NOTE / NOTE

Yellow-bellied marmot hiding time is sensitive to variation in costs

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Abstract: Many species use refugia to avoid predators, but remaining in a refuge is costly because foraging and engaging in other beneficial activities are curtailed while in a refuge. Thus, we expect that the duration of refuge use will be optimized. We tested a key prediction of this optimization hypothesis in yellow-bellied marmots, *Marmota flaviventris* (Audubon and Bachman, 1841), by providing supplemental food next to their burrows to manipulate the costs of remaining in a refuge. We then systematically walked towards a subject that was foraging on supplementary food or a subject that was not foraging on supplementary food until the individual disappeared into its burrow. We found a significant effect of our feeding treatment; subjects with supplementary food emerged from their burrows sooner than those without it. We also found a complex interaction between our feeding treatment and immergence distance (i.e., the distance subjects were at when they disappeared into their burrows). Individuals that tolerated close approaches emerged sooner when food was present, while those that were intolerant of approaching humans took longer to emerge and emerged sooner when food was not present. Juveniles emerged significantly sooner than adults, while there was no detectable difference between emergence times for adults and yearlings. This is the first demonstration in a mammal that hiding time is sensitive to the cost of remaining in the burrow. A number of previous studies on hiding times have focused on ectothermic species. More generally, our results suggest that endotherms are also likely to optimize the time that they remain in a refuge.

Résumé : De nombreuses espèces animales échappent à leurs prédateurs en s'abritant dans un terrier. Cependant, cela ne va pas sans coût, car tant que l'animal reste réfugié, toute activité profitable, comme la recherche de nourriture, est suspendue. Par conséquent, une optimisation de la durée pendant laquelle l'animal se cache serait à prévoir. Nous avons testé cette hypothèse sur les marmottes à ventre jaune, *Marmota flaviventris* (Audubon et Bachman, 1841). Pour cela, nous avons manipulé les coûts reliés au fait de rester réfugié, en apportant de la nourriture supplémentaire près de l'entrée du terrier. Un expérimentateur a ensuite systématiquement marché en direction soit d'un sujet consommant les apports de nourriture, soit d'un individu occupé à d'autres activités, jusqu'à ce que l'animal disparaisse dans son terrier. Les résultats montrent un effet significatif de notre traitement alimentaire: les sujets en présence de nourriture supplémentaire ressortent plus vite de leur terrier que ceux qui n'en ont pas eue. Nous avons, de plus, trouvé une interaction complexe entre le traitement alimentaire et la distance de « perte de vue » (c'est-à-dire la distance entre l'expérimentateur et le sujet au moment où ce dernier disparaît dans son refuge). Les individus tolérant une distance faible entre l'expérimentateur et eux-mêmes ressortent plus vite en présence de surplus de nourriture. Les sujets intolérants mettent globalement plus de temps à réapparaître et ressortent plus vite quand il n'y a pas de surplus de nourriture. Les jeunes de l'année émergent significativement plus tôt que les adultes et les jeunes de 1 an qui mettent un temps semblable à émerger. Notre expérience constitue la première démonstration chez un mammifère que le temps passé à se cacher est soumis aux coûts du retrait dans un terrier. Un certain nombre d'études précédentes sur le temps passé dans un refuge concernent les espèces ectothermes. Nos résultats laissent croire plus généralement qu'il est aussi probable que les endothermes optimisent leur temps dans les refuges.

Introduction

Escaping predators has costs as well as benefits and a variety of species have been shown to minimize costs of escape (Ydenberg and Dill 1986; Cooper and Vitt 2002). Most individuals will eventually flee an approaching predator. There is a large body of literature demonstrating that the decision to initiate flight is based on economics (Bonenfant and Kramer 1996; Kramer and Bonenfant 1997; Cooper and Vitt 2002), and recent findings suggest that animals may of-

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ten initiate flight specifically to avoid on-going assessment costs (Blumstein 2003; Cárdenas et al. 2005). For species that have refugia, remaining in a refuge is an additional decision that individuals can make about escape behaviour; however, remaining in a refuge is not without costs (e.g., Mauck and Harkless 2001; Cooper and Vitt 2002; Jennions et al. 2003; Martín et al. 2003; Hugie 2003, 2004). For instance, the ability to assess the exact risk of predation is no longer possible while in a refuge, and animals in refugia will not be able to forage, thermoregulate or be active at potentially thermally optimal times of the day, or engage in other beneficial activities (Dill and Fraser 1997; Martín 2001; Hugie 2003, 2004).

Recent studies have shown that some species are sensitive to the costs and benefits of remaining in their refugia. For instance, tubeworms (*Serpula vermicularis* L., 1767) alter the duration that they remain hidden dynamically based on short-term fluctuations in food availability in ways which reduce the costs of immergence (Dill and Fraser 1997). Energetic state or body condition is known to influence hiding behaviour in barnacles (Dill and Gillet 1991), fish (Krause et al. 1998), lizards (Martín and López 1999; Martín 2001), and birds (Koivula et al. 1995). However, virtually nothing is known about the economics of hiding behaviour in mammals, and we might expect endothermic species to be less sensitive to remaining in a thermally neutral burrow than ectotherms, whose activity is tightly coupled with ambient temperature (e.g., Huey and Kingsolver 1989; Martín and López 1999).

We asked whether yellow-bellied marmots, *Marmota flaviventris* (Audubon and Bachman, 1841), which are medium-sized mammals that dig burrows to create predator-free refugia, were sensitive to the costs of remaining in their burrows following simulated predator attacks. We experimentally manipulated the costs of remaining in their burrows by providing supplementary food that would likely disappear if the subjects remained hidden too long (e.g., Martín et al. 2003), and after which we experimentally approached subjects until they fled into their burrows under these different feeding treatments and recorded their hiding times (i.e., the time that they remained in their burrows).

Marmots are particularly well suited for this study because much is known about their anti-predator behaviour. Individuals of all species dig numerous burrows throughout their home ranges (Blumstein et al. 2001). Golden marmots, *Marmota caudata aurea* (Blanford, 1875), are sensitive to the distance that they are from their burrows when engaged in different activities (Blumstein 1998). Several species adjust the costs and benefits of their flight-initiation distance (Bonenfant and Kramer 1996; Kramer and Bonenfant 1997; Runyan and Blumstein 2004) or escape speed (Blumstein 1992; Blumstein et al. 2004). However, virtually nothing is known about what influences the decision to emerge from their burrows once they have fled into them.

Methods

We studied yellow-bellied marmots around The Rocky Mountain Biological Laboratory, Gothic, Colorado (38°57′N, 106°59′W), during June–August 2004. These 2–4 kg ground-dwelling sciurid rodents are moderately social and live in matrilines (female kin groups) in subalpine meadows, rocky slopes, and clearings (Frase and Hoffmann 1980). Yellow-bellied marmots avoid predators by allocating a considerable amount of their time to vigilance (Blumstein 1996; Blumstein et al. 2001; Blumstein et al. 2004), and flee to their burrows when they detect a predator.

All experiments were conducted on individually identified yellow-bellied marmots during their peak activity periods (0630–1000 and 1600–1900) in six study sites (River, Bench, Town, Marmot Meadow, Lower Picnic, and Stonefield). Five of the study sites had more than a single matriline. Subjects were regularly livetrapped and permanently marked with ear tags, and we used fur dye to identify subjects from afar (Armitage 1982). A single observer (D.P.) experimentally approached all yellow-bellied marmots. We alternated non-feeding treatments with feeding treatments, where we first placed a handful of Omalene 100 horse food (Ralston Purina Inc., St. Louis, Missouri) 1–2 m in front of a main sleeping burrow (i.e., locations where yellow-bellied marmots were known, by previous observations, to spend the night). There was no significant difference in the distance to the burrow in these two treatments (Wilcoxon's signed-ranks test, $P = 0.121$). The time (mean ± SD) between trials was 4.1 ± 6.14 days. Trials began from "standard" observation points where we could observe marmots without affecting their behaviour. These locations varied by study site, but in all cases, burrows were behind the yellow-bellied marmots (see Kramer and Bonenfant 1997).

When we targeted a "fed" subject, we waited until an individual began foraging on the bait. Otherwise, we waited until an identified subject was relaxed (i.e., not engaged in high vigilance). We then walked directly towards the focal subject at a constant pace of 1.07 ± 0.12 m/s (mean ± SD). Humans are routinely used as standardized alarming stimuli (e.g., Kramer and Bonenfant 1997; Ebensperger and Wallem 2002; Frid and Dill 2002). We recorded the distance (in metres) from the observer that the yellow-bellied marmot disappeared into its burrow (hereinafter, immergence distance), and at which time we started a stopwatch. We continued walking up to the burrow to standardize the risk associated with approaches, whereupon we turned around and walked back to the location where we began our experimental approach (the return took <1 min). We then waited until the yellow-bellied marmot first emerged from its burrow, whereupon we stopped the stopwatch and recorded the number of seconds the subject was out of sight in its burrow. Pups were not experimentally approached until they had been active above ground for ≥3 weeks and were thus fully independent from their mothers.

Our goal was to obtain two experimental approaches on each subject: one with food and one without food. We were able to do this for 42 subjects, but 12 other subjects had only a single experimental approach each. Because of the unbalanced nature of the data set, and because the immergence distances varied for each of the treatments, we fitted a linear mixed-effect model to analyze these data (McCulloch and Searle 2000; Skrondal and Rabe-Hesketh 2003). We report the results of the full data set, but analyses of the balanced data set produce qualitatively identical results. Our dependent variable was time in the burrow (measured in seconds). Feeding treatment (food / no food) and age (pup, yearling,

Table 1. Coefficient estimates from the linear mixed-effects model that predicts the time (in seconds) that a yellow-bellied marmot, *Marmota flaviventris*, was out of sight in its burrow (hiding time) following an experimental approach.

Parameter	*B* value	*P* value
Intercept	738.358	<0.001
Food		
0	688.002	0.004
1	0	
Age		
Pup	–495.392	0.013
Yearling	–252.054	0.213
Adult	0	
Immergence distance	12.341	<0.001
Immergence distance × food = 0	–11.746	0.004
Immergence distance × food = 1	0	

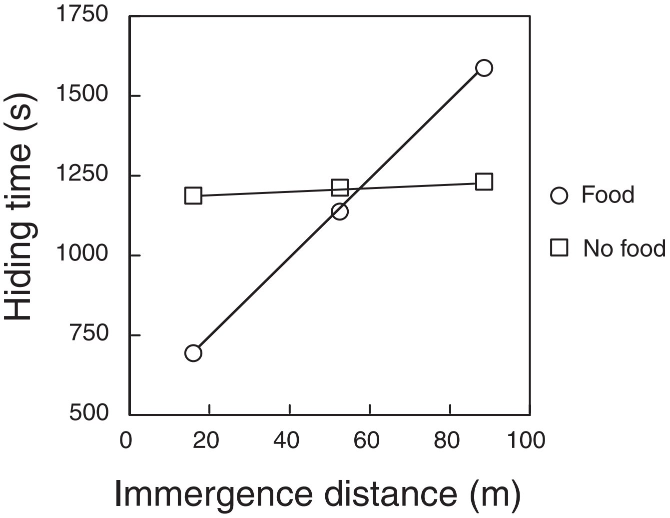
or adult) were fixed factors. Subject was repeated for most individuals, and we included the immergence distance as a random covariate. We also tested for an interaction between food treatment and immergence distance because we expected that “flighty” subjects (i.e., those that had greater immergence distances) might assess risk differently. The variation in time out of sight in the burrow was not significantly affected by food treatment (Levene’s test, $P = 0.198$). We therefore fitted the linear mixed-effect model with a compound symmetry covariance structure. Finally, we studied the immergence distance indirectly by seeing if the immergence time (i.e., the time subjects remained in their burrow) with and without food was significantly different when the marginal mean immergence distance was set to the mean (±1 SD) distance (e.g., Aiken and West 1991). To do this, we used the EMMEANS commands in SPSS® version 12 (SPSS Inc. 2003). Throughout, we interpret $P < 0.05$ as significant, and $0.05 < P < 0.1$ as representing a nonsignificant tendency.

Results

We experimentally approached a total of 54 subjects (21 adult females, 6 adult males, 6 yearling females, 7 yearling males, 4 female pups, and 10 male pups). We found significant main effects of food ($P = 0.004$), age ($P = 0.039$), and immergence distance ($P = 0.003$), as well as an interaction between food and immergence distance ($P = 0.004$). Yellow-bellied marmots remained out of sight longer without food than with food (Table 1). Moreover, pups remained in the burrow for a significantly shorter time than adults, while yearlings did not have significantly longer immergence times than adults (Table 1).

We found that food had opposite effects on the time subjects remained in their burrows when we examined the effects at 1 SD below the mean immergence distance and 1 SD above the mean immergence distance (Fig. 1). Yellow-bellied marmots that tolerated close approaches before entering their burrows remained in their burrows for significantly less time when food was present ($P = 0.008$). There was no significant difference when yellow-bellied marmots immerged at the marginal mean distance ($P = 0.571$). In contrast, when food was present, yellow-belied marmots that had greater immergence distances had a tendency to stay out of sight longer ($P = 0.078$).

Fig. 1. The effect of the marginal mean immergence distance on hiding time (the total time marmots remained in their burrows) of yellow-bellied marmot, *Marmota flaviventris*, as a function of whether supplementary food was presented or not. The hiding time at the marginal immergence distances (mean ± 1 SD) are plotted to illustrate the interaction.



To see if yellow-bellied marmot identity alone was responsible for this, we regressed immergence distance with presence of food against immergence distance without food. We found a significant relationship ($R = 0.305$, $P = 0.047$), suggesting that some of the variation in how animals respond to experimental approaches is a function of individual variation in the subjects themselves (e.g., Blumstein et al. 2004).

Discussion

Although predation is an important cause of yellow-bellied marmot mortality in our study site (Van Vuren 1991; Armitage 2004), it is rare to observe encounters between yellow-bellied marmots and their predators. Thus, it was impractical to study the natural economics of burrow use (sensu Hugie 2004). Rather, we focused on studying whether the decision to remain in a burrow was potentially influenced by the costs of remaining in a burrow. We have shown that the decision to remain in a burrow is influenced by energetic considerations. This is the first time such a decision has been studied experimentally in a mammal; it extends findings from ectothermic animals (e.g., Martín and López 1999; Martín et al. 2003), suggesting that the costs and benefits of hiding (Martín 2001), like other aspects of escape behaviour (Ydenberg and Dill 1986), are balanced and may be optimized. We expect that this decision is naturally part of a “waiting game’ (Hugie 2003) between yellow-bellied marmots and their predators, and our results suggest that future studies on the waiting behaviour of yellow-bellied marmot predators (Jennions et al. 2003) would be especially revealing.

Specifically, we found that the yellow-bellied marmots' decision to remain in a burrow is influenced by the costs of remaining in the burrow; yellow-bellied marmots remained in the burrow significantly longer if food was not present. However, this effect was not simple, and the interaction between immergence distance and food treatment was complex. For "tolerant" yellow-bellied marmots (i.e., those that permitted a close approach), food significantly influenced the time subjects remained in their burrows in an intuitive way — more tolerant subjects emerged sooner if there was food present. Animals that were not overtly alarmed should be sensitive to the costs of their escape behaviour. In this case, yellow-bellied marmots were sensitive to the lost opportunity cost of remaining in the burrow.

In contrast, "flighty" subjects (i.e., those that did not tolerate a close approach) were more likely to emerge sooner if there was no food present. We are unable to explain this finding, but point out that the effect was due completely to the presence of food. Yellow-bellied marmots exposed to the no food treatment had similar hiding times at different levels of immergence distance (Fig. 1). Moreover, because we found a significant relationship between immergence distance for subjects flushed with and without food (see also Runyan and Blumstein 2004), we believe that some of the variation in hiding time was explained by the subjects themselves. Antipredator behaviour varies in the degree of exogenous control (Blumstein et al. 2004), and developing a deeper understanding of the fitness consequences of systematic individual differences is essential (Sih et al. 2004*a*, 2004*b*; Blumstein et al. 2004). It is also possible that some individuals engage in nonadaptive behaviour.

Age had a significant influence on hiding time. Pups emerged significantly sooner than did adults, while yearlings did not emerge significantly sooner than adults. We might expect that young subjects must learn how to respond to predators (e.g., Cheney and Seyfarth 1990), and our finding is consistent with this hypothesis. Perhaps a more likely hypothesis is that the relative value of food is greater for recently weaned pups, because they must gain sufficient mass to survive hibernation in a relatively short period of time before the vegetation dries out (Arnold 1993; Lenihan and Van Vuren 1996). Like lizards (Martín et al. 2003), young yellow-bellied marmots are especially sensitive to the opportunity costs of remaining in their refugia. Future studies that manipulate nutritional state directly are needed to experimentally test this hypothesis.

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