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The Economics of Fleeing from Predators

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I. INTRODUCTION

The business of avoiding and fleeing from predators is one of the most important tasks faced by any prey animal. The reason is simple: failure to do so results in an abrupt end to any future contributions to fitness, and so there is strong selection pressure for individuals that are successful at escaping from predators. Statements based on this principle seem so self-evident as to be hardly contestable. For example, Myers (1983) suggests that prey faced with conflicting demands should ". . . let the less important slide while focusing on the more critical, as might occur when trading off foraging (where lessened efficiency may not result in death) versus predator avoidance (where mistakes are fatal)."

In this article we try to show that, at best, this may be a very misleading viewpoint. We do so by focusing on the distinction between "detection" and "response." Much behavioral literature has equated these processes, and this has led to possible misinterpretations. For example, data which show a positive correlation between flight distance from an approaching predator and flock size (e.g., Kenward, 1978) are commonly cited as evidence that animals in groups detect predators sooner. The assumption implicit in this is that animals flee as soon as predators are detected; that is, detection is equivalent to response (allowing for some small physiological lag). This is a false premise, because it is not possible in the absence of any discernible response to ascertain whether or not an animal has detected a predator. It is logically possible that animals actually detect approaching predators long before they flee, but that the decision to escape is delayed for some reason (Lazarus, 1979; Greig-Smith, 1981; Seghers, 1981; Magurran *et al.*, 1985).

As a second example, Hoogland (1981) placed models of predators near prairie dog (*Cynomys* spp.) colonies and measured the time until the predators were discovered; large colonies gave the alarm sooner than smaller colonies, and Hoogland's conclusion was that small colonies were less efficient in monitoring the surroundings for predators. Similarly, Rothstein (1982) has concluded on the basis of many experiments with model cuckoo eggs that some songbird species are incapable of discriminating between their own eggs (or young) and those of nest parasites. There are many other examples. Our point is not that these conclusions are necessarily wrong, but merely that they critically depend on the implicit assumption that prey ought to give the alarm as soon as a predator is detected, or that songbirds ought always to eject cuckoo eggs.

The detection–response dilemma is just one aspect of a pervasive problem in any of the behavioral sciences—that of distinguishing between "knowledge" and "decision" (T. Getty, personal communication). Has a forager ignored a food item because it failed to encounter it, or did it decide to pass it over in favor of searching for a more profitable item? Have the prey not fled because they have not yet detected the predator, or are they ignoring it for the moment while continuing to feed? One way out of this dilemma is to record the activity of individual neurons in order to determine at the most basic level whether or not a stimulus has been detected. A second method relies on formulating hypotheses about the function of behavior that consist of predictions about which responses ought to occur (based on fitness considerations) and a set of constraints which define which responses are feasible. Essentially, these are hypotheses about "decisions."

As an example, let us consider decisions about breeding in the sowbug (*Armadillidium vulgare;* Lawlor, 1975). These common garden isopods may reproduce either once or twice each summer; Lawlor observed that small females reproduced only late in the summer, while large females reproduced in the spring as well. Why didn't the small females also breed twice? It is possible that they were constrained in some way, perhaps by their small body size, so that breeding in the spring was impossible. In fact Lawlor was able to show that small females were fully capable of breeding, but that the strategy of foregoing early breeding in favor of continued growth produced more offspring over the whole summer.

Lawlor's calculations showed that the optimal size for switching from a single- to double-brooded strategy was about 30 mm, which corresponded closely to the mean observed in the field. Hence the hypothesis that small body size constrained some females from breeding twice could be refuted.

Our general point is that hypotheses about constraints on behavior are incomplete without an analysis of when responses ought to occur at all. In this article we will contrast two approaches to the question of how the distance at which animals flee from predators is determined. The first type, which we term the "perceptual limit hypothesis," is a hypothesis only about constraints: it states that flight distance from an approaching predator is constrained by a prey animal's ability to detect the predator, and it assumes that prey flee as soon as predators are detected. The constraint may be morphological or physiological (acuity), or it may be behavioral (vigilance). This is the approach that most workers have implicitly adopted.

In contrast to this constraint hypothesis we prefer to formulate the problem as an economic one which considers goals as well as constraints. This approach to questions about behavior has been used by behavioral ecologists ever since the pioneering work of Brown (1964) and MacArthur and Pianka (1966). It has since gained widespread usage in models of feeding (Krebs *et al.*, 1983), fighting (Maynard Smith, 1982), reproductive (Charnov, 1982), and social behavior (Vehrencamp, 1983). These models make predictions about the choices animals make between alternative behaviors in each of these contexts. We will consider decisions that prey animals make about fleeing from an approaching predator. As the distance between the predator and prey shrinks, the prey can be thought of as continually choosing between staying where it is and fleeing: our model makes predictions about the distance at which the prey chooses to flee. Of course, this is only one aspect of predator avoidance behavior; we might instead consider a response measure such as choice of feeding site (e.g., Sih, 1980), or feeding rate (e.g., Milinski and Heller, 1978), but in general our approach will apply to any situation, as long as prey make choices between alternative behaviors while a predation threat exists.

One way to view the relationship between the two hypotheses we present is to consider the perceptual limit hypothesis as the limiting case of the more general economic hypothesis. When visibility is severely restricted, for example due to high turbidity or reduced contrast under water, low light levels, or dense vegetation, an attacking predator may be detected only after it is inside the distance at which the prey would otherwise have fled. There are no trade-offs to make in such a situation, and the prey should flee as soon as the predator is detected (Ellis, 1982). This may be a common situation (e.g., ambush predators) but in the more general case, we believe that the decision to flee from an approaching predator may be deferred due to economic considerations.

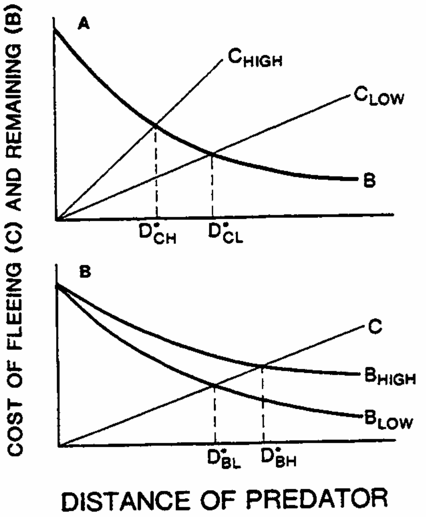


FIG. 1. A simple economic model of flight distance. The cost of remaining when a predator is at a particular distance is directly proportional to risk of capture, which increases to a maximum when $D = 0$. Costs of flight such as lost foraging opportunity increase with distance (time to attack) in a linear fashion. The animal should choose flight over continued feeding when $B > C$. The crossover of the B and C curves thus defines an optimal flight distance (D^*). (A) Increasing the cost of flight decreases the optimal flight distance ($D^*_{CH} < D^*_{CL}$). (B) Increasing risk (cost of remaining) has the opposite effect ($D^*_{BH} > D^*_{BL}$).

II. AN ECONOMIC HYPOTHESIS

The basis for hypothesizing that flight distance may vary in an economic fashion is that flight has costs as well as the obvious benefits. An animal must cease what it is doing (e.g., feeding) in order to flee. If food density is high, a few seconds extra feeding time may compensate for the increased risk of capture which results from a reduced flight distance. Alternatively, if cover is far away so that the chances of escaping are reduced, an animal may flee sooner than if cover is close at hand. These arguments are summarized graphically in Fig. 1. The line C represents the costs of flight (e.g., lost feeding opportunity) as a function of distance to the predator, while the curve B represents the cost of remaining when a predator is at that distance; B is high if the risk of capture is great. The prey animal is hypothesized to choose at every distance the behavior (fleeing or remaining) with the lowest cost. This general model makes the predictions that flight distance should increase with increasing cost of remaining (i.e., risk of capture) and decrease with increasing cost of flight. The cost of fleeing will be an increasing function of distance if the prey must hide until the predator passes. (This will not be true of all predator–prey interactions, but the general predictions of the model will not be affected even if the cost of flight is constant.) Alternatively, one may view cost as the cumulative cost of fleeing from predators at a given distance even when many such predators may have a low probability of attack. In either case "flightier" prey spend more time in flight than "bolder" prey, and therefore give up more time for other activities, such as feeding.

The way in which we have formulated the model is similar in some ways to models of motivation (McCleery, 1978, 1983). In these models an animal orders its activities by consistently switching to that behavior which has the highest tendency. Such models predict not only the sequence of behaviors, but also the timing of switches between activities. The structure of these models is very suitable for our purposes since we can think of an animal deciding to change from one behavior to another, and can use the model to see how changes in the relative costs of the activities affect the timing of the decision. We do not necessarily mean that decisions about fleeing are made in a cognitive way. Animals may follow simple rules to decide when to flee in the same way that they use foraging rules of thumb (Ydenberg, 1984). For example, Dill (1974a) has shown that the zebra danio (*Brachydanio rerio*), a small tropical freshwater fish, flees from approaching objects when the rate of change of the angle subtended by the object at the danio's eye (the "loom" rate) exceeds some threshold (see Section III).

The discussion which follows is divided into two parts. We first examine a variety of evidence to show that escape responses may often not immediately follow from detection in predator–prey encounters. Then, we consider a number of predictions made by the simple economic model outlined above, review the evidence available in the literature, and report new data on waterstriders (*Gerris remigis*).

III. Awareness and Escape

According to our economic hypothesis, a prey may be aware of the predator well before it decides to flee. Measurable neurophysiological responses, such as changes in heart rate, would indicate awareness of the predator's presence. Such responses have been recorded, and often precede flight by a considerable time (e.g., Gabrielsen *et al.*, 1977).

Several examples are known in which changes in behavior occur in response to predators outside the ultimate flight distance. Sticklebacks (*Pygosteus* and *Gasterosteus*) stop and fixate potential predators; flight is only one of several responses which may follow (Benzie, 1965). Banded killifish (*Fundulus diaphanus*) have distinctly separate detection (orientation) and flight responses to approaching predators (Hanson, 1984). According to Ewer (1968, p. 42) most prey become alert upon detecting an approaching cheetah (*Acinonyx jubatus*), but do not flee until it has approached within a certain distance. Gobies (*Cryptocentrus steinitzi*) retreat into their burrows at the close approach of a predator model, but signal danger to their alpheid shrimp symbionts when the model is further away (Karplus and Ben Tuvia, 1979). Eastern swamphens (*P. porphyrio*) approached by a man tailflick at distances greater than those which elicit retreat (Woodland *et al.*, 1980).

The zebra danio flees in response to an enlarging black spot projected on a screen, when the loom rate exceeds a value of 0.156 rad sec^{-1} (Dill, 1974a,b). A predator 2.5 cm in diameter, approaching at 150 cm sec^{-1}, would produce a flight distance of 49 cm in naive danios (from equation in Dill, 1974a). Previously unreported is the observation that 76% of the danios tested showed an approach response to the stimulus at some prior point in the filmed sequence. For naive danios, the loom rate at the start of the approach response was 0.054 ± 0.006 (SE) rad sec^{-1}. This would produce an approach distance of 83 cm to the same hypothetical predator described above. Similarly, Magurran *et al.* (1985) reported that minnows (*P. phoxinus*) made investigative approaches to pike models from which they later fled.

The evidence outlined in this section shows that flight is often preceded by neurophysiological and behavioral changes which indicate that the prey was aware of the predator before deciding to flee. It is also worth noting that such evidence as there is shows that animals are capable of detecting objects of smaller apparent size than those which cause them to flee (e.g., Breder and Halpern, 1946; Boulet, 1960; Ewert, 1970; Scaife, 1976). Therefore flight distance cannot be determined solely by the (visual) acuity of prey animals.

IV. THE ECONOMICS OF FLIGHT DISTANCE

We will now proceed to consider a number of predictions made by the simple economic model we outlined above, and review the evidence for these. Basically, the model (Fig. 1) predicts that the distance at which an animal flees from an approaching predator is determined by a balance between the costs of fleeing and remaining. As the costs of fleeing increase, flight distance decreases; as the costs of remaining increase, flight distance increases. We consider four more specific predictions here.

A. FLIGHT DISTANCE INCREASES WITH RISK

If other things are equal, the risk of death in a given encounter with a predator should increase with the approach velocity of the predator and the distance to effective cover; it should decrease with the attainable escape velocity of the prey.

TABLE I

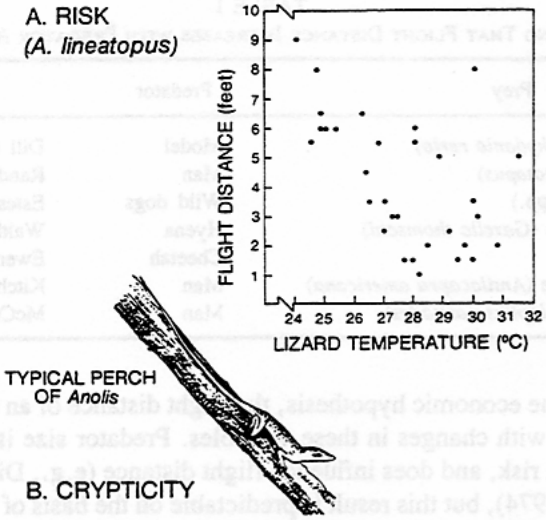
STUDIES REPORTING THAT FLIGHT DISTANCE INCREASES WITH PREDATOR APPROACH VELOCITY

Prey	Predator	Reference
Zebra danio (*Brachydanio rerio*)	Model	Dill (1974a)
Lizard (*Anolis lineatopus*)	Man	Rand (1964)
Gazelle (*Gazella* spp.)	Wild dogs	Estes and Goddard (1967)
Thomson's gazelle (*Gazella thomsoni*)	Hyena	Walther (1969)
African ungulates	Cheetah	Ewer (1968)
Pronghorn antelope (*Antilocapra americana*)	Man	Kitchen (1974)
Tule elk (*Cervus elaphus nannodes*)	Man	McCullough (1969)

According to the economic hypothesis, the flight distance of an individual should therefore vary with changes in these variables. Predator size is also likely to be correlated with risk, and does influence flight distance (e.g., Dill, 1974a; Hurley and Hartline, 1974), but this result is predictable on the basis of acuity considerations alone.

Prey flight distances have been shown to increase with predator approach velocity in a variety of species (Table I), although this is not universally true (e.g., Hurley and Hartline, 1974; Hutson, 1982). It has been proposed that, on a proximate level, the velocity effect results from the fact that flight is elicited by a threshold loom rate, which itself may be subject to behavioral modification (Dill, 1974a). This interpretation is supported by behavioral data in a variety of species (e.g., Hayes and Saiff, 1967; Webb, 1981) and by some neurophysiological data (e.g., Regan and Cynader, 1979). Such a hypothesis provides a proximate causal mechanism consistent with the economic hypothesis.

To our knowledge no study has examined the influence of distance (or more precisely, time) to cover on flight distance. This is an obvious area for future research. However, prey running ability has been shown to influence flight distance in a manner consistent with the economic hypothesis. For example, the flight distance of female blesbok (*Damaliscus dorcas phillipsi*) is greatest just after the birth of their young, which accompany them but cannot run well (Rowe-Rowe, 1974). Rand (1964) found that lizards (*Anolis lineatopus*) had greater flight distances at lower environmental temperatures (Fig. 2A), presumably to compensate for lower running speeds (see also Bennett, 1980; Hertz *et al.*, 1982). In contrast, Bauwens and Thoen (1981) found that gravid female lizards (*Lacerta vivipara*), which like the young blesbok are incapable of moving quickly, have shorter flight distances than males or nongravid females. In this case Bauwens and Thoen believe that running may attract a predator's attention, and that gravid females therefore adopt a more cryptic tactic. Although these latter two cases may appear to contradict one another, it is worth pointing out that neither result is explicable on the basis of perceptual capabilities alone (unless



CAMOUFLAGE (% unobserved at 5 m)	45	30	20
	A. stratulus	*A. cristatellus* *Females & juveniles*	*A. cristatellus* *Adult males*
APPROACH DISTANCE (cm)	50	110	150
n	35	55	42

FIG. 2. The economics of fleeing from predators in *Anolis* lizards in the West Indies. These animals have a stereotyped escape response. Anoles normally perch head downward on tree trunks where they can survey the surroundings, as shown in the vignette. When danger threatens they initially remain motionless but eventually flee by darting around the tree trunk and scuttling up to a higher perch. (A) Cooler lizards cannot move as rapidly and do not allow predators to approach as closely before fleeing, presumably to compensate for the increased risk that predators pose under such conditions. Each point on the graph represents one individual lizard, whose flight distance from an approaching man was measured. After fleeing the lizards were captured and their cloacal temperature taken. The relationship is highly significant ($r = 0.572$, $n = 31$, $p < 0.01$). The data are redrawn from Rand (1964). (B) Cryptic lizards wait longer before fleeing. The data shown here are from Heatwole (1968). Camouflage was assessed by counting the number of lizards that two observers stationed on opposite sides of a tree could spot at 5 m. The lizards were then flushed and the total number counted. The most cryptic lizards (*A. stratulus*) wait longest on average before fleeing, while the noncryptic males of *A. cristatellus* flee soonest.

they are influenced by temperature or by pregnancy). However, it is clear that the predictions of the economic hypothesis need to include the possibility that a prey's other defensive tactics (e.g., crypsis or armor) influence risk. We consider this further below (Section IV,C).

Not all large moving animals detected by prey will be dangerous predators, nor will all predators sighted represent equal risk, since this will vary with their diet. Thus prey should be selected to assess risk. The ability to make such distinctions has been demonstrated in several species. Reef fishes on Aldabra Atoll do not flee in response to large jacks (*Caranx* spp.), which apparently seldom eat them, but respond to smaller individuals (Potts, 1981). The distance which damselfish (*Chromis caeruleus*) maintain from models depends on mouth shape and size (Karplus *et al.*, 1982). Another species of damselfish (*Dascyllus aruanus*) withdraws more closely to its coral head when predators are presented than when nonpredators of the same size are used as stimuli (Coates, 1980).

It may be argued that the animals in the examples listed above deferred their escape responses because they had not categorized the approaching objects as "dangerous." Our objection to the categorization hypothesis as a sufficient explanation for flight distance is that it is one about constraints, incomplete without an analysis of how much information should be gathered before "categorizing" an approaching object as dangerous or not.

A prey's estimate of risk will vary with past experience of a particular predatory stimulus, and flight distance may therefore change with repeated presentation. Increasing flight distance with experience has been reported in zebra danios (Dill, 1974b) and three-spined sticklebacks (Benzie, 1965). Habituation to aversive stimuli has been reported in turtles (Hayes and Saiff, 1967), guppies (*Lebistes reticulatus*) (Russell, 1967), mallard ducks (*Anas platyrhynchos*) (Melzack, 1961), and goldfish (*Carassius auratus*) (Rodgers *et al.*, 1963). These observations are consistent with the economic hypothesis, and the fact that orienting responses to the stimuli persisted after habituation of overt flight in the last three studies lends further weight to this interpretation.

B. Flight Distance Decreases with Increasing Cost of Flight

The second prediction we consider is that as the cost of flight increases, flight distance should decrease.

Bellman and Krasne (1983) observed the reactions of feeding crayfish (*Procambrus clarkii*) to a threat (a moving net). Crayfish eating large food items (liver) had a lower probability of flight than did nonfeeding controls; crayfish feeding on small pieces of liver had an increased probability of flight, and more frequently fled at a distance. Since escaping crayfish almost always carry small items but usually drop large ones, the cost of flight is greater in the latter situation, supporting the economic hypothesis.

In a series of experiments in our laboratory we tested the flight reactions of waterstriders in a similar situation, and were able to replicate the results obtained by Bellman and Krasne (1983). Waterstriders feed by sucking the contents out of insects they capture on the water's surface. In our experiments, the waterstriders

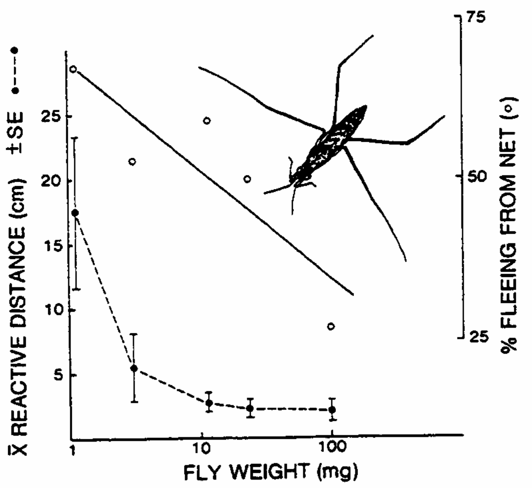


FIG. 3. Waterstriders (adult *Gerris remigis*) vary their response to an approaching net, depending upon the size of the fly on which they are feeding at the time. Both the proportion showing flight responses (upper line; $r^2 = 0.77$, $p = 0.05$), and the flight distance of those which flee (lower line; ANOVA $F_{4,64} = 4.90$, $p = 0.002$) decrease significantly with increasing fly size. Twenty to 23 gerrids in each prey size class were tested individually after they had been feeding on the fly for 10 min, and again 1 min after they had returned to the fly and recommenced feeding. (Gerrids which did not react at a distance jumped from the fly when the net bumped it.) If the gerrid reacted both times, its average flight distance was used as a datum. All trials (two per gerrid) were pooled to obtain the proportion responding. The gerrids were starved 24+ hr before testing. The net measured 8 × 10 cm and was moved by hand at 4.7 ± 0.4 (SE) cm sec^{-1} from an initial distance of 50 cm. The dipteran flies used were *Drosophila melanogaster* (ebony strain, mean wet weight 1.1 mg); *D. gibberosa* (3.0 mg); onion fly, *Hylemya antigua* (11.3 mg); blowfly, *Phaenicia sericata* (23.7 mg); and flesh fly, *Sarcophaga bullata* (97.8 mg).

were allowed to feed on a fly affixed to a pin near the center of a large shallow tank. A net was moved toward the fly and the distance at which the waterstrider left the fly and fled was recorded. Five fly sizes ranging from 1.1 to 97.8 mg were used. Since the waterstrider had to release the fly in order to flee, we assumed that the cost of fleeing was greatest for large flies, and predicted that the tendency to flee would therefore be greatest on small flies. Both the proportion of waterstriders which fled at all, and the flight distance of those which did flee, were greatest when the prey were small (Fig. 3). We think it unlikely that this outcome is an artifact of using a net rather than a real predator, and we consider both this study and that of Bellman and Krasne (1983) as good support for our prediction that flight distance will diminish when the cost of flight increases.

Barnard (1980b) reported that the members of house sparrow (*Passer domesticus*) flocks who remained behind following disturbances were the individuals who had the lowest pecking rates prior to the disturbance. By taking advantage of lower competition following the departure of their flock mates, they were able to double their pecking rate. Seen from the point of view of the economic hypothesis, these birds had the most to lose by leaving, since they would have foregone the opportunity to feed at a high rate (relative to the rate usually available to them). When the other flock members returned, these birds were once again displaced to the poorer feeding places and fed more slowly.

Barnard's (1980a) work with house sparrows also provides a second example. When he compared different feeding sites Barnard found that the flight distance of house sparrow flocks to a standardized approach by a terrestrial predator (Barnard himself) decreased as seed density increased. This result may be confounded by the fact that birds pecked more rapidly on sites with high seed densities and hence may have been less vigilant. A control for this is provided by comparing different observation days rather than different feeding sites. Barnard noted that seeds became increasingly unavailable (due to freezing) as the temperature declined, and he found a strong effect of temperature on flight distance. As before, the flight distance decreased with increasing seed availability (i.e., temperature), but this could not be attributed to a reduced vigilance capability since the rate of looking up did not change consistently with temperature.

C. Flight Distance and Alternative Prey Defense Tactics

Animals that rely on crypsis have a lower cost of remaining at a given distance from an approaching predator than have noncryptic animals, since the former are less likely to be detected. They may actually increase vulnerability by fleeing too soon, since they may draw the attention of an otherwise unaware predator. We therefore predict that a well-camouflaged species will have a shorter flight distance than a less cryptic species. Heatwole's (1968) study of lizards provides support for this prediction. *Anolis stratulus* is better camouflaged than is its sympatric congener *A. cristatellus*, and female and juvenile *A. cristatellus* are better camouflaged than males. The flight distance of individuals to the author was inversely correlated with the degree of camouflage, as expected (Fig. 2B). There is no reason to suppose that the better camouflaged lizards were less vigilant, since all the animals perched quietly, head downward, on low branches. Kettlewell (1973, p. 73) reports analogous observations on moths. Interestingly, Orians (1981) interprets these same findings as evidence that noncryptic prey have evolved greater visual acuity (a constraint hypothesis).

Since flight is costly in terms both of energy and lost opportunity, a prey species with effective morphological protection may be expected to have a shorter flight distance than a less well-protected one. Benzie's (1965) experiments on inexperienced sticklebacks support this prediction: the flight distance of *Pygosteus* to pike exceeds that of the better protected *Gasterosteus*, with its large, sharp spines and heavy plates.

D. FLIGHT DISTANCE AND GROUP SIZE

The relationship between group size and flight distance has often been investigated, particularly among birds. Usually these studies have aimed to test the prediction of the early warning hypothesis that larger flocks flee sooner from approaching predators because they are better able to detect them. We have already elaborated why this prediction does not necessarily follow from the early warning hypothesis, and in this section we will attempt to test predictions about the flock size–flight distance relationship based on economic arguments. The economic hypothesis predicts that if risk of predation or foraging efficiency varies with group size, then this will be reflected in flight distances.

The major problem in comparing flight distances for groups of different size is that a number of important variables may be confounded in such comparisons. (1) Dilution of risk: in many instances (e.g., Kenward, 1978) predators capture only a single prey from a group, and so the chance that any particular individual will be the victim of a successful attack declines with group size. (2) Food density: it is often the case that larger groups form on sites with a higher food density (e.g., Krebs, 1974). (3) Site safety: groups may be larger in areas where (or at times when) it is more dangerous (e.g., Caraco *et al.*, 1980; Pulliam and Mills, 1977; van Schaik *et al.*, 1982a). (4) Behavioral changes: virtually universally, animals apportion more time to feeding and less to vigilance as group size increases. In spite of this, corporate vigilance of the group increases at least up to a group size of about 5–10, and thereafter quickly reaches an asymptote (Pulliam, 1973).

These considerations greatly complicate the business of quantifying how the costs in groups of different size change as a predator approaches. Owing to the dilution effect, the cost of remaining (at any given distance) may be smaller in large flocks, and the flight distance may be reduced. In addition, if animals in large groups have high feeding rates compared to those in smaller groups, the benefit of extra feeding may delay the response to an approaching predator. Conversely, if interference increases with group size, such that the feeding rate drops, then flight distance should increase in large groups. Yet another alternative is that the net benefit is equivalent in groups of all sizes, since the animals array themselves across available feeding sites so that the benefit each obtains is equal (Fretwell, 1972; Harper, 1982). In this case no relationship between flight distance and flock size should be observed.

In Table II we have summarized those studies which have measured the flight distance of groups of animals to predators. The main conclusion from these studies is that there is great diversity in the form of the relationship between group size and flight distance. While this does provide some evidence against the interpretation that flight distance is determined solely by vigilance capabilities, there is no support per se for the economic hypothesis, since only four of the studies in Table II have attempted to quantify or control the benefits of membership in groups of various sizes.

TABLE II
Reported Relationships between Flight Distance (FD) and Group Size (GS)

Species	Predator	Range in group size	Shape of FD–GS relationship	*Comments*[a]	Reference
Starling (*Sturnus vulgaris*)	Falcon silhouette	1 or 10	Flocks of 10 react 0.9 sec sooner	Birds may have been constrained by enclosure	Powell (1974)
Laughing dove (*Streptopelia senegalensis*)	Model hawk	1–34	Concave down, maximum FD at GS = 15	Drinking doves at small waterholes	Siegfried and Underhill (1975); reanalysis by Krebs and Barnard (1980)
Brent goose (*Branta bernicla*)	Walking man	6–400	Positive		Owens (1977)
Woodpigeon (*Columba palumbus*)	Goshawk	1–50+	Positive		Kenward (1978)
Quelea (*Quelea quelea*)	Goshawk	1, 2, 4, 8, 16, 32	Flat	Birds' view almost certainly constrained by enclosure	Lazarus (1979)[b]
House sparrow (*Passer domesticus*)	Walking man	1–30	Flat		Barnard (1980a)
Barred ground dove (*Geopelia striata*)	Walking man	1–9+	Concave up, minimum FD at GS = 3		Greig-Smith (1981)
Long-tailed macaque (*Macaca fascicularis*)	Walking man	1–25	Significantly exponentially increasing	Observational	van Schaik *et al.* (1982a)
Pig-tailed macaque (*Macaca nemestrina*)	Walking man	1–8	Significantly logarithmically increasing	Observational	van Schaik *et al.* (1982a)
Lar gibbon (*Hylobates lar*)	Walking man	1–5	No significant increase	Observational	van Schaik *et al.* (1982a)

(continued)

TABLE II (*Continued*)

Species	Predator	Range in group size	Shape of FD–GS relationship	Comments[a]	Reference
Thomas' leaf monkey (*Presbytis thomasi*)	Walking man	1–15	No significant increase	Observational	van Schaik *et al.* (1982a)
Big game animals	Walking man	—	Solitaries flee sooner than groups	Observational	Altmann (1958)
Sheep	Walking man	—	Solitaries flee sooner than groups		Hutson (1982)
Spottail shiner (*Notropis hudsonius*)	Model pike	1–15	Solitaries flee sooner than groups		Seghers (1981)
Banded killifish (*Fundulus diaphanus*)	Model white perch	1–80	No effect		Godin and Morgan (1985)
	Model	1–15	Concave down, maximum FD at GS = 2–5		Hanson (1984)
Marine waterstrider (*Halobates robustus*)	Model bird	1–250	Asymptotically increasing		Treherne and Foster (1980)
Waterstrider (*Gerris remigis*)	Large conspecific	1–5	Concave down, maximum FD at GS = 2		Dill and Ydenberg (1986)
Minnow (*Phoxinus phoxinus*)	Model pike	3–20	Solitaries flee sooner than groups but show other responses later		Magurran *et al.* (1985)

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[a] Lazarus (1979) reports response latency, which is inversely related to FD.
[b] All studies are experimental unless noted otherwise.

Powell (1974) measured the time that starlings (*Sturnus vulgaris*) spent feeding, and observed that it increased from 53% for solitary birds to 88% for individuals in groups of 10. Assuming that this reflects the benefit of feeding (and thus the opportunity cost of fleeing), the economic hypothesis predicts that solitary birds should flee from an approaching predator sooner than birds in a flock. However, Powell found that captive flocks of 10 birds fled on average 0.9 sec sooner than solitary birds when a model hawk was towed over the experimental cage. In these experiments the predator suddenly appeared approximately 6 m from feeding birds, well inside the distance at which they would otherwise have fled. Considering that the corporate vigilance of flocks of 10 was about 5 times that of solitary birds, it is not surprising that flocks were able to flee sooner. In any case, since the prey were prevented from spotting the predator before it suddenly appeared extremely close by, this study does not provide a test of the economic hypothesis. It does give good evidence that larger flocks have a greater capability to detect predators, since it seems reasonable to assume in this case that the birds should have fled as soon as the predator was spotted.

Barnard's (1980a,b) studies of house sparrows, which we have already described, showed that flight distance varied inversely with seed density. Barnard's own interpretation of this was that vigilance was constrained by the feeding rate, since the birds looked up less when feeding on dense patches. As we outlined above (Section IV,B), a comparison between days of different temperature suggested that the true causal relationship was with seed density. Low temperatures lowered the availability of food and increased the flight distance, in spite of the fact that there was no consistent effect of temperature on the rate of looking up. Thus, as the economic hypothesis would predict, higher feeding rates led to a reduced flight distance; there was no relationship with the flock size per se (Table II).

Van Schaik *et al.* (1982a) found that two macaque species in the Sumatran rain forest reacted sooner to potential predators (men on the ground) when the monkeys were in large parties. The authors hold that the larger parties detect predators sooner. This is not unlikely, given the denseness of forest foliage, but again this conclusion does not necessarily follow from these results. van Schaik *et al.* (1982b) have also shown that for one of these species at least, the long-tailed macaque (*Macaca fasciculatis*), increasing interference results in diminished food intake in the larger parties; the observed result is therefore also predicted by the economic hypothesis.

A second experiment with waterstriders in our laboratory examined the relationship between group size and flight distance (Dill and Ydenberg, 1986). We measured the distance at which first instars feeding on flies in groups of one to five fled from the approach of a cannibalistic adult. The greatest flight distance was shown by pairs, while groups of five remained the longest (a concave down relationship). The hunger state of the first instars was controlled in these experiments.

In contrast, Treherne and Foster (1980) found the flight distance of the marine waterstrider (*Halobates robustus*) to be an asymptotically increasing function of group size. They hypothesized that this was due to larger groups having a greater level of general arousal owing to high encounter rates between individuals. Among fishes, two studies have produced conflicting results. Seghers (1981) found that the flight distance of the spottail shiner (*Notropis hudsonius*) to a model pike was shorter for schools than for individuals, but there was no effect of school size. The flight distance of the banded killifish to model predators has been variously reported to be independent of school size (Godin and Morgan, 1985) or to be maximal in intermediate-sized schools (Hanson, 1984).

The main conclusion of this section is that there is a great diversity in the form of the relation between flight distance and group size. In many species it increases, but in others it decreases over part of the range or is flat. In general, since the "perceptual limit" hypothesis would predict an overall nondiminishing reaction distance with increasing group size, we can conclude that the perceptual properties of groups cannot account entirely for the observed variability in flight distances. Greig-Smith's (1981) study is especially interesting as the flight distance appears to decrease as the flock size increases from one to three, and thereafter increases again (see Fig. 4). The studies of Siegfried and Underhill (1975, as reanalayzed by Krebs and Barnard, 1980), Hanson (1984), and Dill and Ydenberg (1986) likewise show maximum or minimum flight distances at intermediate group sizes. There are no exacting tests of the economic hypothesis, but studies which have measured feeding benefit and flight distance show a general qualitative agreement. Great difficulties lie in making an exact quan-

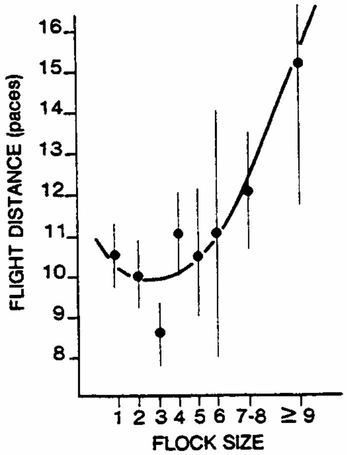

FIG. 4. Flight distance of flocks of the barred ground dove (*Geopelia striatus*) in the Seychelle Islands, from a study by Greig-Smith (1981). An observer measured the flight distance by walking toward flocks at a set pace. The line is predicted by a quadratic equation, which is not quite significant ($0.05 < p < 0.10$).

titative test, since the action of many variables tends to confound the measurement of costs and benefit as a function of group size.

V. SUMMARY AND CONCLUSIONS

We have outlined a simple economic model which predicts in a qualitative way how costs (lost feeding opportunity and risk) interact to produce an optimal flight distance from approaching predators. Our hypothesis is not really new. As early as 1957 Passano wrote, "Most animals must feed on their animal prey yet in turn be fed upon by other organisms; the success of these animals means that a judicious balance between recklessness and care, effective capture of food and preventitive caution in the presence of enemies, has been achieved." More recently, Lazarus (1979) and Greig-Smith (1981) have alluded to the need to consider bird flock size–flight distance relationships in a cost–benefit framework, while Seghers (1981) and Magurran *et al.* (1985) have suggested the same for fish schools.

In spite of this, most studies of flight distance have implicitly assumed that animals flee as soon as they detect approaching predators. We have termed this the "perceptual limit" hypothesis, since it implies that flight distances are determined by animals' perceptual capabilities. We have pointed out that this hypothesis is incomplete, since it does not distinguish between situations in which no response should follow a stimulus, and those in which the stimulus is not detected. These are both logically possible outcomes whenever a stimulus is presented. Our argument is that a statement of when responses ought to occur is required to complete the structure of a good hypothesis. This statement can take any number of forms. In the case of the songbirds whose nests are parasitized by cowbirds, it is clear that a failure to respond always results in a tremendous fitness penalty (Rothstein, 1982), and so we may safely conclude that some constraint prevents nondiscriminating songbirds from ejecting cowbird eggs. More often the costs of no response are less clear-cut (perhaps even for hosts of some nest parasites; cf. Smith, 1968) and a more complete statement of costs and benefits is required. We present our statement in a simple graphical model (Fig. 1) which depicts the way that the fitness costs of fleeing change as the distance between a prey animal and an approaching predator shrinks. The evidence is considered in relation to four specific predictions of the model: (1) flight distance increases with the risk of capture; (2) flight distance decreases with increased cost of fleeing; (3) flight distance changes with the effectiveness of alternative defense tactics such as crypsis, or spines; and (4) flight distance varies with the fitness benefit attached to membership in groups of various sizes.

We found good evidence for predictions 1–3, but the evidence for the fourth prediction was equivocable, since many variables operate simultaneously, so that it is impossible as yet to make any general statement about fitness and group size. There is a great diversity in the nature of the relationship between group size and flight distance, and the studies which considered the costs and benefits in detail were consistent with the economic hypothesis. The perceptual limit hypothesis would have predicted in all cases a positive correlation between flight distance and flock size, and was clearly not upheld.

We conclude that animals often defer the decision to flee from an approaching predator and continue with their ongoing activities. Our view is that a profitable approach to the problem of why such decisions are deferred, and how they eventually are made, is to view the process as an economic one in which the relative costs of fleeing and staying change as a predator approaches. We suggest that this economic approach will prove useful in analyzing many aspects of predator–prey interactions.

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