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The influence of distance to burrow on flight initiation distance in the woodchuck, *Marmota monax*

Marjolaine Bonenfant and Donald L. Kramer
Department of Biology, McGill University, 1205 Docteur Penfield Avenue, Montreal, Quebec H3A 1B1, Canada

We used woodchucks (*Marmota monax*) to test predictions of a cost-benefit model of antipredator behavior that flight initiation distance would increase with distance to refuge and with predator approach velocity. We also examined the effects of distance to refuge and predator approach velocity on escape velocity and on both temporal and spatial margin of safety (expected time and distance between predator and burrow at the time of the woodchuck's arrival). The observer, assumed to be perceived as a potential predator, approached juvenile woodchucks from the direction opposite to the burrow at a slow (1.24 m/s) or fast (1.79 m/s) walking pace. When the woodchuck started to flee, the observer recorded the woodchuck's distance from the observer and from its burrow, the time spent running, and whether the woodchuck stopped before reaching its burrow. Flight initiation distance increased consistently with distance to the burrow over the entire observed range (0–25 m) but was not significantly affected by observer approach velocity. Escape velocity was not significantly influenced by the observer approach velocity and was approximately constant over the range of 2–25 m, but was slower for woodchucks less than 2 m from their burrows. Both temporal and spatial margins of safety increased with distance from the burrow. The temporal margin of safety increased with distance from the burrow more rapidly for slow than for fast observer approach velocity. Woodchucks fleeing from greater than 2 m usually stopped near the burrow before entering, but those from closer distances usually entered directly. These results support the assumption that antipredator behavior is sensitive to the costs and benefits of alternative escape decisions. *Key words:* antipredator behavior, escape velocity, margin of safety, Sciuridae. *[Behav Ecol 7:299–303 (1996)]*

One of the most widespread antipredator responses is fleeing when potential predators come too close (Edmunds, 1974). The distance at which animals start to flee—flight initiation distance (FID)—can vary considerably within a species, depending on the species of predator, demographic class, physiological state, environmental conditions, and past experience (e.g., Altmann, 1958; Bauwens and Thoen, 1981; Lagory, 1987; Rand, 1964; Rowe-Rowe, 1974; Walther, 1969). Ydenberg and Dill (1986) noted that since flight has costs in addition to its benefits of reducing risk of predation, FID should be optimized rather than maximized. That is, animals should not necessarily flee as soon as they detect a potential predator. Using a simple graphical model, they predicted that distance to a secure refuge would affect FID. They argued that the optimal FID in response to an approaching predator would be at the point where the cost of staying exceeded the cost of fleeing. Since the risk of capture is expected to be higher (for a given FID) for animals farther from a refuge, the cost of staying, and hence, the optimal FID, should increase with the distance from the refuge. This prediction was subsequently tested and supported in field studies on gray squirrels (*Sciurus carolinensis*; Dill and Houtman, 1989) and brook trout (*Salvelinus fontinalis*; Grant and Noakes, 1987) and in laboratory studies on African cichlid fish (*Melanochromis chipokae*; Dill, 1990) and banded killifish (*Fundulus diaphanus*; McLean and Godin, 1989), but not on two species of sticklebacks (*Gasterosteus aculeatus* and *Pungitius pungitius*; McLean and Godin, 1989).

Dill (1990) noted that the original hypothesis had assumed flight velocity to be constant; FID might change less or not at all if flight velocity increased with distance to cover. Dill proposed that animals might choose a combination of FID and velocity to provide a constant margin of safety, that is, the time between arrival at the refuge by the animal and the expected time of arrival by the predator. In the fish studied, however, there was no clear evidence for an effect of distance to cover on flight velocity, although there was a suggestion of a constant margin of safety.

Predator approach velocity is another factor that could affect FID (Ydenberg and Dill, 1986). Since a more rapidly moving predator has a greater chance of capturing the prey before the prey reaches cover, the effect of approach velocity should be qualitatively similar to the effect of distance from cover. For an animal that does not change its FID or flight velocity, the margin of safety would decrease as predator speed increases. FID has been reported to increase with predator velocity in some species, [e.g., the zebrafish (*Brachydanio rerio*; Dill, 1974), the anole (*Anolis lineatopus*; Rand, 1964), and in Thompson's gazelle (*Gazella thompsoni*; Walther, 1969)], but not in other species [e.g., damselfish (*Chromis cyanea*; Hurley and Hartline, 1974) and domestic sheep (Hutson, 1982)].

Here we report the results of a study of escape behavior in woodchucks (*Marmota monax*) in response to an approaching human. We tested the predictions that FID would increase with distance to refuge and with predator approach velocity. We also examined the effects of distance to refuge and approach velocity on escape velocity and margin of safety. In addition, we noticed that woodchucks often stopped before entering their burrow, and we investigated the effect of distance from the burrow on this behavior.

MATERIALS AND METHODS

Woodchucks are large (about 3 kg), diurnal, solitary, folivorous sciurids widespread in eastern North America. They dig

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Table 1
Results of least squares regression analysis relating four measures of predator avoidance behavior in woodchucks to distance to burrow

Variable	Treatment	r^2	Slope (SE)	p_1	Intercept (SE)	p_2
Flight initiation distance (m)	S	.469	0.843 (0.144)	<.001	8.990 (1.395)	<.001
	F	.443	0.867 (0.150)	<.001	9.476 (1.089)	<.001
Velocity (m/s)	S	.382	0.083 (0.017)	<.001	1.582 (0.164)	<.001
	F	.442	0.124 (0.021)	<.001	1.379 (0.156)	<.001
Temporal margin of safety (s)	S	.718	1.150 (0.115)	<.001	6.859 (1.121)	<.001
	F	.653	0.714 (0.080)	<.001	4.805 (0.583)	<.001
Spatial margin of safety (m)	S	.717	1.426 (0.143)	<.001	8.512 (1.393)	<.001
	F	.653	1.279 (0.144)	<.001	8.601 (1.044)	<.001

Treatment: S = slow approach (n = 41 woodchucks); F = fast approach (n = 44); p_1 = probability that slope is different from zero; p_2 = probability that intercept is different from zero.

a burrow or occupy an abandoned one which they use for sleeping and to evade predator attacks. Burrows typically have two entrances and are situated along edges of gently sloping, well-drained fields. We studied a relatively dense population on Notre Dame and Sainte Hélène Islands in the St. Lawrence River near Montreal (45°31′ N, 73°32′ W). The area is public parkland, with mowed grass, scattered deciduous trees, and patches of forest and brush. Compared to animals with less exposure to humans, the animals can be approached quite closely. Observations were made from 13:00 h to 18:00 h on dry, mainly sunny days from 13 September to 3 October 1993. At this time of year, most adults have entered hibernation while juveniles are still active (Barash, 1989).

The observer moved slowly around the study site, which had been previously surveyed to identify burrow locations. When a woodchuck was found, the observer moved to position herself so that the woodchuck was on a straight line between the observer and the burrow while remaining far enough away to avoid disturbing the animal. After ascertaining that the woodchuck had detected the observer, as indicated by raising its head and looking in her direction, but had returned to normal foraging, the observer began to walk toward the woodchuck. When the animal began to move toward its burrow, the observer started a stopwatch, dropped a marker to indicate her position, and noted the woodchuck's position. She continued to move at the same pace until the animal entered its burrow. If the animal stopped running before entering its burrow, the location and the time spent running to that location were noted. The observer continued her approach, and the location of the woodchuck and observer at the second flight initiation and the duration of the second flight were recorded. Then all locations were marked and the distances (±1 dm) from the observer to the woodchuck and from the woodchuck to the burrow at each flight initiation were noted.

Woodchucks were identified by burrow location. The first observation on a given individual was randomly chosen for a slow (mean ± SD = 1.24 ± 0.02 m/s, n = 10) or fast (1.79 ± 0.03 m/s, n = 10) walking approach. If the animal was encountered again on another day, it was tested at the other approach velocity. Data were not included if there were extraneous sudden disturbances (e.g., a dog barking) that may have affected the flight behavior. The final data set included 41 animals tested with the slow approach and 44 with the fast; because not all individuals could be tested at both velocities 59 different individuals were involved.

The primary measures were distance to burrow at first flight (DB), distance to observer at first flight (or flight initiation distance, FID), distance to burrow at second flight (DB2), distance to observer at second flight (FID2) and time spent moving by the animal (T). From these we calculated escape velocity [EV = (DB − DB2)/T] and margin of safety. Temporal margin of safety (TMOS) was the expected time between the arrival of the woodchuck and the observer at its burrow entrance [TMOS = [(FID + DB)/AV] − (DB/EV)], where AV is the approach velocity of the observer. Spatial margin of safety (SMOS) was the expected distance between the observer and the burrow entrance at the time when the woodchuck arrived at its burrow [SMOS = (DB + FID) − [AV(DB/EV)] = DB[1 − (AV/EV)] + FID].

Regression analyses of FID, EV, TMOS, and SMOS versus DB were performed on untransformed data separately for each approach velocity. T tests were then used to determine whether the slopes and the intercepts differed significantly from zero and from each other. For regressions, each observation was considered a separate point. For clarity of graphical presentations, data were grouped into categories of DB: 0–0.9 m, 1.0–1.9 m, 2.0–3.9 m, 4.0–7.9 m, 8.0–15.9 m, and ≥16 m; means were calculated and plotted at the midpoint of the DB range on a $\log_{10}$ scale. Chi-square analyses were performed to examine differences in the number of individuals stopping at different distances. All the analyses were performed using Systat 5.1 for the Macintosh.

RESULTS

Habituation to the observer

Although it seemed unlikely that there would be significant habituation between trials because of the high frequency of encounters with humans at the site, we checked for the effect of repeated testing by comparing the 28 trials in which woodchucks were approached first at the slow velocity with the 13 trials in which woodchucks were approached second at the slow velocity; similarly, we compared the 31 trials where the fast velocity was tested first with the 13 trials where it was second. Regression of FID, EV, TMOS, and SMOS on DB differed in only one case (EV slopes for the fast approach; t = 2.57, df = 40, p < .02). We therefore combined data from first and second trials for the same approach velocity.

Flight initiation and velocity

There was a highly significant positive relationship between FID and distance to burrow for both the slow and the fast approach (Table 1 and Figure 1a). There was no evidence that FID reached a maximum within the range of distances tested. Differences were very large, ranging from 8 m at less than 1.0 m from the burrow to over 25 m for animals greater than 16 m from their burrow. There was no indication that FID was affected by approach velocity (Table 2 and Figure 1a).

Escape velocity also increased with distance to burrow for both approach velocities (Table 1). However, Figure 1b sug-

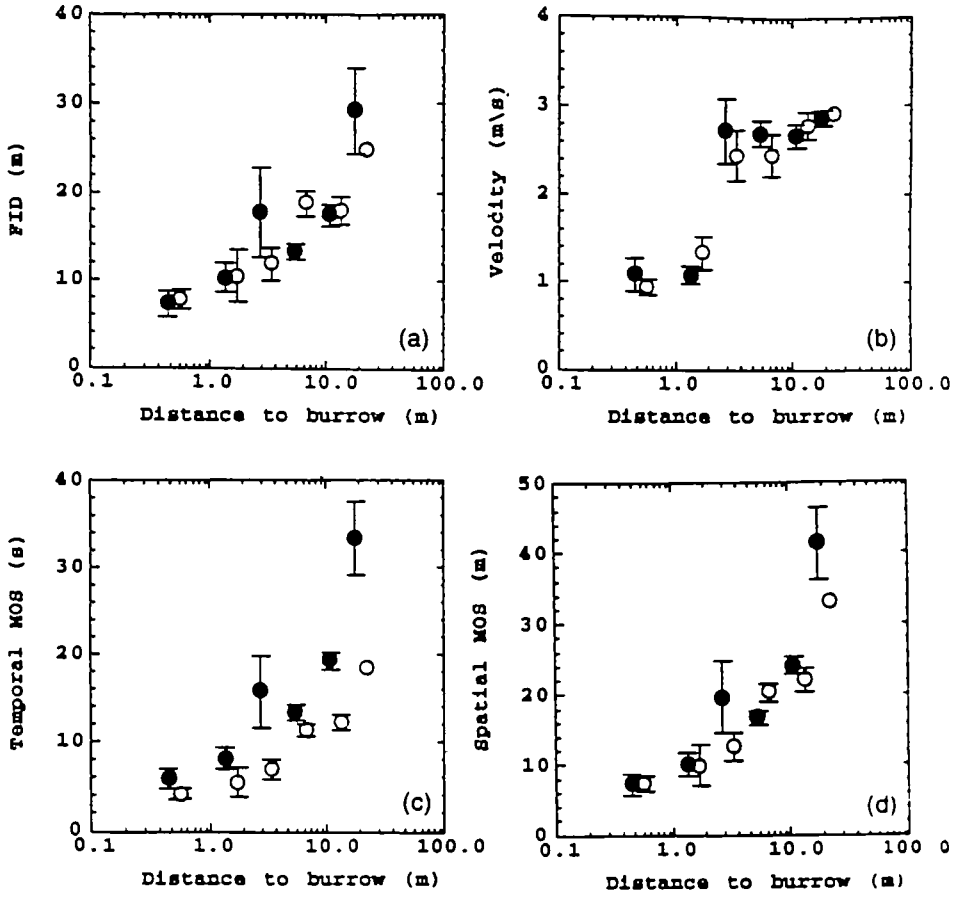

Figure 1
The relationship between distance to burrow and four measures of antipredator behavior in woodchucks: (a) flight initiation distance (FID), (b) escape velocity of fleeing animal, (c) temporal margin of safety, and (d) spatial margin of safety. Dots are for slow approach; open circles for fast approach. Bars represent 1 SE. Data are grouped into six distance categories and the sample size for the slow approach and the fast approach, respectively, for each distance category are as follows: (1) 0–0.9 m (9,11); (2) 1.0–1.9 m (5,5); (3) 2.0–3.9 m (5,7); (4) 4.0–7.9 m (7,10); (5) 8.0–15.9 m (11,10); and (6) 16 m and more (4,1). Points for the same distance are separated for visual clarity.

gests a nonlinear pattern. At distances <2 m, the velocity was about 1.1 m/s; at distances ≥2 m, velocity was about 2.7 m/s, and increased only slightly with distance. When observations at less than 2 m from the burrow were excluded, regressions between escape velocity and distance were nonsignificant for both the slow approach (slope ± SE = 0.008 ± 0.015, r^2 = .013, p = .574, n = 27) and the fast approach (0.041 ± 0.027, r^2 = .083, p = .138, n = 28). The slopes and the intercepts of the regressions between escape velocity and distance for the two approach velocities were also not significantly different from each other (Table 2). However, escape velocities did differ for woodchucks <2 m and ≥2 m from their burrows (slow approach: t = 10.793, df = 26.7, p < .001; fast approach: t = 9.670 df = 42.0, p < .001). Again, there were no differences in escape velocities between approach velocities for a given distance (<2 m: t = 0.189, df = 25.6, p = .852; ≥2 m: t = 0.875, df = 48.4, p = .386).

Temporal and spatial margins of safety increased strongly with distance to burrow for both approach velocities (Table 1 and Figure 1c, d). For the temporal margin of safety, the slope for the slow approach was significantly steeper than for the fast approach (Table 2 and Figure 1c), but this was not the case for the spatial margin of safety (Table 2 and Figure 1d).

Table 2
The effect of the observer approach velocity on the relationship between four predator avoidance behaviors and distance to burrow in woodchucks

Variable	Slope		Intercept	
	t	P^a	t	P^a
Flight initiation distance (m)	0.115	NS	0.275	NS
Velocity (m/s)	1.517	NS	0.897	NS
Temporal margin of safety (s)	3.112	<.01	1.626	NS
Spatial margin of safety (m)	0.724	NS	0.051	NS

[a] Two-tailed probability of a difference between responses to slow and fast approach (t test).

Stopping near the burrow

Woodchucks stopped before reaching the burrow on about 87% of their flights from distances ≥2 m, but stopped much less frequently when the distance to the burrow was less (Figure 2; slow: χ^2 = 13.141, df = 1, p < .001 and fast: χ^2 = 21.891, df = 1, p < .001). There was no effect of approach velocity on the frequency of stopping at either distance grouping (<2 m: χ^2 = 0.403, df = 1, p = .675; ≥2 m: χ^2 = 0.208, df = 1, p = .705). Nearly all animals that stopped were within 1 m of their burrow entrance, with the majority between 0.2 and 0.8 m (Figure 3). There was no apparent relationship between the distance from the burrow at which animals stopped (DB2) and their second flight initiation distance (FID2) for either approach velocity (slow: n = 26, r^2 = .024, p = .455; fast: n = 27, r^2 = .005, p = .727). However, the intercepts differed significantly from zero (slow: 7.129 ± 1.351, p < .001; fast: 8.017 ± 1.544, p < .001). Therefore, it seems that once they are close to safety, woodchucks use a flight distance of about 7–8 m regardless of their exact distance away from their burrow.

DISCUSSION

Animals that have detected an approaching predator may continue their previous activity for some time or initiate escape

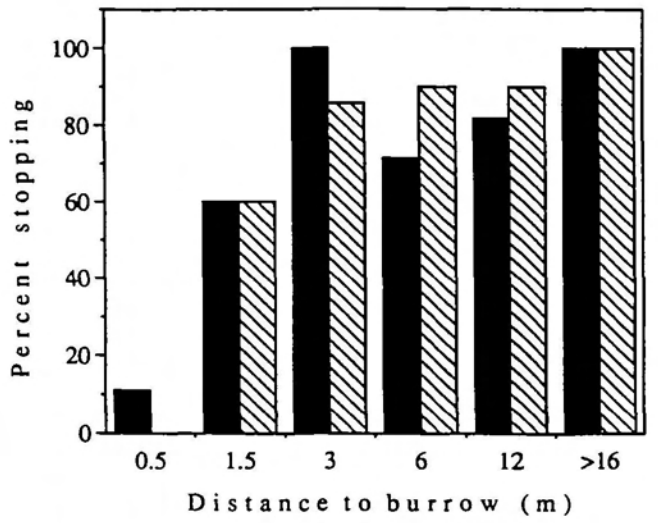

Figure 2
The relationship between distance to the burrow and the percent of woodchucks that stopped before entering their burrow. Black bars indicate data from slow approaches and hatched bars data from fast approaches. Data are grouped into six distance categories and the sample size for the slow approach and the fast approach, respectively, for each distance category are as follows: (1) 0–0.9 m (9,11); (2) 1.0–1.9 m (5,5); (3) 2.0–3.9 m (5,7); (4) 4.0–7.9 m (7,10); (5) 8.0–15.9 m (11,10); and (6) 16 m and more (4,1).

behavior. When they flee, they must choose among alternative escape velocities and escape routes and they must stop fleeing at some point. The costs and benefits associated with these alternatives are likely to vary significantly with specific aspects of each encounter. One might therefore expect flexibility in escape behavior, but this topic has been explored much less than variability in foraging decisions. Indeed, it was the unsupported assumption of consistent minimization of predation risk that Ydenberg and Dill (1986) challenged with their economic models. Our study shows that woodchucks exhibit considerable flexibility in their flight behavior, permitting a human observer to approach as close as 8 m when they are near the burrow entrance, but fleeing at more than 25 m when they are more than 16 m from the burrow. Dill and Houtman (1989) showed an effect on FID of distance from the nearest refuge tree in gray squirrels, but they tested distances only up to 5 m, and their data suggested a leveling out of the response after 3 m. For woodchucks, our study shows that FID continues to increase with distance. It might be expected that the optimal FID would continue to increase with distance, but there are few data on the dynamics of predator-prey interactions in relation to refuge distances with which to develop more than qualitative general predictions.

Previously only Dill (1990) had investigated escape velocity in relation to distance to cover. His results for cichlid fish showed a nonsignificant tendency for escape velocity to increase with distance to refuge. Our results indicate that woodchucks more than 2 m from their burrow did not increase escape velocity significantly with distance, but that running speeds were significantly lower for woodchucks initially less than 2 m from their burrows. In golden marmots (*Marmota caudata aurea*), Blumstein (1992) also concluded that animals closer to their burrow tended to have lower velocities, but the precise relationship between distance and velocity could not be ascertained from his multivariate analysis. These results suggest that changes in velocity in relation to distance from the burrow are at best a minor component of escape strategy. Studies of mammalian running energetics suggest that the cost per unit distance does not increase with velocity (Schmidt-Nielsen, 1979). Therefore it is surprising that woodchucks would not flee at maximum velocity. However, there may be energetic costs of accelerating to higher velocities, as well as increased risk of injury or threat from predators other than the one that precipitated the escape movement. Woodchucks may have changed their gait from walking when less than 2 m from the burrow to galloping when farther. If there are optimal velocities for different gaits, one would expect escape strategies to vary primarily through adjustments in FID.

Dill (1990) proposed the concept of a constant margin of safety, calculated as the difference in time to reach cover by prey and predator. Our study considered margin of safety in both time and distance and has shown that it increases greatly with distance from the burrow. This increase is, of course, a necessary outcome of a situation in which the woodchuck

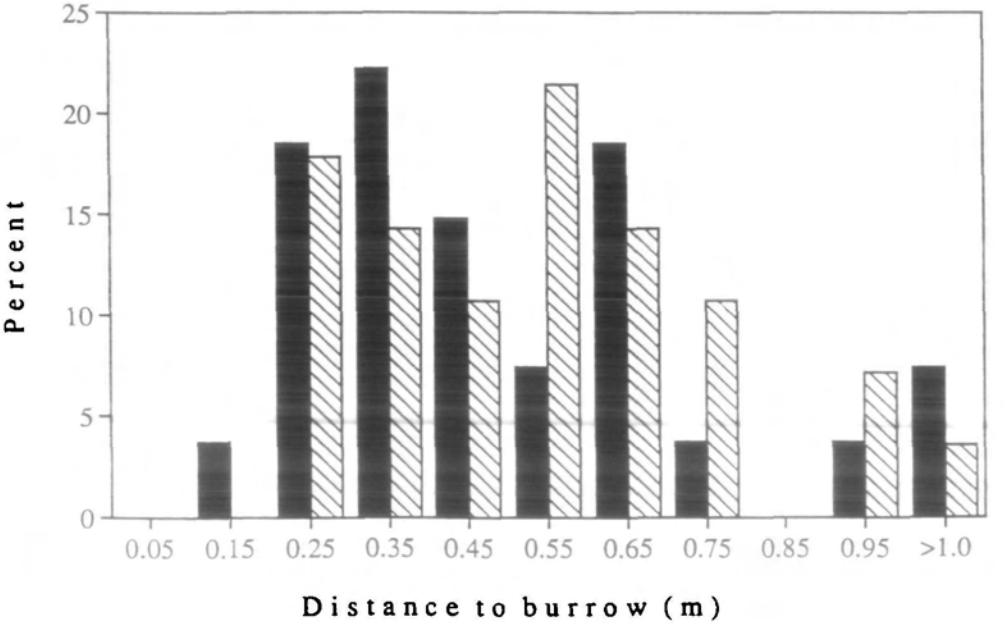

Figure 3
Frequency distribution of distances from the burrow at which woodchucks stopped after fleeing an approaching observer. Data are grouped into six distance categories and the sample size for the slow approach (black bars) and the fast approach (hatched bars), respectively, for each distance category are as follows: (1) 0–0.09 m (0,0); (2) 0.10–0.19 m (1,0); (3) 0.20–0.29 m (5,5); (4) 0.30–0.39 m (6,4); (5) 0.40–0.49 m (4,3); (6) 0.50–0.59 m (2,6); (7) 0.60–0.69 m (5,4); (8) 0.70–0.79 m (1,3); (9) 0.80–0.89 m (0,0); (10) 0.90–0.99 m (1,2); and (11) 1.00 m and more (2,1).

runs at an average velocity that is greater than that of the observer and increases FID with distance from the burrow. Similar relationships explain why the margin of safety would increase more quickly with the slow than the fast approach, although this was statistically significant only for the temporal margin of safety. If a prey is not fleeing at its maximal speed, it has the potential to increase velocity if the predator accelerates. This flexibility may be more important when the predator and prey are farther from the burrow. The greatest risk may come not from the fastest moving predator but from the one with the fastest maximum velocity. Such species would require larger margins of safety. In future studies, it would be interesting to see if margins of safety are adjusted independently of FID.

The lack of an effect of approach velocity on FID and escape velocity is surprising because predator velocity as been reported to influence FID in numerous studies (e.g., Dill, 1974; Rand, 1964; Walther, 1969), although this is by no means universal (Hurley and Hartline, 1974; Hutson, 1982). Perhaps the lack of an effect of approach velocity was a result of the small difference between treatments in our study.

Our finding that woodchucks often pause before going in their burrow confirms an observation by Schoonmaker (1966: 114): "Very often chucks will scurry to their dens at the first sign of danger, but once there they may stop, turn about and endeavor to see just what frightened them." A similar behavior was described in *Marmota olympus* by Barash (1989: 100): "they may enter it, or enter partially and then look outside, with their bodies either partially within the burrow or near the entrance." We examined this behavior further and found that the majority of animals go directly in their burrow when their initial distance to burrow is small (<2 m) and pause near the entrance of the burrow when this distance is more than 2 m. Animals being pursued very close to their burrow may have few other choices. When they are initially far from a refuge, stopping to check whether they are still being pursued may reduce costs such as lost opportunity to forage or inability to monitor the predator's position if the animal is not being immediately pursued.

Ydenberg and Dill's (1986) model used cost minimization as the optimization criterion, proposing that the animal should choose whichever action, stay or flee, has the lowest fitness cost. Since the cost of staying is equivalent to the benefit of fleeing, as recognized by Dill and Houtman (1989), Ydenberg and Dill (1986) in effect assumed that the animal should flee as soon as the benefits of fleeing exceed the cost. However, an animal that tolerated the approach of a potential predator until the difference between benefits and costs was maximal would have higher fitness than one that fled as soon as the benefits exceeded the costs. The benefits of fleeing should be interpreted as the sum of all increasing components of fitness resulting from fleeing versus staying; these would be primarily increases in survivorship. Similarly, the costs should be interpreted as the sum of all decreasing components in fitness resulting from fleeing versus staying; these would be the energetic cost of fleeing, the opportunity cost (time that could be spent in other activities such as foraging), and any increases in predation risk that might result from attraction of predators to the fleeing animal. This change in currency would not change the qualitative predictions, and the potential for measuring the benefits and costs to provide quantitative predictions seems remote at present. Nevertheless, it should be noted that increasing the distance from the burrow should increase the costs of fleeing as well as the benefits of a given FID. Thus the prediction that FID will increase with distance to refuge depends on the predominance of the effect of distance on the benefit curve. The positive relationships between FID and distance to refuge could be used to argue that the importance of the benefits of fleeing outweigh the costs. Given that one is survival and the other foraging time, this may not be too surprising (but see Abrams, 1993). However, the reverse pattern could be predicted when flight is very costly and its survival benefit slight.

Overall our findings and the results of many recent studies support the notion that animals take into account both the benefits and the costs of their actions in determining how to escape when they are facing an approaching predator. This supports the economic approach to antipredator behavior proposed by Ydenberg and Dill (1986). It suggests that simple, qualitative models can provide useful insights into flexible predator avoidance tactics. But it also indicates that progress will be limited until a way is found to obtain quantitative data on the consequences of alternative tactics.

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