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Direction of predator approach and the decision to flee to a refuge

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Abstract. How close should an animal allow a potential predator to approach before fleeing to a refuge? Fleeing too soon wastes time and energy that could be spent on other important activities, but fleeing too late is potentially lethal. A model to predict flight initiation distance was developed, based on the assumption that animals would flee at a distance that allows them to reach the refuge ahead of the predator by some margin of safety. This model predicts that (1) flight initiation distance should increase with distance from the refuge (which has been supported by studies on several species) and (2) the rate of increase of flight initiation distance with distance from a refuge should be higher when the refuge is between the predator and prey (prey runs towards the predator) than when the prey is between the predator and the refuge (prey runs away from the predator). Prediction 2 was tested by approaching juvenile woodchucks, *Marmota monax*, along an imaginary line between the animal and its burrow entrance and measuring the distance between the observer and the animal at the moment it started its flight. As predicted, the rate of increase in flight initiation distance was higher when the burrow was between the observer and the woodchuck than when the woodchuck was between the observer and the burrow. The slopes were appropriate for predators with pursuit speeds about twice the escape speed of the woodchucks. The difference between the slopes was 1.78 m flight distance/m distance to refuge, close to the value of 2 m flight distance/m distance to refuge predicted by the model. The intercept indicated that woodchucks allowed a margin of safety of about 7.6 m. The model permits quantitative evaluation of the principal elements of flexible escape decisions of animals and provides a measure of how predation risk increases the cost of space use in relation to distance from a refuge.

Animals often avoid predators by using refuges in which they are less vulnerable to capture. Foraging and other activities, however, necessitate leaving this protection. Predation risk from an encounter with a predator thus depends on distance to the refuge and to the predator when the prey starts to flee in relation to the relative speeds of the predator and prey. Since fleeing has costs in energy and time taken away from other important activities, animals should not necessarily flee as soon as a predator is detected (Ydenberg & Dill 1986). Instead, risk of capture should be traded off against the costs of fleeing, and animals should flee only when predators are a serious threat. Ydenberg & Dill (1986) developed a qualitative general model for flight initiation distance (distance from a predator at which a prey begins to flee) based on the assumption that animals would choose to flee or remain according to which had lower costs. Since remaining would be more risky when the distance to a refuge was greater, they predicted that flight initiation distance would increase with distance to a refuge. We have developed a quantitative model for the relationship between flight initiation distance and distance to a refuge. This model predicts that flight initiation distance should depend on the relative positions of the predator and the refuge. We tested these predictions in a field study of flight initiation distances in woodchucks, *Marmota monax*.

For a given distance of the prey from the refuge (DP), we define the critical attack distance (AD_{crit}) as the distance between the refuge and the predator at the initiation of an attack that will result in predator and prey reaching the refuge at exactly the same time. When $AD > AD_{crit}$ at the

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time the prey starts its flight, the prey will be safe; when $AD<AD_{crit}$, the predator will be able to capture the prey. Since the time to cover the critical attack distance is the same as the time for the prey to cover the associated distance to its refuge, then $DP/PV=AD_{crit}/AV$, where PV and AV are the running speeds of the fleeing prey and attacking predator, respectively. Therefore, $AD_{crit}=DP(AV/PV)$; critical attack distance increases directly with the prey's distance from the refuge and with the ratio of predator attack speed to prey flight speed. The critical flight initiation distance FID_{crit} for an approaching predator is the distance between the predator and prey at the time the predator reaches AD_{crit}. If an animal delays its flight until the FID_{crit}, slight errors in the estimation of either its own or the predator's distance or speed could be fatal. Therefore, one might expect some 'margin of safety' (MOS; Dill 1990) to be added to the AD_{crit}, and the expected flight initiation distance FID_{exp} should be the distance between predator and prey at the time the predator reaches AD_{crit} plus MOS. FID_{exp} will be strongly affected by the direction of the predator's approach relative to the refuge (Fig. 1a). If the predator is on the same side of the refuge as the prey, but further away, the prey will be running away from the predator and the FID_{exp} will be the difference between $AD_{crit}+MOS$ and DP. If the predator is on the side of the refuge opposite the prey, the prey must run towards the predator. AD_{crit} and MOS do not change, but FID_{exp} will be the sum of $AD_{crit}+MOS$ and DP. Thus, $FID_{exp,\ same}=DP[(AV/PV)-1]+MOS$ and $FID_{exp,\ opposite}=DP[(AV/PV)+1]+MOS$ (Fig. 1b). The slopes of the relationship between FID_{exp} and DP will be $(AV/PV)-1$ and $(AV/PV)+1$ for $FID_{exp,\ same}$ and $FID_{exp,\ opposite}$, respectively. The slopes are therefore expected to differ by two units of flight initiation distance per unit of distance to refuge.

Studies have supported the prediction that flight initiation distance would increase with distance to a refuge, although this relationship has not been found in all species or the full range of distances tested (Grant & Noakes 1987; McLean & Godin 1989; Dill & Houtman 1989; Dill 1990; Bulova 1994; Bonenfant & Kramer 1996). To our knowledge, the effect of the direction of predator approach has not been previously examined.

Our study species was the woodchuck. Woodchucks are large, terrestrial sciurid rodents that feed on leaves of a wide range of plants, often in open fields and meadows (Hamilton 1934). Burrows with one to several entrances are dug in open fields or along fences and hedgerows adjacent to such fields. Animals retreat to these burrows when disturbed and use them for sleeping, hibernating and rearing their young. Except for females with

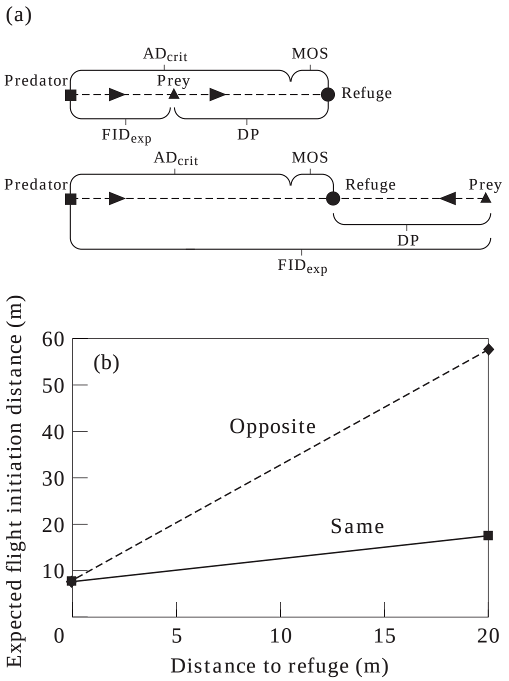

Figure 1. (a) Flight initiation distances for prey (triangle) exposed to a predator (square) approaching from the same side (above) and opposite side (below) as the refuge (filled circle) along the prey–refuge axis (dashed lines). The direction of predator and prey movement are shown by arrows. The prey's distance from the refuge (DP) and the ratio of predator to prey speeds define the critical attack distance (AD_{crit}) at which the predator can reach the refuge at the same time as the prey. If the prey allows a margin of safety (MOS), its expected flight initiation distance (FID_{exp}) is the distance between prey and predator when the predator reaches the critical attack distance plus the margin of safety. FID_{exp} equals $AD_{crit}+MOS-DP$ for a predator approaching from the same side and $AD_{crit}+MOS+DP$ for a predator approaching from the opposite side. (b) The relationship between distance to refuge and expected flight initiation distance for predators approaching on the same (solid line) and opposite (dashed line) sides of the refuge. The values shown are for a ratio of predator to prey speeds of 1.5 and a margin of safety of 8 m.

young, only one animal usually occupies a single burrow during the active season. We studied a relatively dense population occupying a public park with rolling terrain and a mixture of lawns, meadows and flower beds, shrubs and patches of forest, on Ile Notre Dame and Ile Sainte Hélène near Montreal. These woodchucks frequently encounter humans and are not as wary as hunted or unhabituated populations. Unlike grey squirrels, *Sciurus carolinensis*, and chipmunks, *Tamias striatus*, in similar situations, however, they are not tame and typically avoid approaching humans. In late autumn when this study was carried out, most adults are already hibernating, but young born that year are independent of their mothers and still actively foraging (Barash 1989). In a previous study (Bonenfant & Kramer 1996), we showed that flight initiation distance in response to an observer approaching from the same side of the refuge increased with distance from the animal to its burrow. Whether the observer approached at a slow or fast walking speed did not appear to affect flight initiation distance. The present study was carried out on the same population and at the same season as the previous study, but two years later. We tested the prediction that flight initiation distance would increase more steeply with distance to refuge when the observer approached from the direction of the refuge than when the observer approached from the direction opposite the refuge.

METHODS

The study area was searched so that locations of active burrows were known in advance. Then, from 6 September to 10 October 1995, one observer (M.B.) carried out all experimental trials as follows. When a woodchuck was found out of its burrow with no obstructions preventing it from running directly to its burrow or from having a clear view of the approaching observer, the observer randomly chose one of the two treatments. Then she aligned herself with the woodchuck and its nearest burrow entrance so that the woodchuck was between herself and the burrow (same side treatment) or the burrow was between herself and the woodchuck (opposite side treatment). She waited until the woodchuck had indicated that it had seen her by raising its head and looking in her direction, but had returned to foraging. The observer then began to walk towards the woodchuck at a slow pace (mean ± SD = 1.23 ± 0.002 m/s). When the animal began to move towards its burrow, she noted its position, started a stopwatch, dropped a marker to indicate her position, and continued to move towards the burrow at the same pace. When the animal either stopped running or entered its burrow, she stopped the stopwatch and again noted the position. Animals almost never stopped running more than 1 m from the burrow entrance, but sometimes stopped before entering (Bonenfant & Kramer 1996). Data were not included in a few cases when the woodchuck began running before the observer was in position or in three trials (all approaches from the opposite side) in which the animal ran to cover other than its burrow.

After the trial, all positions were marked and distances measured (± 10 cm) with a measuring tape. Measurements were distance from the animal to the observer at the time of flight initiation (FID), distance from the animal to the refuge (burrow) at the time of flight initiation (DP), distance run (this was slightly less than distance to the refuge if the animal stopped outside its burrow), and running time. Dividing distance run by running time gave running speed (PV). In a set of separate trials, a second observer was used to estimate inter-observer variation in determining the woodchuck's position. Differences in estimated flight initiation distances ranged from 0 to 0.6 m (0.22 ± 0.04 m, $N = 14$). This difference was less than 1% of the mean flight initiation distances in these cases. For a given treatment, each trial used a different individual as determined by burrow location. Some animals were tested a second time with the alternative treatment but never on the same day. The final data set included 31 animals tested on the same side, with 24 of these receiving the treatment first and 7 second, and 27 animals tested on the opposite side, with 18 tested first and 9 tested second.

Results were analysed by regression analyses using Systat 5.1 for the Macintosh. Slopes and intercepts are given ± 1 SE. Comparisons between slopes and intercepts were based on one-tailed *t*-tests. Preliminary analyses revealed no effect of testing order, so data from animals tested first and second with a given treatment were combined. Paired analyses were not feasible because of the limited number of individuals tested with both treatments, and because distance to the refuge often differed between tests for the same individual.

RESULTS

When the observer approached from the same side of the burrow, FID = DP × 1.09 (± 0.17) + 7.74 (± 1.20), where FID is flight initiation distance in metres and DP is the woodchuck's distance from the burrow in metres ($r^2 = 0.580$, $P < 0.001$). When the observer approached from the side opposite the burrow, FID = DP × 2.87 (± 0.39) + 7.41 (± 2.36) ($r^2 = 0.680$, $P < 0.001$; Fig. 2). The intercepts were not significantly different ($t_{54} = 0.124$, NS), but the slopes were ($t_{54} = 4.129$, $P < 0.0005$). The slope and intercept of flight initiation distance with the observer on the same side of the burrow did not differ significantly from values obtained at the same approach speed in the previous study (FID = DP × 0.84 (± 0.14) + 8.99 (± 1.39); Bonenfant & Kramer 1996). The difference between the slopes for approaches on the opposite and same side of the burrow was 1.78 m FID/m DP, quite close to the expected difference of 2.0 m FID/m DP.

As in Bonenfant & Kramer (1996), woodchuck running speeds were slower for animals close to their burrows, but did not change strongly with distance for animals further away. Slopes of regressions of PV versus DP for animals with DP greater than 3 m were 0.006 ± 0.030 (m/s)/m ($r^2 = 0.002$, NS) for animals approached on the same side and 0.04 ± 0.02 (m/s)/m ($r^2 = 0.18$, $P = 0.074$) for animals approached on the opposite side. For animals more than 3 m from their burrow, average running speeds were very similar for animals approached on the same side (2.61 ± 0.23 m/s) and opposite sides (2.51 ± 0.14 m/s). These values were very similar to the value of about 2.7 m/s obtained in the previous study.

If the margin of safety is not influenced by distance to refuge, the slope of the relationship between flight initiation distance and distance to refuge will equal the ratio of predator:prey running speeds minus one and plus one, for approaches on the same and opposite sides, respectively (see Introduction). We can therefore estimate the woodchuck's expectation of the ratio of predator:prey running speeds (AV:PV) as slope + 1 = 2.09 for approaches on the same side and slope − 1 = 1.87 for approaches on the opposite side.

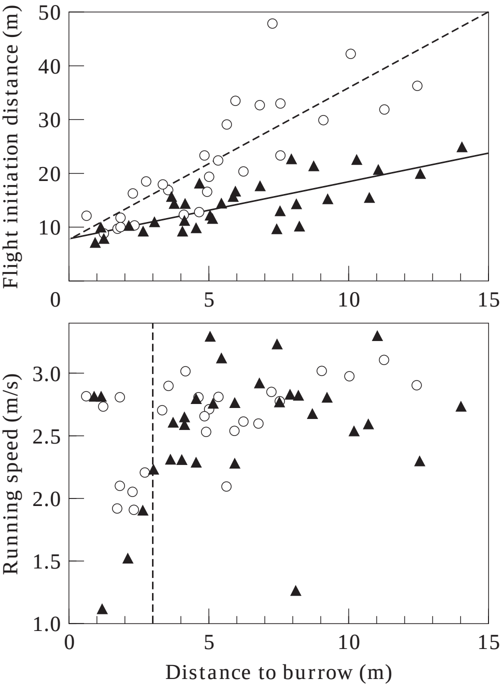

Figure 2. (a) The relationship between flight initiation distances and distance to burrow for woodchucks approached by an observer on the same side of the burrow as the woodchuck (▲, solid line) or on the opposite of the burrow from the woodchuck (○, dashed lines). (b) The relationship between running speed and distance to burrow for woodchucks approached by an observer on the same side (▲) or opposite side (○) of the burrow from the woodchuck. The vertical dashed line separates the observations into those in which the woodchuck was greater than or less than 3 m from its burrow entrance.

DISCUSSION

Woodchucks typically responded to the approach of the observer by fleeing towards the burrow as they would in response to a predator. As predicted by our model and the cost minimization model of Ydenberg & Dill (1986), flight initiation distances increased with distance between the woodchuck and its burrow. The experiment also supported the prediction of our model that flight initiation distance would increase more quickly with distance from the burrow when the observer approached from the side opposite the burrow than when the observer approached from the same side as the woodchuck. Therefore, woodchuck flight initiation decisions take into account the position of the threat relative to the location of the refuge as well as the animal's own distance from the refuge. The difference between the slopes also approximated the predicted value of 2 m FID/(m DP). This result suggests that the animal does not alter its assessment of risk and of running speeds in relation to its absolute distance from the predator.

Lotka (1928, 1932) developed a model for predator–prey interactions, showing that for a given prey position relative to the refuge, the critical attack distances for predators approaching from all directions form an ellipse, centred on the refuge with the prey position as one focus. In Lotka's model, the critical attack distance lay closer to the refuge for predators located off the prey–refuge axis than for those along the prey–refuge axis, because he assumed that the predator would remain oriented towards the fleeing prey during the entire attack and would therefore follow a curvilinear path. If the predator was able to identify the refuge and run directly towards it, the critical attack distance would be a circle centred on the refuge. In either case, critical attack distance would be the same for predators approaching along the prey–refuge axis, whether on the same or opposite side, and these two positions represent the minimal and maximal predicted flight initiation distances. However, the critical attack distance and therefore the flight initiation distance for predators approaching from other directions should depend on whether the predator orients towards the prey, towards the refuge, or somewhere in between, for example by attempting to intercept the flight path of the prey (Curio 1976).

Our model implicitly assumed that fleeing animals would run at their maximal speed, and hence that flight speeds would be independent of distance from the burrow. Actual running speeds of woodchucks in this study were approximately 2.6 m/s and were not strongly related to distance from the burrow, except that some individuals ran more slowly when they were within 3 m. Garland (1983) reported a maximal running speed of 4.4 m/s for woodchucks. In a study of adult golden marmots, *Marmota caudata*, Blumstein (1992) reported a mean running speed of 4.4 m/s in animals released after handling. Thus, the woodchucks in our study appeared to be running at speeds well below the species maximum. To what extent they were running below their own individual maxima is less clear, because they had not reached adult size and were carrying a large fat load just prior to hibernation. Running at less than maximal speeds could be advantageous for several reasons. Avoiding speeds that rely on anaerobic metabolism should reduce the total energy cost of the run and prevent fatigue (Kenagy & Hoyt 1989). High speeds may also reduce the quality of visual perception (Probst et al. 1986), so slower speeds may help avoid obstacles or predators other than the one that precipitated the flight. If increasing speeds have increasing costs, a modulation of speed with risk would not be surprising. However, despite running at less than their maximum speeds, the woodchucks did not adjust their speed to their distance from the burrow except when they were very close. It would be interesting to know whether running speed would change with different species of attackers or different types of approach. For example, would the woodchucks have run faster if the observer had accelerated instead of maintaining the same pace when the woodchuck started to run?

Flight decisions should be sensitive to the pursuit speed of the predator. Some evidence suggests that flight initiation distance increases with predator approach speed (reviewed in Ydenberg & Dill 1986). A safer option, however, would be to adjust flight initiation distance to the maximal pursuit speed of the predator; otherwise, a predator could get within the critical attack distance by moving slowly then accelerate for the capture. The slope of the relationship between woodchucks' flight initiation distances and distance to the burrow were appropriate for a ratio of attack speed to escape speeds of about 2. For a woodchuck with a running speed of 2.6 m/s, this would be 5.2 m/s close to maximal aerobic speeds of humans (5.6 m/s Garland 1983). For the maximal running speed of 4.4 m/s, the estimated predator speed of 8.8 m/s is considerably below maximal running speeds of humans in athletic competitions (11 m/s, Garland 1983). Other potential terrestrial predators such as dogs, *Canis familiaris*, and coyotes, *C. latrans*, have maximal aerobic speeds of 11 m/s and maximal running speeds of 18 m/s (Garland 1983). Little is known, however, about the relationship between maximal running speeds and the speeds actually used by predators while pursuing prey. It would be interesting to determine to what extent flight initiation distances are adjusted to the maximal speeds of different predators and what cues the woodchucks use to estimate maximal speeds.

Bonenfant & Kramer (1996) calculated margins of safety from the expected distance between the observer and the burrow at the time the woodchuck reached the burrow and the expected difference between the time the woodchuck reached its burrow and the time the observer would have reached it. These calculations assumed that the observer continued to approach at the same speed and led to the conclusion that margins of safety increased with distance to the burrow. As with running speed, however, an animal should probably base margin of safety decisions on the potential pursuit speed of a predator rather than the current pursuit speed. Thus, the margin of safety is probably better calculated from the intercept of the relationship between flight initiation distance and distance to burrow. This calculation indicates that woodchucks in our study area show a spatial margin of safety of about 7–8 m. Margin of safety calculated in this way did not differ with direction of approach and might be constant for a given set of conditions. However, trade-offs between predation risk and benefits of remaining away from the burrow might be expressed as changes in the margin of safety. By using a model in which all components can be measured, our approach should permit future quantitative investigations of hypotheses concerning how effects on different components of the escape process should affect anti-predator decisions.

Anti-predator decisions in relation to refuge location have important implications for the use of space. Because the area of danger increases with distance from a refuge, predation risk may set an upper limit to the distance that animals can travel from a refuge. If refuges are limited and escape speeds low relative to attack speeds of predators, this could result in an optimal home range size less than that predicted by foraging economics and resource defence considerations (Lotka 1932; Covich 1976; Taylor 1988). On the other hand, if refuges are naturally available or can be constructed at different locations, the home range can be expanded (Covich 1976). Other marmot species dig additional refuge burrows at a distance from their main sleeping burrow (Holmes 1984), and woodchucks move from one burrow system to another during the active season (Merriam 1971). Even within a relatively safe home range, anti-predator behaviour could have important implications for space use. First, the area in which a predator is a threat increases as animals move further from their refuge. This may necessitate greater scanning effort or increase the chance of a predator actually getting within the critical attack distance. Secondly, animals that respond to potential threats will have to retreat to the refuge on more occasions when a larger area is involved, and each trip is longer and hence more costly. Therefore, the net benefits of areas further from the refuge will be much lower than those predicted by foraging economics alone.

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REFERENCES

Barash, D. P. 1989. *Marmots: Social Behavior and Ecology*. Stanford, California: Stanford University Press.

Blumstein, D. T. 1992. Multivariate analysis of golden marmot maximum running speed: a new method to study MRS in the field. *Ecology*, **73,** 1757–1767.

Bonenfant, M. & Kramer, D. L. 1996. The influence of distance to burrow on flight initiation distance in the woodchuck, *Marmota monax*. *Behav. Ecol.*, **7,** 299–303.

Bulova, S. J. 1994. Ecological correlates of population and individual variation in antipredator behavior of two species of desert lizards. *Copeia*, **1994,** 980–992.

Covich, A. P. 1976. Analyzing shapes of foraging areas: some ecological and economic theories. *A. Rev. Ecol. Syst.*, **7,** 235–257.

Curio, E. 1976. *The Ethology of Predation*. Berlin: Springer-Verlag.

Dill, L. M. 1990. Distance-to-cover and the escape decisions of an African cichlid fish, *Melanochromis chipokae*. *Environ. Biol. Fish.*, **27,** 147–152.

Dill, L. M. & Houtman, R. 1989. The influence of distance to refuge on flight initiation distance in the gray squirrel (*Sciurus carolinensis*). *Can. J. Zool.*, **67,** 233–235.

Garland, T., Jr 1983. The relation between maximal running speed and body mass in terrestrial mammals. *J. Zool., Lond.*, **199,** 157–170.

Grant, J. W. A. & Noakes, D. L. G. 1987. Escape behaviour and use of cover by young-of-the-year brook trout, *Salvelinus fontinalis*. *Can. J. Fish. Aquat. Sci.*, **45,** 1390–1396.

Hamilton, W. J., Jr 1934. The life history of the rufescent woodchuck, *Marmota monax rufescens* Howell. *Ann. Carneg. Mus.*, **23,** 85–179.

Holmes, W. G. 1984. Predation risk and foraging behavior of the hoary marmot in Alaska. *Behav. Ecol. Sociobiol.*, **15,** 293–301.

Kenagy, G. J. & Hoyt, D. F. 1989. Speed and time-energy budget for locomotion in golden-mantled ground squirrels. *Ecology*, **70,** 1834–1839.

Lotka, A. J. 1928. Families of curves of pursuit and their isochrones. *Am. Math. Month.*, **35,** 421–424.

Lotka, A. J. 1932. Contribution to the mathematical theory of capture. I. Conditions for capture. *Proc. natn. Acad. Sci. U.S.A.*, **18,** 172–178.

McLean, E. B. & Godin, J.-G. J. 1989. Distance to cover and fleeing from predators in fish with different amounts of defensive armour. *Oikos*, **55,** 281–290.

Merriam, H. G. 1971. Woodchuck burrow distribution and related movement patterns. *J. Mammal.*, **52,** 732–746.

Probst, T., Brandt, T. & Degner, D. 1986. Object-motion detection affected by concurrent self-motion perception: psychophysics of a new phenomenon. *Behav. Brain Res.*, **22,** 1–11.

Taylor, R. J. 1988. Territory size and location in animals with refuges: influence of predation risk. *Evol. Ecol.*, **2,** 95–101.

Ydenberg, R. C. & Dill, L. M. 1986. The economics of fleeing from predators. *Adv. Study Behav.*, **16,** 229–249.