007) study of Nubian Ibex vigilance. Both organisms showed the same preference to forage close to safety. This reluctance to forage suggests that individuals assess food at these far distances to be associated with a higher predation risk.

Although marmots interpreted the risk of predation to increase with increased distance from the burrow, the FID data showed that marmots were no more or no less alert to potential predators as they traveled into the higher risk areas farther from the burrow. The consistency in alert distance and flight initiation distance across stations suggests that individual marmots are equally aware of predators and equally responsive to approaching threats no matter the distance they are from a burrow. This lack of distance effect was surprising considering Bonenfant and Kramer (1996) found the flight initiation distance of ground hogs (*Marmota monax*) to increase consistently as individuals moved farther away from a burrow.

Although it is apparent that marmots perceived a greater predation risk farther from the burrow, I found no significant change in the proportion of time the individual spent vigilant and foraging as they traveled alone to higher risk areas. This does not mean that marmots failed to change their anti-predator vigilance strategies in response to an increased predation risk. Rather, it may be that differences in individual personalities and body condition result in individuals using different anti-predator vigilance strategies. Some individuals, for example, may increase

anti-predator vigilance behaviors and decrease foraging when they interpret greater risk (Unck et al. 2009; Holmes 1984). Others may decrease anti-predator vigilance and focus, instead, on maximizing food consumption while decreasing exposed feeding time (Blumstein et al. 2001; Favreau et al. 2009; Pays et al. 2009). These differences between individuals may account for the failure to see a significant change in time allocation for marmots overall as the distance foraging from burrow increased. The difference among individuals could also explain the lack of significant change between the anti-predator vigilance strategies of adult marmots and yearlings as distance from refuge increased.

When additional marmots were within 10m of the focal animal, there was no significant change in the proportion of time allocated to anti-predator vigilance and foraging with the exception of the 5m station. Here, the focal individual significantly increased the proportion of time allocation to foraging and decreased the proportion of time allocated to anti-predator vigilance. This pattern has been well documented in many species of birds and mammals (Roberts 1995). This change in time allocation suggests a nonlinear relationship in how marmots rely on others for assistance in detecting predators. At a distance directly next to refuge (the 1m distance from burrow for example), the foraging individual may not need to rely on the vigilance of others to escape which could explain the non-significant change in vigilance and foraging time allocation. When foraging at moderate distance from burrow, however, individuals may find it beneficial to rely on the vigilance of conspecifics (Roberts 1995). This pattern could emerge because, at these distances, the alerts of others could substantially reduce the time it takes the individual to return to a burrow (Pulliam 1973; Powell 1974; Dehn 1990). Because of this social safety net, the individual can afford to increase foraging and decrease anti-predator vigilance. Yet at greater distances (such as the station 10m from burrow), marmots may no longer benefit

from the vigilance of others because this would not substantially reduce the total time to return to safety (Roberts 1995). Overall, it appears that at a certain distance from refuge, yellow-bellied marmots will stop benefiting from the alerts of others and rely only on their own anti-predator vigilance for survival. This suggests that there is a distance limit in which a marmot individual will rely on conspecifics to alert them to threats.

This non-linear relationship in reliance on conspecifics could be related to body size and running speed because these factors can influence the amount of time an individual can afford to spend in risky situations. Marmots, for example, can run at a speed of approximately 4 m/s (Blumstein et al. 2004) in short vegetation, meaning that it takes less than a second for them to enter the burrow at 1m, 1-2 seconds to reach the burrow at a distance of 5m, 2-3 seconds coming from a distance of 10m, and 5 seconds to reach the burrow from 20m. One must also assume a greater latency to reach the burrow due to the time required to both recognize the threat and then decide to flee. It is possible that a time span of greater than 2 seconds to reach safety is perceived as too risky for an individual foraging marmot causing the individual to forgo dependence on conspecifics for predation alerts.

Further inquiry into the relationship between the effects of burrow distance and the presences of conspecifics on anti-predator vigilance of foraging individuals is needed to increase the understanding of anti-predator behavior and its effects on the survival of individuals. Similarly, additional research on the possible distance limit in which foraging individuals will rely on conspecifics to alert them to predators could provide insight into the costs and benefits of social grouping.

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Figures

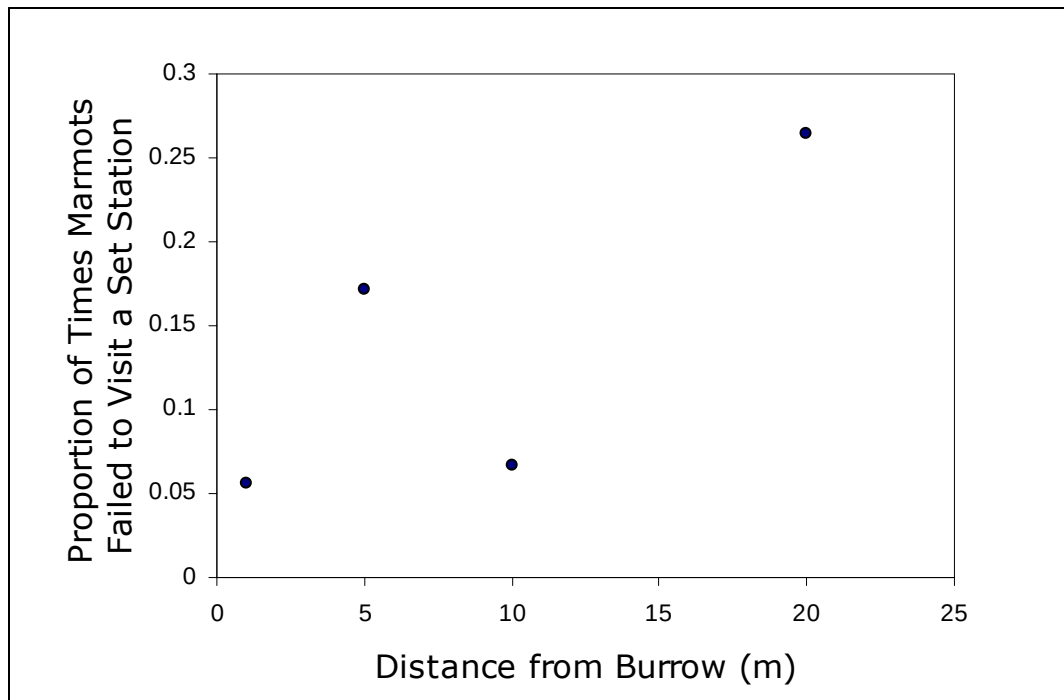


Figure 1. Reluctance to Forage. Proportion of times marmots failed to visit a set feeding station at designated distances from the burrow.

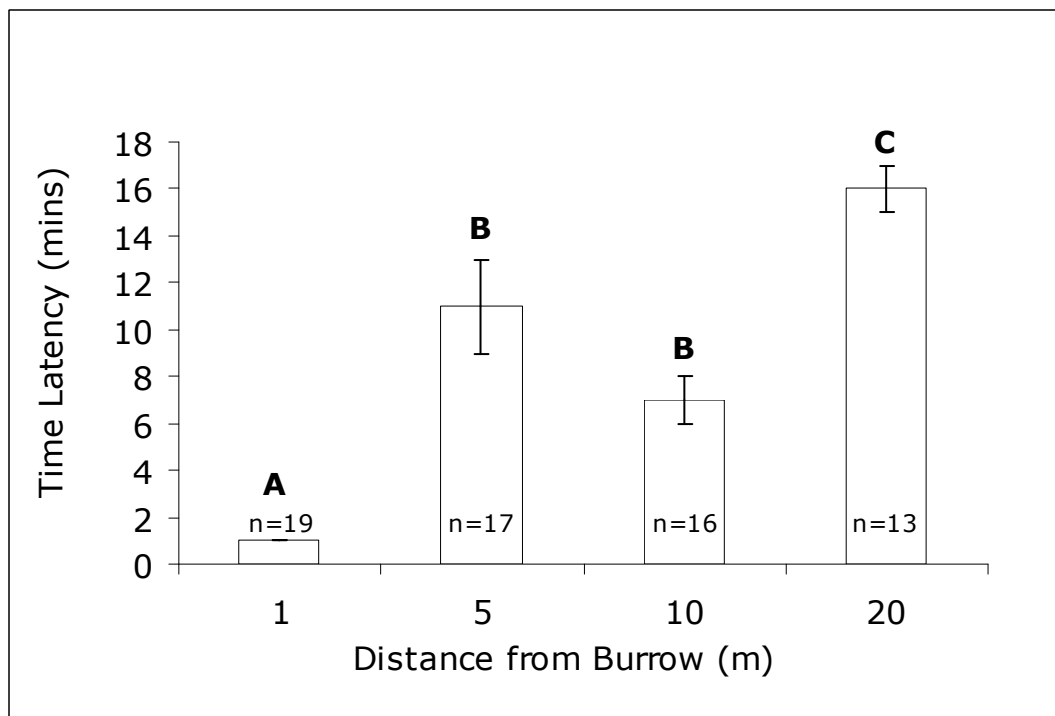


Figure 2. Mean ($\pm$ SD) latency (min) to forage. Letters denote statistical significance (see Table 1(a)).

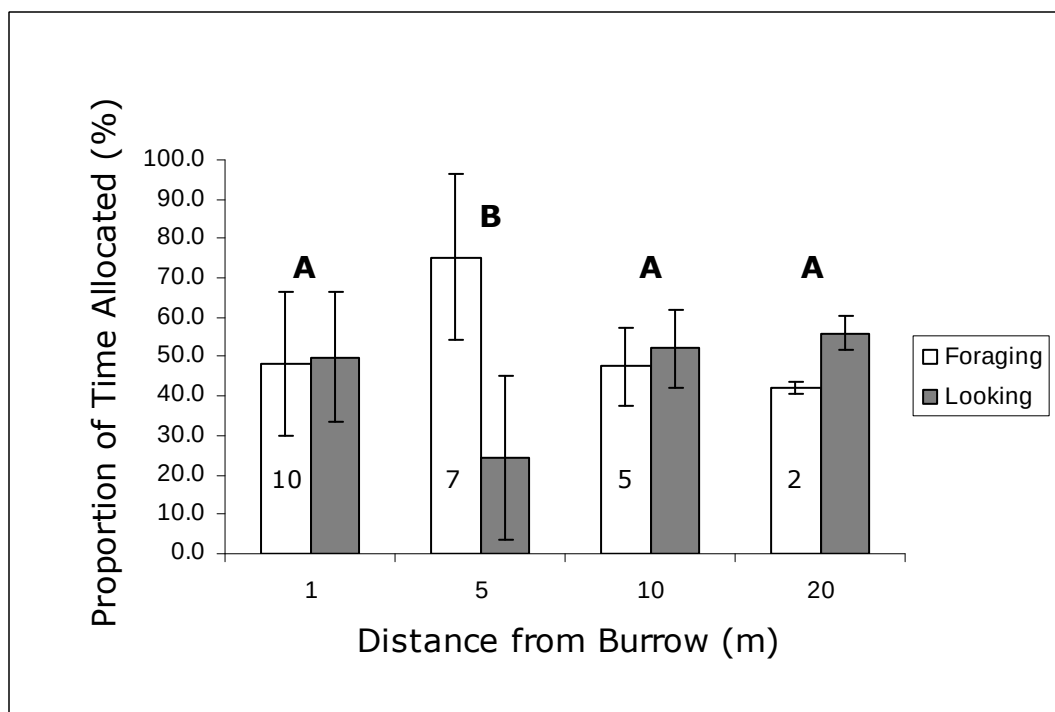


Figure 3. Mean ($\pm$ SD) time allocated to foraging and looking in the presence of conspecifics as a function of distance to the burrow. Sample size is included in the bars; letters denote statistical significance (see Table 1(b,c)).

Factor	$\bar{\theta}$	HPD95 lower	HPD95 upper	P_{MCMC}	$\bar{\theta}$	HPD95 lower	HPD95 upper	P_{MCMC}	$\bar{\theta}$	HPD95 lower	HPD95 upper	P_{MCMC}
	(a) Latency to forage (min)				(b) Proportion of time foraging (%)				(c) Proportion of time vigilant (%)			
(Intercept)	0.648	-1.226	2.623	0.507	47.936	7.661	88.230	0.021	50.879	9.869	90.859	0.018
Station $_{5m}$	1.196	0.560	1.816	<0.001	-2.640	-14.852	9.660	0.673	4.027	-7.699	16.103	0.506
Station $_{10m}$	1.197	0.542	1.189	<0.001	3.476	-8.655	16.784	0.587	-2.3768	-15.924	9.236	0.717
Station $_{20m}$	1.979	1.301	2.653	<0.001	7.651	-5.414	21.655	0.261	-6.513	-20.017	6.680	0.328
Other marmots	0.624	-0.089	1.326	<i>0.081</i>	-0.409	-2.690	1.986	0.736	-4.1732	-17.898	10.161	0.551
Order	-0.046	-0.156	0.0637	0.409	-0.409	-2.690	1.986	0.736	0.293	-2.097	2.543	0.799
Age $_{Yearling}$	-0.381	-2.221	1.541	0.695	-0.793	-43.741	37.291	0.981	0.682	-40.276	40.231	0.979
Age $_{Adult}$	0.372	-1.523	2.257	0.701	-3.980	-45.541	35.402	0.856	4.412	-37.349	43.731	0.831
Station $_{5m}$ x marmots	-1.625	-2.712	-0.550	0.003	25.484	2.802	48.093	0.024	-25.839	-48.334	-4.497	0.023
Station $_{10m}$ x marmots	-0.193	-1.475	1.001	0.753	-5.665	-30.683	19.262	0.661	6.483	-17.785	30.920	0.603
Station $_{20m}$ x marmots	-0.0636	-2.138	0.950	0.420	-12.431	-42.533	20.338	0.425	11.667	-18.740	43.444	0.448

Table 1. Results from the linear mixed effect models explaining variation in the latency to forage, the proportion of time foraging, and the proportion of time vigilant. The factor, mean parameter estimate $\bar{\theta}$, along with the lower and upper 95% confidence intervals for the estimate are reported. The p-value comes from 10,000 Markov-Chain Monte Carlo simulations. Significant p-values ($p < 0.05$) are bold, while those $0.1 > p > 0.05$ are italicized.

<i>Factor</i>	$\bar{\theta}$	<i>HPD95 lower</i>	<i>HPD95 upper</i>	P_{MCMC}
<i>(Intercept)</i>	-5.372	-12.751	2.071	0.146
<i>Station_{5m}</i>	-2.583	-7.401	2.143	0.293
<i>Station_{10m}</i>	-0.554	-5.282	4.260	0.827
<i>Station_{20m}</i>	-4.397	-10.032	1.734	0.133
<i>Other marmots</i>	1.998	-2.557	6.417	0.378
<i>Alert distance</i>	0.938	0.739	1.122	<0.001
<i>Age_{Yearling}</i>	0.593	-3.333	4.469	0.764

Table 2. Results from the linear mixed effect models explaining variation in flight initiation distance. The factor, mean parameter estimate $\bar{\theta}$, along with the lower and upper 95% confidence intervals for the estimate are reported. The p-value comes from 10,000 Markov-Chain Monte Carlo simulations. Significant p-values ($p < 0.05$) are bold.