Distance-to-cover and the escape decisions of an African cichlid fish, *Melanochromis chipokae*

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Synopsis

The risk to a prey individual in an encounter with a predator increases as the distance to protective cover increases. Prey should therefore initiate their flight to cover at longer distances from an approaching predator (i.e. sooner) and/or flee at greater velocities, as the distance to cover increases. These predictions were tested with an African cichlid fish, *Melanochromis chipokae* presented with a looming stimulus simulating an attacking predator. The fish varied their flight initiation distance as predicted, but there was no significant effect of distance-to-cover on escape velocity. Nevertheless, the cichlids appeared to choose a combination of flight initiation distance and escape velocity which ensured they reached cover with a constant temporal 'margin of safety'.

Introduction

Animals which flee to cover to escape their predators must choose both a distance from the predator at which to initiate their flight and an escape velocity. In general, these are not expected to be the maximal distance and velocity achievable, but rather those which maximize the prey individual's fitness, taking into account the costs of escape (primarily lost opportunity to engage in other activities; Ydenberg & Dill 1986). Since risk of capture should increase as the prey's distance-to-cover increases (see, for example, the simulation results of Dill 1973), flight initiation distance might be expected to be greater for prey further from cover. This appears to be true in both the gray squirrel, *Sciurus carolinensis* (Dill & Houtman 1989), and the brook charr, *Salvelinus fontinalis* (Grant & Noakes 1987). Escape velocity was not measured in either of these studies, however, but was assumed to be invariant.

If escape velocity (EV) were indeed constant then distance-to-cover (DC) would be directly proportional to time-to-cover (TC), the critical parameter from the prey's point of view. However, most prey can probably vary their escape velocity, and therefore might control time-to-cover in that way, since TC = DC/EV. As long as the prey reaches cover before the predator can get there, the prey will be secure. The purpose of the study reported here was to test the hypothesis that small cichlid fish escaping to the shelter of rocks will vary flight initiation distance and/or escape velocity with distance to cover. The results suggest that the fish do in fact choose values of these two behavioural parameters which assure them of reaching cover with a fixed margin of safety.

Methods

The subject fish were three individuals of *Melanochromis chipokae* (Johnson 1975) purchased from a

local aquarium store. These fish are members of the 'mbuna' group of rock-dwelling cichlids from Lake Malawi (Fryer & Iles 1972). They were chosen because of their characteristic escape behaviour: attacked by a predator, they flee to a refuge provided by rocks. The three fish averaged 4.9, 5.5 and 5.7 cm total length at the time of the experiments. Data were collected over a 10 month period, but the fish grew little during this time. Although the sample size is small, it proved impossible to obtain additional specimens of this species.

The test aquarium (Fig. 1) consisted of a long rectangular tank (122 × 14.5 × 20.5 cm high) with a glass bottom; water depth was 16.5 cm. Two rocks positioned on reference marks on the bottom provided a refuge for the fish at one end. A feeder could be hung in the tank at calibrated distances from the front edge of these rocks, and immediately in front of a small 45° mirror spanning the width of the tank. A black styrofoam ball (10.2 cm diameter) was positioned 117 cm directly above the centre of the mirror, attached with monofilament line to a pulley driven by a 6 V DC motor. The motor unwound the line, lowering the ball at a controlled speed (averaging 14.2 cm s^{-1}). The length of the line was such that the ball reversed direction just as it touched the water surface.

The feeder consisted of an orange plastic hanger with a small depression drilled in it to hold a tablet of dry food (Tetratabs TM). The test fish had been conditioned to approach an orange feeder in their home tanks, and to graze on the tablet, much as they probably graze algal slime from rocks in the field (Fryer & Iles 1972). The feeder was placed so that a feeding fish had to be positioned sideways in the tank, its left eye always toward the mirror. Once the ball began to fall the fish experienced a black solid looming toward it; such a stimulus is effective at eliciting escape in other small fishes (Dill 1974a). The mirror, feeder and overhead motor moved as a single unit, so that the ball always fell in the same part of the mirror and at the same height as the food tablet, producing a consistent stimulus. An opaque piece of plexiglass directly above the feeder prevented the fish from seeing the falling ball directly. The entire apparatus was surrounded with black plastic curtain to prevent ex-

ternal disturbance. A video camera was positioned between the feeder and the rocks so as to film (in another 45° mirror beneath the tank) the feeder, the fish, and the ripples caused by the ball striking the water surface. The ball itself was usually not in camera view, and the rocks were not always visible at the longest refuge distances. The camera also filmed two lamps added part way through the experiments. One of these lit when the ball began its descent, and the other lit just as the ball touched the surface of the water. The first lamp made it possible to recognize (and edit from the data set) any startle responses to the noise of the motor. The second lamp was added due to occasional difficulties seeing the ripples. This lamp also allowed the spread of the ripples to be timed so that the instant that the ball hit the water in earlier tests could be determined accurately, even when the ripples could not be seen immediately in any particular trial. Neither lamp was visible to the fish.

Between tests the fish were fed in their home aquaria, using the same tablets in an orange holder, in order to maintain the conditioned association. Feeding was carried out in the afternoon, 18–23 h prior to testing, so that the hunger level of the test fish (and the lost opportunity cost of escape) would be consistently high.

A fish which had been regularly 'hover feeding' in its home tank (i.e., feeding calmly and remaining within 2 cm of the tablet) was chosen for testing. The distance-to-cover was chosen randomly, subject to the constraint that each fish was tested only once at each of 6 distances: 15, 25, 35, 45, 65, and 95 cm from the rocks. The test fish was gently transferred to the pre-arranged test aquarium and allowed free access to it for one hour, after which the loaded feeder was put in place. Once the fish had begun hover feeding the motor was switched on and the response of the fish to the falling ball filmed. A test was aborted if the fish did not hover feed within 20 min. Only trials in which the fish fled rapidly and for at least 10 cm toward the rocks were accepted.

The ball's position above the water surface at the time the test fish began to flee could be determined from the speed of the ball and the subsequent time taken for it to strike the water (noted by the ripples
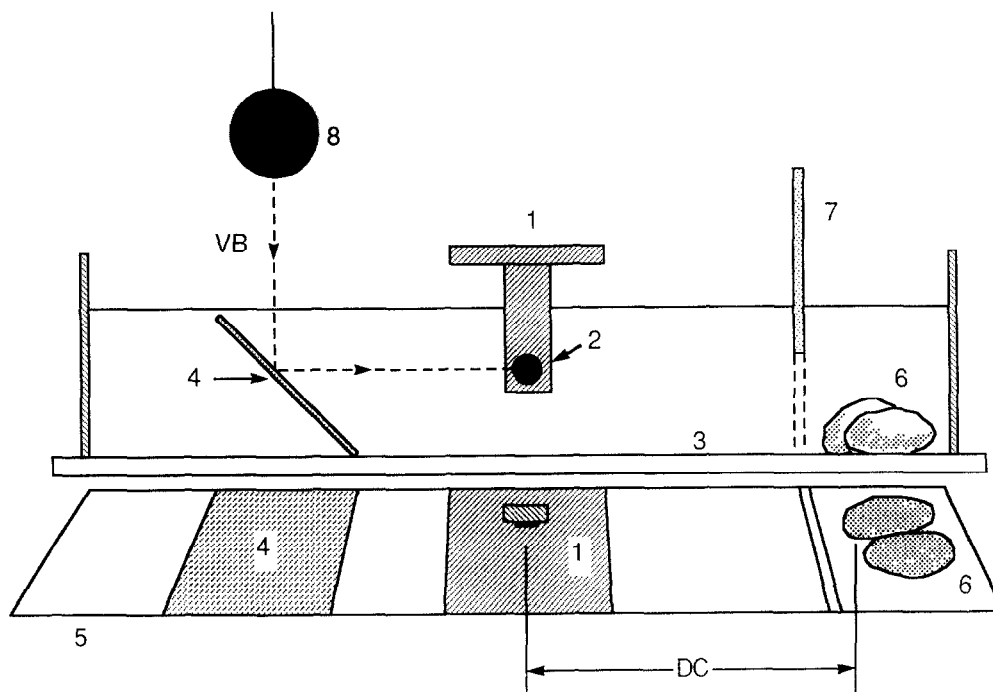
Fig. 1. The apparatus used to measure flight initiation distance as a function of distance-to-cover. (1) orange plastic feeder, containing (2) a food pellet; (3) glass tank bottom; (4) 45° mirror in which the threat stimulus appeared to the fish; (5) 45° viewing mirror; (6) rocks serving as shelter for the fish; (7) sliding door (open during test); and (8) black styrofoam ball connected to an electric motor with monofilament line.

or the lamp). The fish's flight initiation distance was calculated as the sum of this measure plus the distances from the mirror centre to the water surface (5 cm) and to the food tablet (10 cm). The fish's velocity over the first 10 cm of its flight path (or to any pause) was also measured from the videotapes; this was a true vector velocity, measured along the long axis of the tank. Data were collected intermittently from 10.7.1985 to 15.5.1986. The water temperature was 21°C, and the light intensity at the water surface was 750 lux.

Results

Flight initiation distance increased as distance-to-cover increased (Fig. 2), and the overall regression (more than one value of y for each x; Sokal & Rohlf 1969) was highly significant, despite the small sample size (ANOVA; $F_{1,15} = 15.95$, $p < 0.01$). The relationship between flight initiation distance and distance-to-cover was also consistent across fish (dummy variable regression; Kleinbaum & Kupper 1978). Although there is a suggestion of non-linearity in these data, the simple linear regression provides an adequate fit and there is no a priori reason to fit a more complicated model.

The situation with regard to escape velocity was somewhat more complex, owing to missing data points. In 5 of the 18 trials the fish stopped before reaching cover, and in 5 others the rocks were not in the camera field of view. The former cases were not considered further, but escape velocity could be estimated in four of the latter cases by the fish's velocity to a brief pause or change of direction in the flight path. Thus, the sample size for escape velocity is only 12. There was no significant effect of distance-to-cover on escape velocity. However, there was a tendency for relatively long flight initiation distances to be accompanied by relatively low escape velocities (Fig. 3), although this regression was not significant ($F_{1,10} = 1.38$, $p < 0.30$).
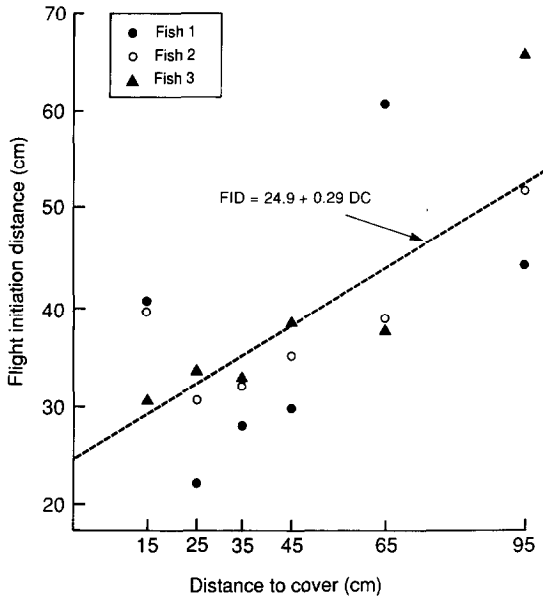
Fig. 2. Flight initiation distance of the three test cichlids in relation to their distance-to-cover. The regression is significant (p<0.01), and consistent across fish.

Fig. 3. The relationship between the cichlids' relative escape velocity in a particular trial $(EV_i / \overline{EV})$ and their relative flight initiation distance in that trial $(FID_i / \overline{FID})$. Mean FID was calculated from the data for all 18 trials; mean EV only from the 12 represented here. EV_i was usually measured directly (●) but had to be estimated from the time to reach a pause in the flight path in 4 cases (○).

This relationship suggests the possibility that the fish may have been controlling some compound temporal variable related to time-to-cover (TC). In particular, they may have varied both flight initiation distance (FID) and escape velocity (EV) in such a way as to reach cover a constant amount of time before the attacking predator. The difference in time between when the prey would reach the rocks (if it continued moving at a constant velocity, EV) and when the model predator would do so (if it also continued moving at constant velocity, VB), can be calculated as:

$$((FID + DC)/VB) - (DC/EV) = MS, \quad (1)$$

where MS is the temporal 'margin of safety'. If the fish chose an EV and FID in order to achieve a constant margin of safety (MS*), then the following relationship should hold:

$$(FID + DC)/VB = MS^* + (DC/EV). \quad (2)$$

A plot of (FID + DC)/VB against DC/EV should therefore yield a straight line with a slope of 1.0 and a y-intercept equal to the achieved margin of safety. This is shown in Figure 4. The regression is
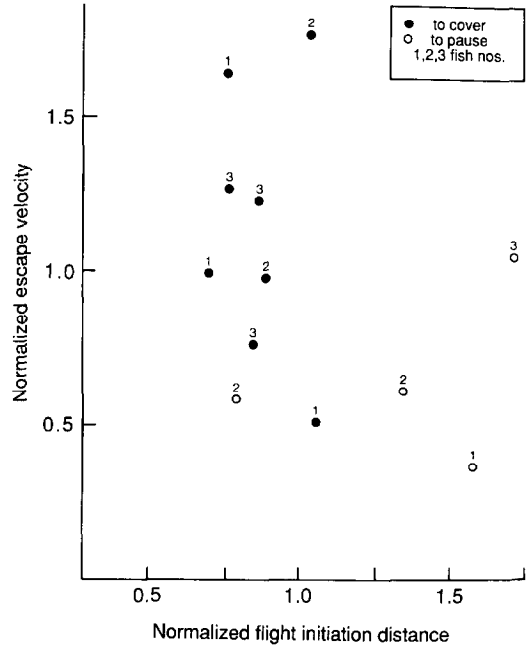
significant $(F_{1,10} = 23.11, p < 0.05)$, and the observed slope does not differ significantly from 1.0. The margin of safety estimated from this regression is 3.4 s. By conditioning the regression to have a slope of exactly 1.0 (as required by the hypothesis), a better estimate of the margin of safety is obtained: 2.34 ± 0.52 (s.e.) s. Of course, a significant correlation in Figure 4 is almost inevitable, given that DC must occur on both sides of eqn. 2. However, the important point is not that they are correlated, but that the slope approximates 1.0, and the intercept is non-zero.

Although the results support the hypothesis that the cichlids aimed to achieve a constant margin of safety, the fish appeared to do so primarily by adjusting flight initiation distance. A larger sample size might reveal dual parameter control of the margin of safety, however. This conjecture is supported by the fact that re-analysis of the relationship between (FID + DC)/VB and DC/EV (Fig.
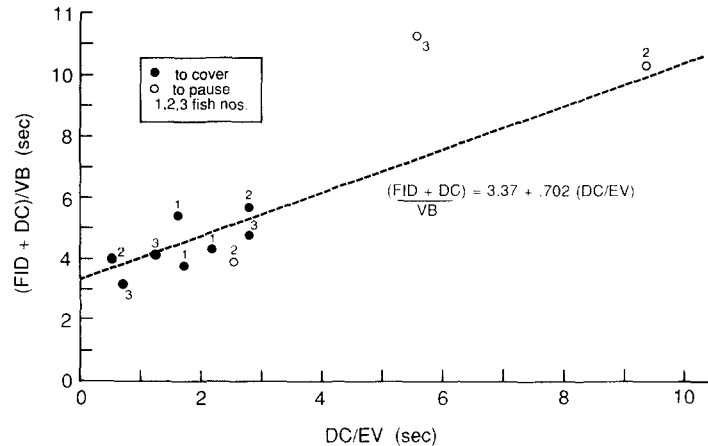
Fig. 4. The time it would take for the 'predator' to reach the cover [(FID + DC)/VB] compared to the time taken for the escaping fish to get there (DC/EV). Symbols as in Figure 3.

4), but using the mean observed value of EV (18.43 cm s^{-1}), results in a slope significantly greater than 1.0. That is, if it is assumed that all the variance in escape velocity is random, there is no evidence for the fish maintaining a constant margin of safety.

Discussion

Having detected an attacking predator, a prey animal can choose the distance from the predator at which to initiate flight, as well as an escape speed and heading. If escape is characteristically toward shelter, as in the present case, then the animal must make decisions only about the first two parameters. These decisions are crucial to the animal's fitness: if the chosen values of either flight initiation distance or escape velocity are too low, the animal will not reach cover in time to escape, but if they are too high, the animal will waste either energy or the opportunity to engage in other fitness-enhancing activities. Thus, in general, these and other parameters of escape behaviour should be optimized rather than maximized (Ydenberg & Dill 1986). Escape velocity might also be varied in a more dynamic fashion than envisioned here, i.e., the fish could accelerate if the predator were gaining ground. However, escape velocity has been considered constant within a flight for simplicity.

As the distance-to-cover increases, the prey must increase either its flight initiation distance, its escape velocity, or both, if it is to maintain the same level of security, i.e., give itself the same odds of escape. The cichlid fish in the present study increased flight initiation distance with increasing distance-to-cover, but appeared not to adjust escape velocity to any great extent. Nevertheless, they appeared to choose values of these two behavioural parameters which allowed them to reach the cover provided by the rocks a constant period of time before the predator would have been expected to do so; i.e., they maintained a constant temporal 'margin of safety'. The evidence, although inconclusive, also suggests that the cichlids might compensate for relatively low choices of flight initiation distance by increasing their swimming velocity. The particular margin of safety chosen by the fish probably ensures a particular probability of escape, given uncertainty in the prey's estimation of the predator's distance, velocity, and ability to accelerate (relative to the prey's ability in this regard). Thus, a 'constant margin of safety' rule can be thought of as a simple rule-of-thumb allowing the prey to achieve a more complex objective.

Other rules-of-thumb are possible, of course. For example, instead of maintaining a margin of safety as defined here, a prey might choose its flight initiation distance and escape velocity so as to

reach cover a constant period of time before the attacking predator can close the initial distance between them. There is no evidence that the cichlids did this, however, since in 7 of the 12 cases their escape velocity exceeded the ball velocity, i.e., the relative velocity of the 'predator' was negative, and it could never close the gap between itself and the prey.

The actual margin of safety which a prey individual should try to achieve is expected to be influenced by a number of features of the interaction, some of which have already been mentioned. These include the acceleration capabilities of both the predator and prey, morphological features of the predator (eg. mouth protusibility), and uncertainty in the prey's estimation of predator velocity and distance (which could be influenced by visibility as well as by viewing distance). The margin of safety is also expected to be influenced by prey group size and other determinants of risk, and by the internal state of the prey. For example, a hungry animal might be expected to take greater risks (i.e., delay flight) than a more satiated one, if the decision to flee entails loss of feeding opportunity; this has been shown in the waterstrider, *Gerris remigis* (Ydenberg & Dill 1986) and the pea aphid, *Acyrthosiphon pisum* (Dill et al., unpublished data). Previous experience with predators ('close shaves') would also be expected to influence FID, as shown earlier in the zebra danio, *Brachydanio rerio* (Dill 1974b). Although an attempt was made to control most of these factors in the present experiments, variation in others (especially prior experience) likely contributed to the variation evident in the data.

The finding that flight initiation distance in *M. chipokae* increases with distance-to-cover confirms previous findings with both gray squirrels and brook charr (Dill & Houtman 1989, Grant & Noakes 1986, respectively). Taken together with recent findings with insects (Ydenberg & Dill 1986, Dill & Ydenberg 1987), the results provide support for the notion that animals take both the costs and benefits of their behaviour into account when making decisions about when and how to escape from their predators.

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