The influence of distance to refuge on flight initiation distance in the gray squirrel (*Sciurus carolinensis*)

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Gray squirrels (*Sciurus carolinensis*) typically run to the nearest tree to escape from predators they encounter while foraging on the ground. As the risk of capture increases with distance from the refuge tree, squirrels feeding far from trees should have greater flight initiation distances than those feeding closer by. This prediction was confirmed: flight initiation distance in response to a motorized model predator (a cat) increased as distance to refuge increased. This could not be attributed to any effect of distance to refuge on vigilance.

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À l'arrivée d'un prédateur alors qu'ils sont en train de se nourrir par terre, les écureuils gris (*Sciurus carolinensis*) ont un réaction typique, celle de grimper dans l'arbre le plus proche. Étant donné que le risque de capture augmente en fonction de la distance de l'arbre le plus proche, il est permis de croire que chez les écureuils qui se nourrissent loin des arbres, le déclenchement de la réaction de fuite se produit à une distance plus grande que chez les écureuils qui se nourrissent près des arbres. Cette prédiction a pu être confirmée : la distance au moment de la fuite à l'approche d'un modèle de prédateur (un chat) monté sur moteur augmente en fonction de l'éloignement de l'abri le plus proche. Cette observation n'a pu être attribuée à aucun effet de la distance animal–refuge sur la vigilance.

Introduction

Animals faced with approaching predators must decide at which distance to initiate their flight, and they are expected to do so in a way that maximizes their fitness (Ydenberg and Dill 1986). As flight has both costs (including lost opportunity) and benefits, there will be in general an optimal flight initiation distance, defined as the first point in a predator's approach at which the benefit of flight exceeds the cost. The benefit of flight is equivalent to the cost of remaining in place or, in other words, to the risk of capture. For animals that run to refuge or cover to escape their predators, risk increases with the distance to or time from the refuge (see, for example, the simulation results of Dill 1973). As the optimal flight initiation distance should increase as the risk of capture increases (Ydenberg and Dill 1986), then animals far from a refuge should have longer flight initiation distances than those closer by. The purpose of this paper is to test this prediction experimentally.

We do so by measuring the flight initiation distances of gray squirrels (*Sciurus carolinensis*) faced with a model predator while feeding on the ground at various distances from the trees to which they characteristically run when attacked. Gray squirrels are good candidates for making such adaptive adjustments to their escape behaviour; they have been shown in previous studies to be capable of making trade-offs between feeding efficiency and risk of predation (Lima and Valone 1986; Lima *et al.* 1985).

Methods

The experiment was carried out between 26 June and 24 July, 1985, at Stanley Park, Vancouver, B.C. The area was lightly forested with a mixture of conifers and deciduous trees, with Douglas-fir (*Pseudotsuga menziezii*) the dominant species. The ground surface was packed soil, fine gravel, or low sparse grass, with scattered leaf litter throughout. All trials were performed between 08:00 and 12:00, on dry days.

A stuffed house cat (*Felis domesticus*), prepared in a crouching position and mounted on the chassis of a radio-controlled car, served as the predator. This allowed control of the timing, speed, and direction of attack. The car's electric engine made a low-pitched whine while running, but this had the advantage of drawing the squirrel's attention to the approaching predator. The model predator's speed was kept as constant as possible, and was measured at 1.31 ± 0.26 $m \cdot s^{-1}$ ($\bar{x} \pm$ SD) from a sample of 20 timings along a known path length in the study area.

The gray squirrel's distribution in British Columbia is limited to Stanley Park, where it was introduced in 1914 (Cowan and Guiguet 1965). Although quite tame toward people, they are frequently attacked by cats from surrounding neighbourhoods (L. LeSage, Stanley Park Zoo Manager, personal communication). Squirrels are well suited for this study, as they sit on their haunches and continue to scan for potential predators while eating (Lima *et al.* 1985). The only time a predator can approach undetected is when the squirrel is bending down to pick up another food item. Therefore, as long as feeding rate is independent of distance to refuge, any patterns in the squirrels' fight initiation distance cannot be explained as being caused by changes in their likelihood of detecting the predator. We checked this by measuring the time squirrels took to eat 10 experimental food items (see below) at three distances from trees ($n = 10$ in each case).

We chose six values of distance to refuge (0.5, 1, 2, 3, 4, and 5 m) for the experiment, and selected the distance for a particular trial at random. The food items (10 unsalted, roasted peanut halves) were placed at a preselected distance from a mature Douglas-fir (diameter at breast height >0.4 m) standing apart from surrounding trees; this tree was the intended refuge and only trials in which the squirrel fled toward that tree are included in the data set. Besides having a tree standing apart, all sites had at least one clear, well-graded predator approach path leading straight toward this tree; the peanuts were always placed on one of these paths.

Trials were performed at seven such sites within the study area. The site used for a particular trial was decided by where a squirrel presented itself for testing. The squirrel first attracted to the peanuts served as the subject. Whenever possible, consecutive trials were performed at different sites, with new subjects. Where no other squirrels were available, the same squirrel was used, but only after at least

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10 min had passed. No squirrel was used more than three times a day. Although an accurate tally of squirrels could not be made, we estimated (from variability in markings and pelage damage) that the study population consisted of at least 10 animals.

Once the subject squirrel was aware of the peanuts, the investigator gently placed the cat on the approach path, at least 8 m away, and sat down beside the path (with radio transmitter in hand), at least 6 m from the squirrel. When the squirrel had been estimated to have eaten four to five peanut halves and had sat up to begin another one, the predator was advanced straight toward the tree and the squirrel. The instant the squirrel began to flee, the investigator noted the position of the predator and stopped its approach. The flight initiation distance (cat to squirrel) could then be estimated. Occasionally a second observer independently estimated the flight distance; there was always good agreement between the two estimates.

Other gray squirrels or native red squirrels (*Tamiasciurus hudsonicus*) often were attracted to the area during a trial. In such cases the trial was aborted, to avoid the effect that varying competition pressure would have on the opportunity cost of flight (Ydenberg and Dill 1986). The presence of other squirrels could also dilute the risk of capture and thus influence the benefit of flight.

Acceptable trials were those in which the subject squirrel ran toward the intended refuge tree. The squirrels often (about 50% of trials) stopped before they had actually reached the tree, but this was probably because the cat's approach had been stopped by the investigator, and such trials were therefore considered acceptable. To maintain a high opportunity cost of flight only those trials in which at least two peanut halves remained were used (remaining peanut halves after a trial averaged 4.4). The experiment was continued until 15 useable trials were obtained for each distance to refuge. Anywhere from 3 to 10 acceptable trials were obtained per day during 18 testing days.

Data were analyzed with ANOVA to test the null hypothesis that flight initiation distance was independent of distance to refuge, using formulae appropriate for the case in which there are many y values for each x value (Sokal and Rohlf 1981). The best fit linear relationship between flight initiation distance and distance to refuge was then determined by regression.

Results

Flight initiation distance (FID) did increase with distance to refuge (DR) (Fig. 1). This trend is highly significant (among groups $F_{[5,84]} = 5.42, p < 0.001$). It appears that flight initiation distance may increase most rapidly at a distance to refuge between 2 and 3 m. Nevertheless, a simple linear regression provides a significant fit (FID = 2.19 + 0.385 DR; $F_{[1,4]} = 11.00, p < 0.05$). Adding trial number (1–90) as a second independent variable does not explain a significant proportion of the remaining variance. Thus, there is no evidence of habituation across the experimental series.

The time taken to eat a peanut half was independent of distance to refuge: it averaged 18.85 s (SE 1.82) at 0.5 m, 21.09 s (1.75) at 2 m, and 16.84 s (0.95) at 5 m ($F_{[2,27]} = 1.68, p > 0.2$). Lima and Valone (1986) and Lima *et al.* (1985) also found the handling time per food item of the gray squirrel to be independent of distance to cover, although it was shorter for items eaten in the open than those carried to cover. As squirrels at all distances could therefore have spent the same proportion of time scanning, we conclude that the effect of refuge distance on flight initiation distance could not have been the result of differential vigilance.

Discussion

According to the economics of escape hypothesis of Ydenberg and Dill (1986), a squirrel should start to flee when its estimate of the benefit of flight (the cost of staying) exceeds its estimate of the cost of flight. As the benefit of flight increases with distance to an effective refuge, the hypothesis predicts that a squirrel's flight initiation distance should increase with its distance to the nearest tree. This prediction was confirmed in the present study.

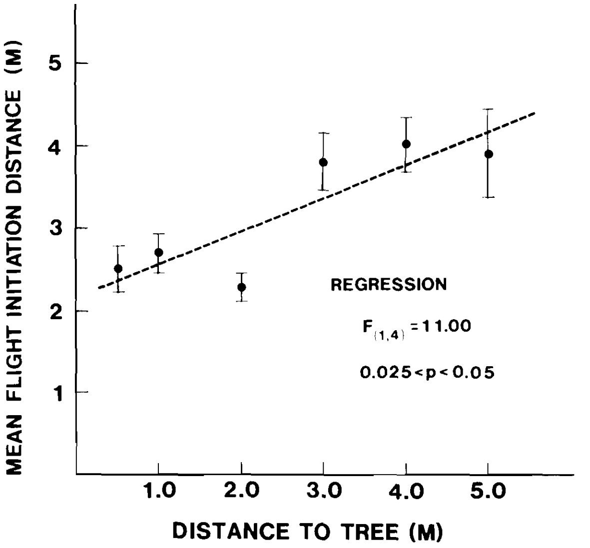

FIG. 1. The relationship between mean gray squirrel flight initiation distance in response to an approaching model predator (n = 15 in each case) and distance to the tree used as a refuge. Vertical bars represent ±1 SE.

Ours is the first experimental test of this prediction, although Grant and Noakes (1987) have recently compared the flight initiation distances of juvenile brook trout (*Salvelinus fontinalis*) to a human observer, in areas of high and low cover availability (corresponding to short and long distances to the nearest cover, respectively). Although the trout's flight distance was greater in areas with long average distances to cover (consistent with our hypothesis), there are several possible confounding factors in their study. For example, prey may have been more abundant in areas of high cover, and flight distances might have been lower there because of the increased opportunity costs of flight (a fleeing prey cannot continue to feed). Such an effect has been demonstrated in the waterstrider *Gerris remigis* (Dill and Ydenberg 1987) and in brook trout in another study stream (Grant and Noakes 1987).

It was apparent that the squirrels in our study were often aware of the approaching model some time before they actually fled, as they were often seen to stop eating and stare intently at it. This provides further evidence that the observed flight initiation distances resulted from behavioural decisions made by the squirrels, and were not due to any effect of distance to refuge on vigilance or detectability. There is also independent physiological evidence that awareness occurs a considerable period of time before flight in gray squirrels (Smith and Johnson 1984).

A slow-moving prey should have longer flight initiation distances than faster individuals, as shown in the lizard *Anolis lineatopus*, whose flight initiation distance is increased at low temperatures to compensate for lower running speeds (Rand 1964). This makes the important point that the critical parameter from the prey's point of view is actually time to cover rather than distance *per se*. We have tacitly assumed (without measuring it) that our squirrels' running speed was fixed, but of course it might be varied adaptively by the animal. In fact, it is possible that the apparent nonlinearity in the flight distance relationship (Fig. 1) was the result of the squirrels choosing to hold flight initiation distance constant over the low range of values of distance to refuge, and to increase their velocity instead. Cichlid fish (*Melanochromis chipokae*) appear to vary both flight initiation distance and escape velocity with distance to cover in laboratory experiments, although only the former effect is significant (L. M. Dill, manuscript in preparation). Another possible explanation of the apparent nonlinearity in Fig. 1 is that the squirrels delayed their flight at intermediate distances to refuge to give a pursuit deterrence signal to the predator (Woodland *et al.* 1980). This tactic is expected to be most beneficial to the prey at intermediate distances to refuge, and is most common at such distances in the zebra-tailed lizard, *Callisaurus draconoides* (Hasson et al. 1989). Unfortunately, we did not film the interactions and therefore cannot reject either of the above possibilities.

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The functional significance of adrenergic pH regulation in fish erythrocytes

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TUFTS, B. L., and RANDALL, D. J. 1989. The functional significance of adrenergic pH regulation in fish erythrocytes. Can. J. Zool. **67**: 235–238.

Experiments were conducted *in vitro* to determine the presence or absence of an adrenergic pH effect in the erythrocytes of *Squalus suckleyi*, *Raja binoculata*, and *Oncorhynchus tshawytscha*. Adrenergic stimulation significantly increased the erythrocyte pH of *Oncorhynchus tshawytscha*, but did not significantly affect the erythrocyte pH of *Squalus suckleyi* or *Raja binoculata*. The results support the view that the functional significance of adrenergic pH regulation in fish erythrocytes is to offset the reduction in blood oxygen carrying capacity caused by the Root effect.

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Des expériences *in vitro* ont permis de déterminer l'existence ou l'absence d'un effet adrénergique du pH dans les érythrocytes de *Squalus suckleyi*, de *Raja binoculata* et d'*Oncorhynchus tshawytscha*. La stimulation adrénergique augmente significativement le pH des érythrocytes chez *Oncorhynchus tshawytscha*, mais n'a pas d'effet significatif chez *Squalus suckleyi* ou *Raja binoculata*. Ces résultats corroborent la théorie selon laquelle le rôle fonctionnel de la régulation adrénergique du pH dans les érythrocytes de poissons est de compenser la diminution de la capacité de transport d'oxygène du sang causée par l'effet Root.

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