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Predicted fitness consequences of threat-sensitive hiding behavior

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In studies of refuge use as a form of antipredator behavior, where prey hide in response to a predator's approach, factors such as foraging costs and the perceived risk in a predator's approach have been shown to influence the hiding behavior of prey. Because few studies of waiting games have focused on mammals, we studied the hiding behavior of the yellow-bellied marmot (*Marmota flaviventris*), a ground-dwelling rodent. We tested the prediction that marmots vary hiding time as a function of predator approach speed and presence and absence of food outside their refuge and that marmots hide differently depending on their relative condition. We conducted "fast approaches" and "slow approaches" in the presence and absence of extra food and evaluated hiding times. Multiple regression analyses demonstrated that the interaction between the approach speed and the presence and absence of food influenced hiding behavior; body condition had a smaller, but nonsignificant effect. We then developed a state-dependent dynamic model to explore potential fitness consequences of these decisions. The model suggested that the overall survival of a population is substantially reduced when individuals make suboptimal decisions. Our research builds on previous studies, indicating that animals integrate both costs and benefits of hiding when determining their hiding times. *Key words:* antipredator behavior, dynamic modeling, hiding behavior, *Marmota flaviventris*, marmots, predation risk, refuge use. *[Behav Ecol 18:937–943 (2007)]*

Many species retreat to a refuge when they encounter a predator (Hugie 2003; Caro 2005). The prey will likely remain in its refuge for some time, attempting to outwait the predator, which may remain in the area. However, in this "waiting game" (Hugie 2003), between predator and prey, there are obvious costs to waiting too long or not waiting long enough. If, for example, the prey waits too long, it will unnecessarily lose a significant amount of foraging time (Hugie 2004).

Refuge use is a daily component of antipredator behavior for many refuging species. Thus, hiding behavior has been studied in several ectotherms, such as marine worms (Dill and Fraser 1997), caddisfly larvae (Johansson and Englund 1995), lizards (Cooper 1999; Martín and López 1999, 2001, 2004; Cooper et al. 2003; Martín et al. 2003), snakes (Shine et al. 2000), salamander larvae (Sih et al. 1992), barnacles (Dill and Gillett 1991; Mauck and Harkles 2001), and fiddler crabs (Jennions et al. 2003; Hugie 2004). In these ectotherms, various factors likely affect the hiding behavior of different species, and this may be partially explained by variation in life history patterns (Eklov and Persson 1996). For instance, lost foraging opportunities (Dill and Fraser 1997; Martín et al. 2003; Blumstein and Pelletier 2005), the type of attack (Johansson and Englund 1995; Cooper et al. 2003), hunger levels (Dill and Gillett 1991; Martín et al. 2003), reproductive opportunities (Cooper 1999), sex (Shine et al. 2000; Jennions et al. 2003), body size (Dill and Gillett 1991; Shine et al. 2000; Jennions et al. 2003), body temperature in ectotherms (Martín and López 1999, 2001; Shine et al. 2000), and group membership (Mauck and Harkles 2001) have all been factors suggested to influence hiding time.

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Endotherms have different energetic needs and costs than ectotherms (Shine 2005), and these intrinsic constraints may influence hiding decisions. Only one previous study of hiding time focused on a mammal—the yellow-bellied marmot (Blumstein and Pelletier 2005). The previous marmot study demonstrated that hiding time is sensitive to lost opportunity costs: marmots emerged earlier when artificially provisioned—that is, when extra food was placed outside their main burrow.

We extended this previous study to focus both on lost foraging opportunities as well as perceived predation risk. Lost foraging opportunities present a major cost to refuge use because it is assumed that hiding prevents an individual from foraging (Dill and Fraser 1997). For that reason, the amount of time spent hiding is lost foraging time (Johansson and Englund 1995). This cost forms the basis for the assumption that animals will attempt to optimize the risks of reemergence (predation) with the benefits of reemergence—that is, the ability to forage (Houston et al. 1993). This has been shown in studies of *Serpula vermicularis*, a marine tubeworm that, using its tube as a refuge, decreased its hiding times when food was experimentally added (Dill and Fraser 1997). Similarly, marmots decreased their hiding times when extra food was placed outside their refugia (Blumstein and Pelletier 2005).

Because prey must assess the risks of reemergence as well as the benefits, we also explored the effect of approach speed on the hiding behavior of marmots. Some species use approach speed as an index of risk (Cárdenas et al. 2005). For instance, the lizard *Lacerta monticola* exhibited longer hiding times when a "predator" (the experimenter) approached quickly rather than slowly (Cooper et al. 2003). A fast approach speed might indicate to prey that the predator is attacking rather than passing through the area.

If marmots were sensitive to both benefits and risks, we predicted either significant effects of both food and speed treatments or significant interactions between treatments. We also explored the effect of body condition on hiding, hypothesizing that any costs of hiding will be more important to individuals in relatively poorer condition, such as pups and lactating females. These energetically challenged individuals may be more sensitive to the benefits of reemergence but perhaps not to the risks. In addition to approach speed, the presence and absence of food, and condition, we also evaluated the effects of age, sex, and the distance at which the marmots submerged (the distance out of sight). Finally, we used empirical results to help us identify potentially important factors and to parameterize them in a stochastic dynamic model that we then used to explore the fitness consequences of hiding. Specifically, we determined optimal hiding decisions for different age–sex categories of marmots given certain body masses and approach types and then explored the fitness costs by forcing them to hide 50% less or 200% longer than optimal.

METHODS

Part I: experimentally studying hiding time

We studied individually identified marmots in and around The Rocky Mountain Biological Laboratory (Gothic, Colorado 106°50′W, 46°52′N). Experiments took place between 6:30 AM and 11:00 AM and 3:00 PM and 5:30 PM, times of peak activity. We conducted 4 treatments: "slow, no food," "slow, with food," "fast, no food," and "fast, with food." "Slow" and "fast" indicate the speed of approach of the "predator" (the experimenter), 0.5 m/s and 1 m/s, respectively. "No food" and "with food" indicate whether or not extra food was placed outside the burrow of the subject. Treatments were randomized to avoid order effects; most subjects (56%) received 2 or more treatments (range 1–4). Prior to with-food treatments, we placed approximately two and a half handfuls of Omolene horse feed (Purina Mills, LLC, St Louis, MO) within 1 m of the marmot burrow opening. To control for the effect of the experimenter approach, the burrow was approached prior to no-food treatments, but no extra food was placed outside the burrow. The placement of food (or no food) occurred before marmots became active in the morning or resumed activity later in the afternoon. We then observed the burrow from points previously demonstrated to not influence marmot behavior. This distance varied according to the social group's familiarity with humans and ranged from 20 to 200 m.

We waited until the focal subject appeared relaxed (i.e., was not actively looking around) and was feeding. A single experimenter (E.R.) then approached the subject quickly and directly from the observation point—at a velocity of 1 m/s (actual approach velocity = 1.1 ± 0.135 m/s) or slowly—at a velocity 0.5 m/s (actual approach velocity = 0.5 ± 0.094 m/s). The experimenter remained in full view of the marmot during the entire approach. Any given individual was approached only once during a day, and any individual visible within the marmot group during an approach on another marmot was not approached that day.

We recorded the time that the approach began and the time the subject retreated into its burrow (the "out of sight" time). The experimenter then returned to the observation point, pacing the distance corresponding to the point at which the subject was observed to retreat into its burrow (the "distance out of sight"). This distance may be expected to change based on the relative boldness or shyness of an individual and so was important to measure as a possible covariate. Finally, the time the subject reappeared and fully emerged from the burrow was recorded.

Marmots increase their body mass throughout their active season. We used data from the most recent trapping (mean = 11.3 days; standard deviation = 11.8; range = 0–55 days) to estimate the body condition of the marmots at the time they were approached. We first performed a linear regression in StatView v. 5.0.1 (SAS Institute, Inc 1998) of weight versus Julian date for each age–sex category to determine the expected body mass for a given date. We used the most recent trapping mass and subtracted the expected mass from this value. Subjects with a negative residual were lighter than predicted and were thus considered in relatively poor condition, whereas subjects with a positive residual were considered in relatively good condition.

Table 1

Results (*B* values and *P* values for potentially important parameters) from multiple regression model with clustering option fitted in Stata

Main effect/interaction	*B* value	*P* value
Distance out of sight	0.07	0.46
Food	−21.45	0.15
Condition	−15.24	0.33
Speed of approach	2.50	0.80
Age	−3.63	0.61
Sex	−10.81	0.35
Condition × food	*28.44*	*0.06*
Speed × food	**−20.53**	**0.04**
Age × food	−4.70	0.65
Sex × food	4.54	0.73
Condition × speed	0.72	0.92
Age × speed	2.62	0.51
Sex × speed	−4.61	0.43
Age × condition	−0.50	0.93
Sex × condition	10.70	0.16
Sex × age	7.26	0.12
Food × distance out of sight × condition	*−0.72*	*0.05*
Food × distance out of sight × speed	*0.62*	*0.07*
Food × distance out of sight × age	0.38	0.30
Food × distance out of sight × sex	0.03	0.94

Significant interactions are highlighted in bold; nonsignificant tendencies are italicized.

Data analysis

A multiple regression model with a cluster option (to account for repeated measures) was fitted to the data to determine the main effects of 6 different variables (approach speed, presence and absence of food, distance out of sight, age, sex, and condition) as well as ten 2-way interactions and four 3-way interactions between these variables (Table 1). The regression was fitted in Stata v. 9 (StataCorp LC 2006). We interpret factors or interactions where $P < 0.05$ as significant and those where $0.05 < P < 0.1$ as potentially important.

Part II: studying fitness costs using a state-dependent dynamic model

We used our empirical results to help parameterize a state-dependent stochastic dynamic model (McNamara and Houston 1986; Mangel and Clark 1988) to study marmot hiding time. Our model included the key factors identified from the multiple regression that influenced optimal hiding time (Table 2). The dynamic model permitted us to examine a marmot's decision making over a period of time steps (t) and under in a variety of different situations and predator approach speeds. The main "currency" in the model was energy, which was either gained or lost based on a marmot's hiding behavior. The energy gained or lost with each decision then defined the marmot's condition at each subsequent time step. We used

Table 2
Parameters of the state-dependent dynamic model

Symbol	Name	Values	Description
t	Time unit	90 min	Time unit equal to 90 min.
T	Final time step	At $t = 20$–50	The time at which the individual goes into hibernation, and fitness is calculated; $T = 50$ indicates 50 days when animals are disturbed by an approach
x	Decision	0, 15, 30, 45, 60, 75, 90	The amount of time for which an individual "decides" to hide, ranging from 0 to 90 min in increments of 15 min
s	State	Min = 0; max = 8	The condition of the individual based on the amount of energy it has gained or lost in the previous time step
s_c	Critical state	$s = 0$	Defined as $s = 0$, the state level at which an individual dies
n	Need	Min = 0.043 (adult males); max = 0.124 (juvenile females)	The amount of energy required for survival for each t, calculated as a percentage of beginning hibernation weight
P	Total predation risk	Min = 0.00 (for an individual that does not emerge); max = 0.60 (for an individual not hiding in a high-risk scenario)	The probability of fatality due to predation is proportional to time spent in the open and increases for high-risk approaches.
ρ	Environmental predation risk	0.10–0.50	The risk of predation that is inherent in the environment, independent of decision making
g	Energy acquired	Min = 0 (for an individual that does not emerge); max = 13.83 (for a juvenile female that does not hide)	The amount of energy an individual can acquire from food in a time step based on how much time it spends in the open
G	Net gain	Min = −1.23 (for a juvenile female who does not emerge); max = 12.598 (for a juvenile female that does not hide)	The net amount of energy gained or lost during a step, calculated as the cost subtracted from the gain from food consumption
c	Cost	Proportional to n	The energy cost for 90 min.
F	Fitness	—	The fitness function based on state at time of hibernation (occurring at final T)

this model to examine the fitness consequences of suboptimal behavior for juvenile and yearling males and females. Female marmots live up to 15 years and males live up to 11 years (Blumstein DT, unpublished data; Schwartz et al. 1998). We focused, however, on juveniles and yearlings because they have not reached adult body mass, and thus, missing a foraging opportunity should be especially important for them.

In the model, an individual marmot made various hiding decisions in response to a predator approach; specifically, it could choose to hide for 0, 15, 30, 45, 60, 75, or 90 min (90 min was the longest period of time for which any marmot in the experiments remained in its burrow). Because each time step, t_x, was 90 min, a marmot's decision could potentially be to hide for the entire time step, which would mean that the marmot did not forage during that time step. The marmot "decided" its hiding time using 3 factors: 1) its condition (i.e., state), which was modeled using its body mass; 2) the perceived risk or reemergence (indicated by approach speed); and 3) the benefit of reemergence (quantified by the presence or absence of extra food).

Optimal decisions

It was important to make optimal decisions because individuals needed to both acquire energy and avoid predation, and individuals making incorrect decisions could either starve or be killed. The need to acquire energy was represented by the "need," n, or the amount of energy that a marmot needed to acquire during each time step. Marmots needed to forage enough to not starve during a time interval. The need for each time step was the percentage of the final hibernation weight that an individual needed to gain each day. It was based on the actual weight gain (in g/day) of different age–sex categories of yellow-bellied marmots (juvenile males = 1.91 g/day = 0.12% of mass at hibernation; juvenile females = 1.92 g/day = 0.12% of mass at hibernation; yearling males = 2.38 g/day = 0.07%; yearling females = 1.97 g/day = 0.06) that had been quantified at our study site (Salsbury and Armitage 2003). We calculated the final hibernation weight from the average of asymptotic weight values for each age–sex category within the population in 2005 (Blumstein DT, unpublished data).

The probability of predation was defined to be proportional to the amount of time spent in the open during any given time step (i.e., the time not spent hiding) and was therefore defined as:

$$P = \text{predation} = \rho(t_0/t),$$

where ρ was the baseline predation inherent in the environment and t_0/t indicated the proportion of time spent in the open (with t_0 = time in open).

We varied ρ between 10% and 50% during the active season. This therefore included the 32% risk of active season predation reported for this population (Van Vuren 2001). In a high-risk approach, which represents the experimental slow approach, the chance of predation is increased from that of a low-risk approach by values ranging from 0 to 55%, with smaller increases for less risky decisions within the high-risk approach. This exponential decay of predation risk has been hypothesized in other studies (Cooper and Frederick, forthcoming) and is based on the assumption that a marmot would be in greater danger within the first 15–30 min following an approach, when the predator was more likely to still be in the area, than it would be after 90 min, when there is a greater chance that the predator had left the area.

In any given time step, the marmot had to decide on a hiding time. Its hiding time then dictated how much food it could acquire during that time step. The amount of food acquired was described by the gain function, $g(x)$:

$$g(x) = \text{gain}(x) = [kn(t_0/t)]^2,$$

where k was a proportionality constant that was higher in with-food scenarios and n referred to units of need. Thus, energy acquired, g, can be understood based on its relation to the energy needed. Because individuals with a higher need will gain more value from the same quantity of food, they will thus have a higher relative gain from food acquired. By raising the proportion of time spent in the open (t_0/t) to the exponent $n = 2$, benefits are very high for early emergers (who will have a greater likelihood of getting a share of the extra food in the with-food scenarios before it is devoured by other group members) but decay substantially for late emergers (Cooper and Frederick, forthcoming). (Note: because k is small in no-food scenarios, this spike and decay is less pronounced in those approaches.)

The gain then dictated the "net amount of energy" it gained or lost during that step, which in turn determined its condition at the next time step. An individual's "net gain," G, from a decision was therefore its "gain," g, from the food it acquired minus the energy requirement (c) for that time step:

$$G(x) = \text{net gain}(x) = g(x) - c,$$

where x is a given decision, energy gain is the amount of energy it acquires, and energy cost is the amount of energy used during that time step.

We assumed that marmots could be in 8 discrete condition levels, ranging from dead (condition 0) to a level that prevents animals from starving during the winter hibernation period (condition 8). A marmot's fitness at the final time step, T, was given by a sigmoidal fitness function based on condition, where s = condition (state) and

$$T(fit) = s^2/(4 + s^2).$$

In order to maximize its fitness at the end of the time steps (assumed to be the point at which the marmot enters into hibernation), individuals had to choose the best possible decision at each time step. Although it is impossible to empirically verify a fitness function in marmots, previous dynamic models have used similarly sigmoidal functions to express outcomes of energy stores. For instance, in their dynamic model of the foraging behavior of tits and chickadees, Brodin and Clark (1997) use sigmoidal survival probability functions as a measure of birds' fitness.

The model calculated the optimal decisions for a single marmot over the given period of time steps. Thus, we excluded variables that were not expected to change significantly within individuals. One such variable was distance out of sight (i.e., the immergence distance), which has been shown to significantly explain some variation in hiding time between subjects (Blumstein and Pelletier 2005). As a measure of an individual's shyness, distance out of sight is a useful covariate; individual marmots vary in their "shyness" (Blumstein et al. 2004), but this was not expected to vary significantly within experiments on the same individual.

Fitness consequences

In order to explore the fitness consequences of suboptimal decision-making, we did 2 things. First, we introduced stochasticity into the model by randomizing predation. Therefore, an individual died from predation if a random number generated by the computer (from 0 to 1) was less than the probability of predation. Importantly, this meant that a reduced probability of predation would indicate a lower but not a zero probability of death from predation. Second, to quantify the effect of suboptimal decision making on the percent survival of the population, we simulated populations of marmots hiding suboptimally. We thus simulated 100 marmots starting at condition 5 (representing a population of marmots in modest condition), which were then forced to select nonoptimal hiding times (50% shorter and 200% greater than optimal; see also Bouskila and Blumstein 1992). We studied the consequences of individuals hiding for half of the optimal time (by doubling the predation risk and doubling gain) as well as the consequences of hiding for twice the optimal hiding time (by halving predation risk and gain). In this way, we were able to determine the overall percent survival of nonoptimally behaving populations as compared with optimally behaving populations. Results were standardized with optimal populations' survival at 100%.

RESULTS

Part I: experimentally studying hiding time

Our data set consisted of 82 experimental approaches on 50 different subjects (33 females, 17 males—20 juveniles, 13 yearlings, and 17 adults). Data were collected from 26 June 2005 to 5 September 2005. The raw data suggested that overall, marmots hid for less time in with food treatments than in no food treatments (no food, slow approach: 11.89 ± 2.66 min; no food, fast approach: 17.20 ± 3.85 min; with food, slow approach: 15.12 ± 3.56 min; with food, fast approach: 12.52 ± 2.56 min), but this main effect was not found to be significant in the multiple regression model ($P = 0.15$). The multiple regression model explained 36.4% of variation in hiding time and demonstrated that marmots hid for the least time after fast approaches with the presence of extra food. This was revealed by a significant interaction between approach speed and the presence and absence of food (Table 1); the negative B value for the interaction indicates that hiding time decreased significantly in fast, with food approaches as compared with slow, no food approaches. Although the model had no significant main effects, there were suggestive 3-way interactions ($0.05 < P < 0.1$) between the presence and absence of food, the distance out of sight, and condition and between the presence and absence of food, distance out of sight, and approach speed (Table 1). Rather than asserting the null and possibly making a type 2 error, we selected approach speed, food, and condition as important parameters that would be integrated into our dynamic model.

Part II: studying fitness costs using a state-dependent dynamic model

Optimal decisions

In the state-dependent dynamic model, predicted hiding time varied with risk, food, and condition. Marmots in all age–sex classes hid for less time in fast approaches with food than they did during slow approaches without food (Figure 1). Because shorter hiding times in fast approaches can only make sense if marmots perceive fast approaches as low risk, we refer to fast approaches as low risk. However, the model illustrated that juvenile marmots should be expected to respond differently to scenarios with the same risk level but different food levels.

Although the overall empirical trend of hiding for less time in low risk, no food approaches holds in the model, juvenile males and females hid for less time in high risk, with food scenarios than in high risk, no food scenarios (Figure 1). By contrast, yearling males and females hid for less time in high risk, no food

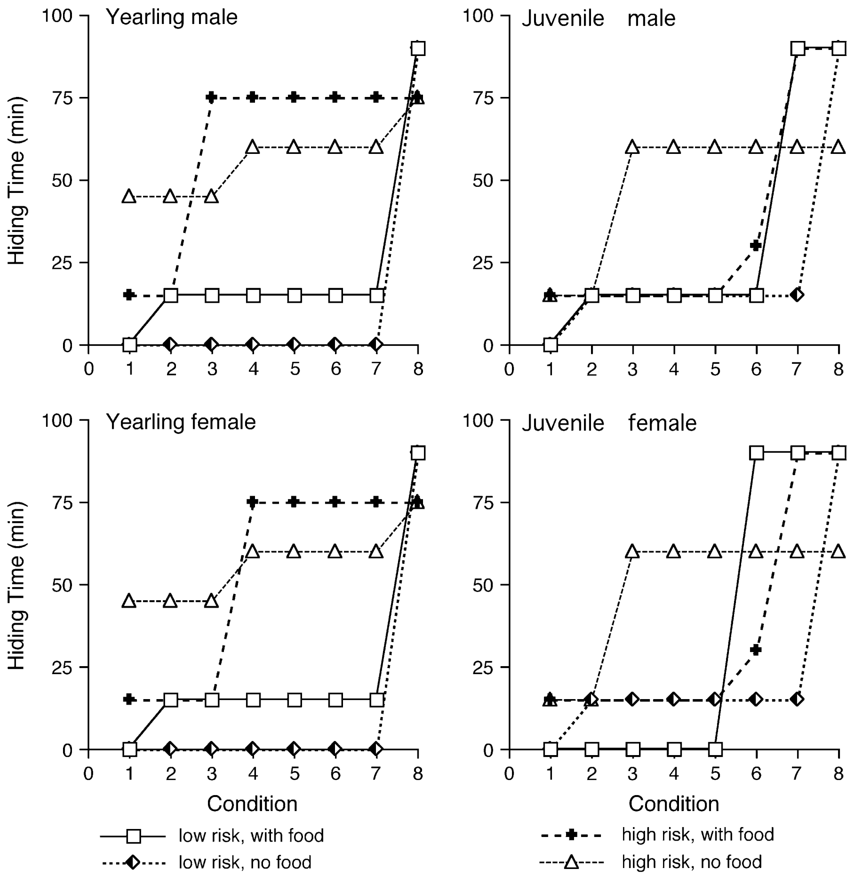

Figure 1
Results from state-dependent model. Graphs illustrate optimal hiding time for yearling males, yearling females, juvenile males, and juvenile females at any of 8 levels of condition given variation in supplementary food and predation risk.

scenarios than in high risk, with food scenarios. The same expected trend was seen in low-risk scenarios. This is likely because yearlings, who have less pressure to gain weight, could afford to wait slightly longer in with food scenarios and use the extra food to gain an adequate amount of energy in less time. Juveniles, however, must gain relatively more weight each day in order to reach a sufficient mass to survive their first hibernation. Thus, juveniles would be under greater pressure to eat as much as possible, and for them, it might be prudent to emerge as early as possible so as to reap all the benefits of extra food.

Finally, the model predicts that marmots in poor condition at a given time step will hide for less time than did marmots in good condition. Thus, marmots in poor condition, for which energy is relatively more important, may be more willing to take risks to acquire energy (Figure 1).

Fitness consequences

Suboptimal decision making is costly. When simulated marmots of all age–sex classes hid for 50% of the optimal time, none survived (Figure 2). In these simulations, all individuals were killed by predators because they hid for too short a time. When simulated marmots hid for 200% of the optimal time, the percent survival decreased by 65% for yearling males, 63% for yearling females, 92% for juvenile males, and 62% for juvenile females (Figure 2). In these simulations, overly cautious marmots starved. Interestingly, females were predicted to have a greater probability of survival than males, reflecting an empirical trend reported in this population (Schwartz et al. 1998).

DISCUSSION

As expected, marmots are responsive to the costs and benefits of hiding decisions. Marmots hid the least in low-risk situations when there was the added benefit of extra food. Furthermore, our model results suggest that assessment of costs and benefits has fitness consequences. Interestingly, these results parallel generalization of Bouskila and Blumstein (1992) that individuals would be favored if they overestimated predation risk rather than underestimated predation risk. This was illustrated in that all subjects would be expected to be killed if predation risk were underestimated, but many individuals would still live if they overestimated risk.

Predation is the primary cause of summer mortality in yellow-bellied marmots (Van Vuren and Armitage 1994), as well as in Vancouver Island marmots (*Marmota vancouverensis*; Bryant and Page 2005). Thus, hiding time is an important decision that marmots should optimize. If marmots hid for too long, they would have a difficult time meeting their energetic needs and may not reach an optimal weight for hibernation, which could reduce their chances of overwinter survival (Salsbury and Armitage 2003). As demonstrated by the model, hiding for too little or too long may have deleterious fitness consequences. We might expect selection against individuals who emerged too soon because their predators might still be in the vicinity. Future studies should focus on predator behavior to better document this game (Hugie 2003).

Marmots in our study hid longer in response to a slower approach; interestingly, the opposite has been shown in lizards (Martín and López 1999, 2005; Cooper et al. 2003). The interpretation for these ectotherms was that they assessed themselves as being at greater risk following rapid approaches because rapid approaches represented an overt attack by a predator relying on speed rather than stealth. A slow approach may be considered more dangerous by marmots because many predators that threaten marmots stalk their prey.

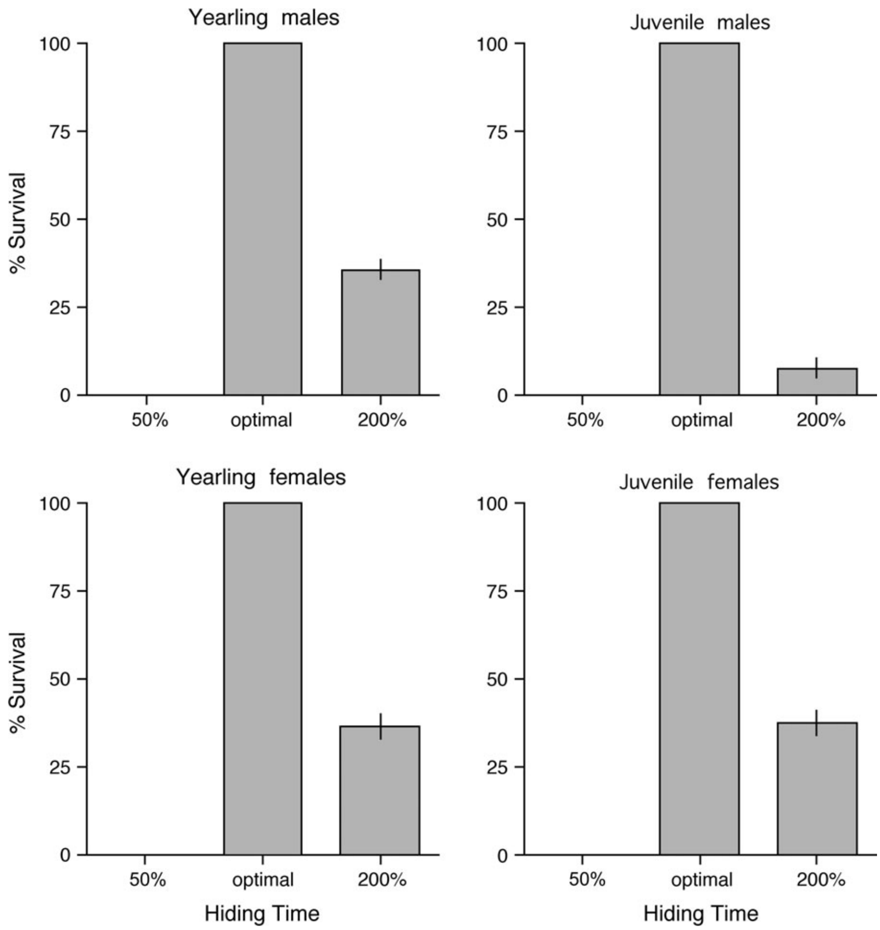

Figure 2
Predicted survival given that individuals select optimal hiding times or nonoptimal hiding times. Graph illustrates that hiding 50% less or 200% more than the optimal hiding time substantially decreases the likelihood of survival.

In a study of the Vancouver Island marmot, for example, wolves and cougars accounted for 59% of the population's annual mortality (Bryant and Page 2005). Marmots in and around Gothic, Colorado, likewise face danger largely from ground predators such as coyotes (*Canis latrans*), bears (*Ursus americana*), badgers (*Taxidea taxia*), and possibly long-tailed weasels (*Mustela frenata*) (Schwartz et al. 1998).

Because our experiments took place in a site with many stalking predators (Schwartz et al. 1998), it may prove illuminating to focus new studies on areas where stalking predators account for only a small percentage of total mortality. Different predators may themselves be influenced by different factors in selecting their optimal decision. These factors may generate unique perceptions of risk for the prey populations they hunt.

It is encouraging that our model produced results that mirrored the observed trend of higher overall female survivorship. This was likely a consequence of a need for greater daily weight gain to reach optimal weight for juvenile males than juvenile females. Their more demanding need function is likely what contributes to higher mortality among juvenile males even when making optimal decisions (Figure 2). In real life, the need to gain weight may be compounded with other problems such as male-biased dispersal. Evidence suggests that these obstacles may have a greater effect on mortality than do the energetic costs of pregnancy and lactation (Van Vuren 2001). With larger sample sizes, subsequent research can strengthen our knowledge of the effects of age- and sex-specific energy costs.

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Erratum

Predicted fitness consequences of threat-sensitive hiding behavior *[Behav Ecol 19:1369–1369 (2008)]*

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The authors inadvertently reported incorrect means and standard deviations for marmot approach treatments. The correct means ± SD are as follows: no food, slow approach: 23.48 ± 11.89 min; no food, fast approach: 26.48 ± 17.20 min; with food, slow approach: 17.81 ± 15.12 min; with food, fast approach: 11.17 ± 12.52 min.

The authors regret the error.