

Behavioral decisions made under the risk of predation: a review and prospectus

STEVEN L. LIMA¹ AND LAWRENCE M. DILL

*Behavioural Ecology Research Group, Department of Biological Sciences, Simon Fraser University,
Burnaby, B.C., Canada V5A 1S6*

Received February 6, 1989

LIMA, S. L., and DILL, L. M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* **68**: 619–640.

Predation has long been implicated as a major selective force in the evolution of several morphological and behavioral characteristics of animals. The importance of predation during evolutionary time is clear, but growing evidence suggests that animals also have the ability to assess and behaviorally influence their risk of being preyed upon in ecological time (i.e., during their lifetime). We develop an abstraction of the predation process in which several components of predation risk are identified. A review of the literature indicates that an animal's ability to assess and behaviorally control one or more of these components strongly influences decision making in feeding animals, as well as in animals deciding when and how to escape predators, when and how to be social, or even, for fishes, when and how to breathe air. This review also reveals that such decision making reflects apparent trade-offs between the risk of predation and the benefits to be gained from engaging in a given activity. Despite this body of evidence, several areas in the study of animal behavior have received little or no attention from a predation perspective. We identify several such areas, the most important of which is that dealing with animal reproduction. Much work also remains regarding the precise nature of the risk of predation and how it is actually perceived by animals, and the extent to which they can behaviorally control their risk of predation. Mathematical models will likely play a major role in future work, and we suggest that modelers strive to consider the potential complexity in behavioral responses to predation risk. Overall, since virtually every animal is potential prey for others, research that seriously considers the influence of predation risk will provide significant insight into the nature of animal behavior.

LIMA, S. L., ET DILL, L. M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* **68**: 619–640.

La prédation est depuis longtemps considérée comme une importante force sélective dans l'évolution de plusieurs caractéristiques morphologiques et éthologiques des animaux. L'importance de la prédation au cours de l'évolution est un phénomène évident, mais les données récentes permettent de plus en plus d'affirmer que les animaux sont également capables d'évaluer et de modifier, par leur comportement, les risques de devenir victimes de prédation durant un temps écologique (i.e., le temps d'une vie). Nous proposons un concept de processus de prédation dans lequel plusieurs composantes du risque de devenir victime sont identifiées. Une revue de la littérature indique que la capacité qu'a un animal d'évaluer et de contrôler, par son comportement, l'une ou plusieurs de ces composantes influence fortement la prise de décision chez les animaux qui se nourrissent, de même que chez les animaux qui doivent décider quand et comment échapper aux prédateurs, quand et comment être sociables, ou même, chez les poissons, quand et comment respirer de l'air. Cette révision met également en évidence qu'une telle prise de décision reflète des compromis apparents entre les risques de prédation et les avantages reliés à une activité donnée. En dépit de cette masse d'informations, plusieurs aspects de l'étude du comportement animal ont rarement été envisagés dans une perspective de prédation. Nous précisons ici plusieurs de ces aspects, notamment celui de la reproduction. Il reste encore beaucoup à découvrir sur la nature exacte du risque de prédation, sur la façon dont les animaux le perçoivent, et sur l'importance de l'influence de leur comportement sur son contrôle. Les modèles mathématiques joueront probablement un rôle prépondérant dans les travaux futurs et nous suggérons ici aux modélisateurs de s'attarder au problème de la complexité des réactions éthologiques du risque de prédation. Dans l'ensemble, comme pratiquement tout animal est une proie potentielle pour un autre animal, les chercheurs qui considèrent l'influence du risque de prédation comme un phénomène important peuvent contribuer considérablement à la compréhension de la nature du comportement animal.

[Traduit par la revue]

Introduction

During any given day, an animal may fail to obtain a meal and go hungry, or it may fail to obtain matings and thus realize no reproductive success, but in the long term, the day's shortcomings may have minimal influence on lifetime fitness. Few failures, however, are as unforgiving as the failure to avoid a predator: being killed greatly decreases future fitness. Predation may thus be a strong selective force over evolutionary time, and it has long been recognized as important in the evolution of adaptations, such as cryptic and aposematic coloration, protective armor, chemical defenses, etc. (Edmunds 1974; Harvey and Greenwood 1978; Sih 1987). Predation has also been

implicated in the evolution of sociality in both the breeding and nonbreeding season (Bertram 1978; Pulliam and Caraco 1984). In addition, many reproductive strategies appear to reflect the importance of predation as a selective force (e.g., Burk 1982).

Thus, an animal is born into a population whose cryptic coloration, for instance, reflects the outcome of the constant interaction between predator and prey over evolutionary time. From such an animal's viewpoint, however, its coloration provides only a "coarse" defense against predators. The reason is simple. While predation pressure may vary little over evolutionary time, during ecological time (i.e., an animal's lifetime) the risk of being preyed upon may vary greatly on a seasonal, daily, or even a minute by minute basis. Since an animal must accomplish more in its lifetime than simply avoiding predation, its antipredator adaptations should some-

¹Present address: Department of Life Sciences, Indiana State University, Terre Haute, IN 47809, U.S.A.

how be sensitive to the current level of predation risk. Such antipredator flexibility may be achieved by integrating gross morphological adaptations with the behavioral decision-making process.

There are many ways in which the risk of predation may influence animal decision making. For example, consider our cryptic animal. A cryptic animal can effectively avoid visually oriented predators as long as it remains motionless, but it must nonetheless move about to locate both food and mates. How should such an animal proceed with its activities so that fitness is maximized? There is a benefit and cost to both movement and remaining cryptic. Since this animal cannot simultaneously be cryptic and active, there will be a conflict in deciding the extent to engage in one behavior over another. This conflict must be resolved in ecological time based upon the animal's assessment of the risk of predation in its environment and the costs and benefits associated with its various behavioral options.

We will examine a growing body of evidence that animals do indeed possess the ability to (i) assess their risk of being preyed upon and (ii) incorporate this information into their decision making. The nature of the above cost-benefit trade-offs will also be examined. The review section of the paper deals mainly with studies that examine decision making in response to explicit alterations (natural or experimental) in the risk of predation; we have largely avoided anecdotal studies. We also emphasize throughout this paper that the risk of predation concerns the decision maker *per se*. Most work satisfying these criteria for inclusion concerns the behavior of feeding animals, and we begin with this. We then consider work in areas not directly related to feeding behavior, such as escape from predators and aspects of sociality. Following the review, we discuss several areas in need of further research, and some of the problems and pitfalls, both practical and philosophical, that may be encountered along the way. However, before proceeding, we first provide a brief discussion of the nature of predation risk, around which we focus much of our review.

The components of predation risk

Many studies deal with predation risk in a very general and often vague manner; thus, the complexity of the behavioral options controlling risk has gone largely unappreciated. Therefore, in this section, we briefly develop a simple abstraction of the predation process in an effort to better define the varied aspects of predation risk that will be encountered below.

The risk of predation is most intuitively defined as the probability of being killed during some time period. Thus, for our present purposes, a simple representation of predation risk is

$$[1] \quad P(\text{death}) = 1 - \exp(-\alpha dT)$$

where α is the rate of encounter between predator and prey, d is the probability of death given an encounter, and T is the time spent vulnerable to encounter (or attack). We refer to α , d , and T as the "basic" components of predation risk (*sensu* Holling 1959). An essential aspect of these basic components is that they are potentially assessable by the prey (see below).

For convenience, an encounter occurs whenever the distance separating prey and predator is less than whichever of their detection radii is greater; we call this an encounter situation. The prey or the predator may detect the other party first, or neither may detect the other, in which case no actual interaction occurs. Treated in this way, α is a purely statistical concept depending on local predator density, search tactics, relative speed of movement through the habitat, habitat structural complexity,

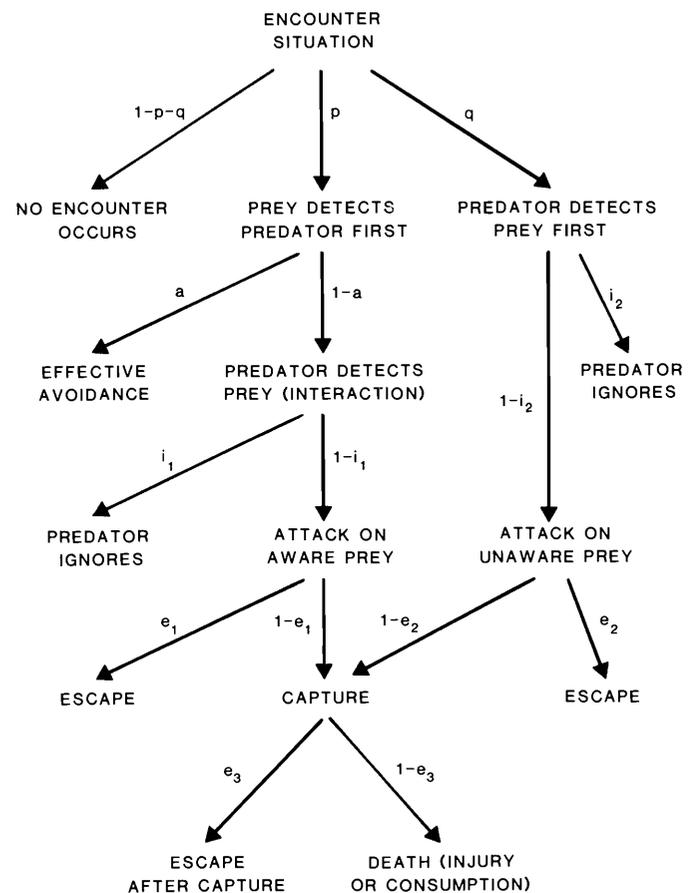


FIG. 1. Flow chart showing the possible outcomes of an "encounter situation" between a prey and its predator (see text). The symbols adjacent to arrows represent the conditional probabilities of following the labelled pathways. Only a proportion (d) of all encounters lead to the death of the prey through consumption or fatal injury; see eq. 2 in text.

etc. Note that α is assessable by potential prey. For instance, if predators tend to remain in an area for a long period of time, then a recent sighting may indicate a high value of α (e.g., Sonnerud 1985). On the other hand, if predators follow regular routes through their territories, then a recent sighting of a predator may indicate a low value of α in the near future. Prey might also assess α via the frequency of predator sightings, or encounters with scats, territory markings, etc.

The probability of death given an encounter situation, d , can be represented as a combination of the probabilities that an actual behavioral encounter occurs and that this is followed by attack, capture, and consumption. These probabilities, or "subcomponents" of predation risk, are outlined in Fig. 1. From this figure, d can be defined as

$$[2] \quad d = [p(1-a)(1-i_1)(1-e_1) + q(1-i_2)(1-e_2)](1-e_3)$$

Most of these subcomponents should be assessable by the prey. For instance, a prey can assess the escape subcomponents (e_1 , e_2) via its proximity to protective cover, the distance between itself and a predator, etc.

The remaining basic component, T , is the time spent vulnerable to an encounter. For some animals, this may be time spent moving or time spent away from protective cover, etc. Generally speaking, T should be easily assessed by potential prey.

We have stressed the assessability of the above components of predation risk because an ability to assess them allows an animal to behaviorally control its risk, at least to some extent. For example, an animal can reduce its risk of predation by reducing the time it spends in areas of high α , d may be reduced by feeding close to protective cover, etc. By whatever means, an animal's ability to control its risk of predation in ecological time is the raw material of the following review. For the studies examined below, we attempt to identify the components and subcomponents that (i) appear to be major determinants of predation risk and (ii) are assessable and under an animal's control. In doing so, we hope to give the reader a greater appreciation of the role of predation risk in animal decision making.

Behavior of feeding animals

We organize this section around a simple hierarchy of decision making, which generally flows from large- to small-scale decisions: when to feed, where to feed, what to eat, and how to consume (or handle) it. Each of these basic hierarchal levels may itself represent a large- to small-scale hierarchy of decision making. For instance, the decision of where to feed may involve broad-scale habitat or patch selection, or merely the choice of feeding site within a patch. While this organizational theme is convenient, the reader will no doubt realize that the distinction between various hierarchal decisions is somewhat blurred.

When to feed

Diurnal patterns

Some times are more dangerous for feeding than others, owing to temporal variation in predator activity and other determinants of risk. Such times are not always predictable to prey in advance, since predator activity may vary with a host of biotic and environmental variables. Consequently, prey animals are expected to assess the prevailing level of risk in deciding when to forage.

Few experimental or even quantitative observational studies on this question have been conducted, although Helfman (1986) provides limited experimental evidence that juvenile grunts (Haemulidae) are sensitive to the local abundance of a predatory lizardfish (*Synodus intermedius*) and adjust their migration times accordingly; their off-reef foraging migrations are delayed when predator densities and simulated attack rates are increased using model lizardfish. Caldwell (1986) suggests that during periods of intense hawk predation, herons (Ardeidae) switch their foraging to safer periods (during rainfall or at dusk), but suffer reduced food intake as a consequence. Additionally, Feener (1988) found that the ant *Pheidole titanus* strongly avoids aboveground foraging activity when dipteran parasitoids are active.

Light level, since it influences the visual abilities of both predator and prey, is an environmental determinant of risk which is easily assessed by prey and ought to affect their foraging decisions. Nocturnal foragers have frequently been shown to reduce their activity during periods of bright moonlight, when the risk of predation is high (Clarke 1983). Lockard and Owings (1974a, 1974b) reported that the surface-feeding activity of bannertail kangaroo rats (*Dipodomys spectabilis*) is inhibited by bright moonlight. Price *et al.* (1984) and Bowers (1988) have reported that another kangaroo rat, *D. merriami*, increases its relative use of areas with cover during periods of bright moonlight. Deer mice, *Peromyscus maniculatus*, and old-field mice, *P. polionotus*, also reduce their foraging activity in bright moonlight (Clarke 1983; Wolfe and Summerlin 1989).

Leach's storm petrels, *Oceanodroma leucorhoa*, avoid returning to their breeding colony from foraging trips when the moon is full, particularly when gull predation is intense (Watanuki 1986). The fruit bat *Artibeus jamaicensis* also avoids searching and feeding when the moon is full (Morrison 1978), but the fact that the effect persists even when the moon is obscured by heavy clouds argues against a risk assessment mechanism. Strong evidence for such a mechanism requires experimental manipulation of light levels. In this way, Kotler (1984a, 1984b, 1984c) has demonstrated that increased artificial illumination causes desert rodents to reduce their foraging in areas without cover; Brown *et al.* (1988) provide further experimental evidence in this regard and demonstrate that these rodents accept lower feeding rates in doing so.

Light level may also influence the foraging activity of diurnal foragers, particularly during crepuscular periods when light level (i.e., risk) changes rapidly. For instance, Lima (1988a, 1988b) found that dark-eyed juncos (*Junco hyemalis*) may be subject to a greater risk of predation in the dim light of early morning, and that they appear to perceive this risk. Accordingly, juncos initiated daily feeding in very dim light only when feeding could take place in the relative safety of cover (Lima 1988a), or when their energy reserves were dangerously low. Clark and Levy (1988), in contrast, suggest that pelagic planktivorous fishes may experience much reduced risk in dim light (twilight), hence their crepuscular feeding habits.

Most of the above studies dealt with predation risk in a general way. However, by reasoning that prey can avoid predation by curtailing feeding when potential predators are active, or when a predator's ability to detect prey is maximal, these studies were clearly concerned with the "encounter" component of risk. However, some subcomponents of d (eq. 2) may come into play. For instance, the decision of when to feed may be influenced by a prey's ability to detect predatory attacks, since this may change with light level (e.g., Lima 1988a).

Resumption of feeding after interruption

Many birds immediately rush to cover upon detecting a nearby predator. In many cases, the birds then lose sight of the predator, although it may be lying in ambush nearby. The birds must, however, resume feeding at some time. In such situations, De Laet (1985), Hegner (1985), and Hogstad (1988a) found that dominant great tits, blue tits (*Parus caeruleus*), and willow tits, respectively, often will not resume feeding until the more (potentially energetically stressed) subordinate individuals have done so (Fig. 2). In tufted titmice, *Parus bicolor*, subordinates do not return to a feeding site before dominants, but do resume activity sooner following an alarm call (Waite and Grubb 1987; see also Breitwisch and Hudak 1989). Although not demonstrated, these dominant birds may be using the subordinates as indicators of a possible encounter situation. Møller (1988) presents an interesting twist to these results. He found that when food is scarce or easily monopolized by dominants, subordinate great tits gain access to it by purposefully using antipredatory alarm calls to create interruptions in the feeding of dominants.

The resumption of feeding following a period of food deprivation may also depend upon predation risk. Morgan (1988b) found that in bluntnose minnows (*Pimephales notatus*), the time delay in initiating feeding increases in the presence of a predator and decreases with both increasing shoal size and the degree of food deprivation. In a related study, Godin and Sproul (1988) found that energy-stressed (i.e., parasitized) three-

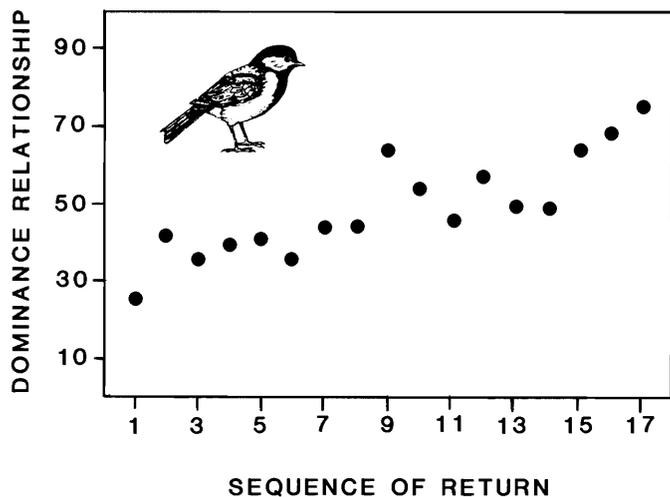


FIG. 2. Relationship between dominance and sequence of the resumption of feeding by great tits that had stopped feeding because of a recent sighting of a sparrowhawk, *Accipiter nisus*. The "dominance relationship" is an index of dominance calculated as the number of birds present that dominated the bird in question subtracted from the number of individuals it dominated; high values indicate more dominant birds. Data are given as average dominance relationships pooled from observations gathered during an entire winter. Generally, dominant birds resumed feeding after more subordinate birds had done so ($r_s = 0.66$, $P < 0.05$). Redrawn from De Laet (1985).

spine sticklebacks resume feeding sooner than nonstressed individuals following a simulated predatory attack. These examples clearly involve encounter situations, but the components of risk involved are not clear. The effect of shoal size in the minnows may reflect diluted risk (e_1) and (or) increased vigilance (p , see below).

Where to feed

Habitat and patch selection

Habitats and patches may vary not only in terms of their foraging profitability, but also in terms of predation risk. When the best areas for foraging are also the most dangerous, the forager must trade off energy gain against the risk of predation in deciding where to feed.

The risk of predation has been equated with habitat- and patch-specific predator abundance in several recent demonstrations of such trade-offs in freshwater organisms, such as the crayfish *Oronectes propinquus* (Stein and Magnuson 1976), the backswimmer *Notonecta hoffmanni* (Sih 1980, 1982), sunfish, *Lepomis* spp. (Werner *et al.* 1983; Mittelbach 1984), the minnow *Campostoma anomalum* (Power and Matthews 1983; Power *et al.* 1985), the dace *Rhinichthys atratulus* (Cerri and Fraser 1983), the creek chub, *Semotilus atromaculatus* (Gilliam and Fraser 1987), the guppy, *Poecilia reticulata* (Abrahams and Dill 1989), and the threespine stickleback, *Gasterosteus aculeatus* (Fraser and Huntingford 1986). These and related aquatic studies have recently been reviewed in detail elsewhere (Milinski 1986; Mittelbach 1986; Dill 1987).

Further examples of habitat and patch selection trade-offs in freshwater systems have also been reported recently. For instance, Holomuzki (1986) found that predaceous beetles (*Dytiscus*) influence habitat use by larval tiger salamanders, *Ambystoma tigrinum*. In the absence of beetles, the salamander larvae forage preferentially in vegetated shallows both day and night. Introduction of beetles causes the salamanders to shift to

deeper, pelagic areas when the beetles are active in the shallows, resulting in reduced food intake by the salamanders. Stoneroller minnows, *Campostoma anomalum*, may shift into shallow habitats in the presence of largemouth bass, *Micropterus salmoides*, but not smallmouth bass, *M. dolomieu*; this difference may reflect activity levels in the two predators (Harvey *et al.* 1988). Fry of pink salmon, *Oncorhynchus gorbuscha*, but not those of chum salmon, *O. keta*, reduce their use of profitable open-water feeding areas when they can see potential predators in an adjoining aquarium. The extent of their shift to a safer vegetated habitat (where food is unavailable) depends on their food intake: the effect is less marked in hungrier fish (Magnhagen 1988a). Similar results were obtained in two gobiid fish species, *Pomatoschistus minutus* and *Gobius niger*, choosing between open and vegetated habitats with and without food, respectively (Magnhagen 1988b). Larval dragonflies (Odonata: Anisoptera) may also shift into pond bottom litter in the presence of bluegill sunfish (Pierce 1988); their use of cover tends to be higher during the day than at night.

Several of these aquatic studies indicate an antipredatory benefit to feeding in vegetation. However, Savino and Stein (1989) showed that such benefits depend upon species-specific antipredator behavior and the foraging behavior of predators. In addition, vegetation may be avoided by sticklebacks if it harbors ectoparasites (Poulin and FitzGerald 1989).

Heads (1986) found that damselfly larvae, *Ischnura elegans*, avoid profitable patches if these also harbor predators, and Wellborn and Robinson (1987) present evidence that larvae of another damselfly, *Pachydiplax longipennis*, choose sites on submergent vegetation in accordance with predation risk and their hunger level. In addition, Feltmate (1987) found that the choice of patch and substrate by caddisfly larvae, *Hydropsyche sparna*, depends upon the presence or absence of predatory stonefly nymphs, *Paragnetina media*; the substrate choice of the stonefly depends in turn on the presence or absence of rainbow trout (Feltmate *et al.* 1986). In a similar fashion, predators have been shown experimentally to influence the habitat use patterns of large species of zooplankton (Raess and Maly 1986), *Ambystoma* salamander larvae (Semlitsch 1987; Stangel and Semlitsch 1987), *Hyla crucifer* tadpoles (Morin 1986), juvenile threespine sticklebacks (Foster *et al.* 1988), European minnows, *Phoxinus phoxinus* (Pitcher *et al.* 1988), and various species of small freshwater fishes (Schlosser 1987, 1988a, 1988b). Jakobson *et al.* (1988) provide evidence for a shift in distribution of threespine sticklebacks in the field in response to predation by Atlantic salmon, *Salmo salar*, but it is inconclusive; the apparent shift could have been due to mortality of sticklebacks in the risky pelagic zone of the lake.

Predation risk may be traded off against habitat characteristics other than food availability. For example, Fischer *et al.* (1987) have shown that the upper avoidance temperature of bluegill sunfish, *Lepomis macrochirus*, is elevated in the presence of a predator (the largemouth bass). The size of the increase (about 4°C) did not depend on the size of either the prey or the predator.

In contrast to the many studies in freshwater systems, few examples of predation risk dependent habitat or patch selection exist for marine systems. One exception is provided by Schmitt and Holbrook (1985) who showed that prey density and risk level (determined by structural complexity) interact to affect patch choice decisions by juvenile black surfperch, *Embiotoca jacksoni*, at least when predators are present during the dimly lit (thus dangerous) dusk period. This species is also sensitive to

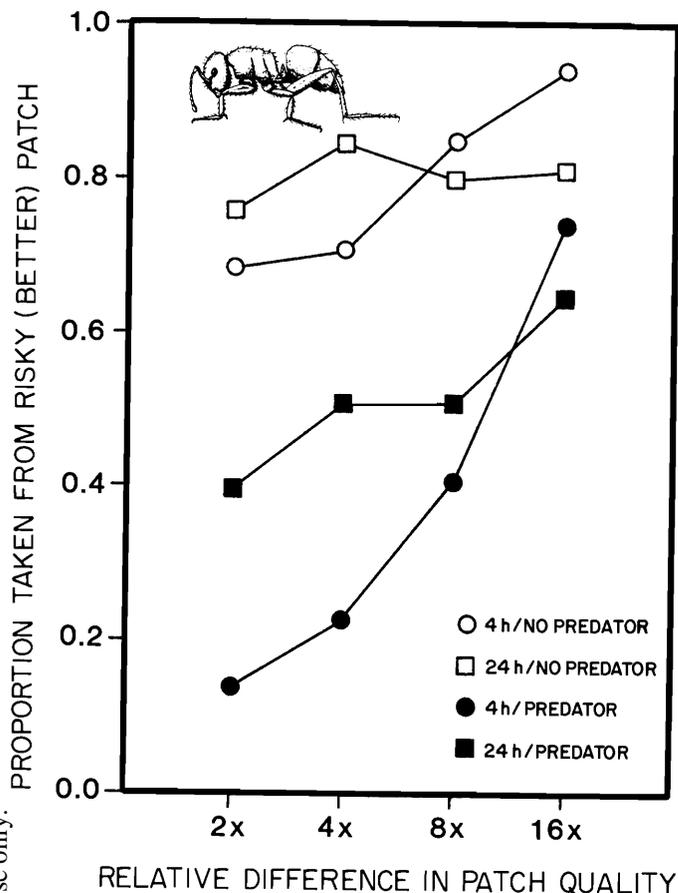


FIG. 3. Predation risk and patch selection by laboratory ant colonies. The ants were given a choice between two patches providing sugar solutions which differed in concentration. The patches were available to the ants for 4 or 24 h per day. In some treatments, a predatory ant was placed in the better quality patch. Behavior is expressed as the proportion of a colony's daily energy intake taken from the better (sometimes risky) patch. Data from Nonacs and Dill (1990a).

the presence of predatory kelp bass, *Paralabrax cathratus*, and trades off food density against risk when choosing feeding patches (Holbrook and Schmitt 1988a, 1988b). In addition, Main (1987) has shown that a caridean shrimp, *Tozeuma carolinense*, responds to the presence of pinfish, *Lagodon rhomboides*, by moving to higher, less vulnerable positions on sea grass blades, and by reducing its walking and feeding rates.

Some recent terrestrial studies also focus on predator abundance or presence as the prime determinant of risk in habitat and patch use trade-offs. For instance, Nonacs and Dill (1990a, 1990b) found that ants (*Lasius pallitarsis*) offered a choice between pairs of sugar solutions of different concentrations preferentially forage from the richer patch (Fig. 3), as expected. However, when a risk of predation (from a larger ant species) is associated with the richer solution, the ants' feeding behavior changes. If the difference between the two solutions is not great, the ants prefer the weaker (but safer) one (Fig. 3) and increase their foraging tempo to keep colony intake rate roughly constant. When the safe solution is too weak for the ants to adopt such a tactic, they forage from the richer patch, accepting a risk of mortality in doing so. In addition, Caldwell (1986) reported that foraging herons switch from areas in which predatory attacks are common (mangroves) to those where predators are rare (reefs and deforested inlets), even though the safe areas are less energetically profitable. Anderson (1986) has shown that small

mammals (primarily deer mice) are more willing to visit feeding stations outside their home range when these are set in areas of high cover density, and caribou, *Rangifer tarandus*, may trade off food availability and risk of predation from wolves when choosing foraging sites (Ferguson *et al.* 1988).

The presence of predators is of obvious importance in decisions concerning habitat or patch use, but other aspects of predation risk may come into play. For instance, Grubb and Greenwald (1982) found that patch selection in house sparrows, *Passer domesticus*, reflects a predation–energy trade-off influenced by the distance to protective cover (safety) and the thermal advantages (energy savings) afforded by cover. Hogstad (1988a) found that willow tits, *Parus montanus*, prefer to feed in patches closest to cover if all else is equal. This is also true of the kangaroo rat *D. merriami* (Bowers 1988) and deer mouse *Peromyscus maniculatus* (Travers *et al.* 1988), particularly on moonlit nights. Gray squirrels, *Sciurus carolinensis*, accept reduced feeding rates in order to feed in patches closer to cover (Newman and Caraco 1987). Kotler (1984b), Brown *et al.* (1988), and Brown (1988, 1989) demonstrated that patch selection by desert rodents is also influenced by the proximity of protective cover. Thus, the escape subcomponents of risk (e_1 and e_2 in Fig. 1) may be of considerable importance in habitat and patch selection.

Choice of feeding site

Here, we are concerned with decisions regarding where to feed within a distinct patch; these decisions are on a smaller spatial scale than those discussed above. There are several ways in which these decisions may come into play, but only a few have received quantitative attention.

Escape subcomponents of risk have been implicated as important determinants of feeding-site selection within a patch of food that borders an area of protective (escape) cover. Schneider (1984) found that white-throated sparrows, *Zonotrichia albicollis*, feed as close to cover as possible in such patches, unless food is greatly depleted close to cover or more dominant individuals force them away from cover; similar observations were obtained in studies on willow tits (Ekman and Askenmo 1984; Ekman 1987). In contrast to these results, Lima *et al.* (1987) found that several finches (Emberizidae) often feed well away from cover. Observations and experimental results suggested that these finches perceive cover as both safety and a source of attacks, and that their behavior reflects a trade-off between the perceived risk of feeding too close to cover versus that of feeding too far away. Some mammals may be similarly influenced by cover. Carey (1985) and Underwood (1982) found that yellow-bellied marmots, *Marmota flaviventris*, and African antelopes, respectively, avoid cover which might obscure and (or) harbor predators; for these animals, cover is not a refuge, but only a source of risk.

Milinski and Heller (1978) and Heller and Milinski (1979) provide an example of feeding-site selection which focuses on the predator detection subcomponents of risk (p , Fig. 1). They found that hungry threespine sticklebacks prefer to attack the denser portion of a swarm of water fleas, *Daphnia pulex*, where they can obtain a high rate of energy intake, while partially satiated sticklebacks prefer lower density portions of the swarm. Milinski and Heller suggested that the visual "attention" necessary to overcome the confusion of feeding in a dense portion of a swarm (caused by many simultaneously moving targets) detracts significantly from a stickleback's ability to detect attack (Milinski 1984; see also Godin and Smith 1988).

Hungry sticklebacks are apparently willing to accept the risk of feeding on dense prey to lower their energetic deficit; partially satiated individuals are unwilling to take such a risk. Interestingly, Milinski (1985) found that parasitized sticklebacks exhibit a much reduced response to predators, which may reflect manipulation by the parasite and (or) differing decision criteria for parasitized fish (see also Godin and Sproul 1988).

Lima (1985) and Lima *et al.* (1985) provide examples of trade-offs in decision making concerning where to actually consume a food item once it has been located. They found that black-capped chickadees, *Parus atricapillus*, and gray squirrels, respectively, sometimes carry food items to protective cover for consumption. In particular, their tendency to carry items to cover increases with both a decrease in the distance to cover and an increase in the size of the food item (see also Phelps and Roberts 1989). This behavior is consistent with an energy – predation risk trade-off where time spent vulnerable to attack (i.e., away from protective cover) is the major component of risk under behavioral control. In a similar study examining several bird species, however, Valone and Lima (1987) present a more complex view of this carrying behavior in which escape subcomponents also appear to be important factors in decision making.

The avoidance subcomponent *a* in Fig. 1 may influence larval mayflies' (*Baetis tricaudatus* and *Ephemera subvaria*) positioning on stones within streambeds (Soluk and Collins 1988). Upon detecting predatory stoneflies (*Agneta capitata*) via chemical and tactile cues, the mayflies prefer the upper surfaces of stones where interactions with stoneflies are reduced. Interestingly, the mayflies do not respond significantly to the presence of a benthivorous fish (*Cottus bairdi*), perhaps because these potential predators cannot be detected easily.

Finally, consider a sit and wait forager deciding when to change feeding sites given its foraging success. The movement necessary to change sites may attract the attention of nearby predators; hence, such decisions may depend upon predation risk. Heads (1985) provides evidence for such a scenario in the sit and wait larval damselfly, *I. elegans*. These larvae change perches less often and move shorter distances in the presence of the predatory water boatman, *Notonecta glauca*, or under well-lit conditions. Such site changes are presumably in response to poor feeding success, but this was not actually demonstrated. In an analogous study, Wong *et al.* (1986) showed that the presence of predatory copepods (but not just their odor) reduces the jumping frequency of a herbivorous copepod, *Diaptomus minutus*. Jumps are used to change feeding sites in the water column, but they also increase the zooplankton's chance of being detected by its vibration-sensitive predators.

What to eat

It may not be obvious that the risk of predation can be a determinant of an animal's diet, since it might appear that choosing the diet which maximizes the rate of energy intake will simultaneously minimize the risk of predation (cf. Schoener 1971). Recent examinations of diet selection, however, yield some examples where this is not the case.

Lima and Valone (1986) found that gray squirrels selecting a diet would reject more profitable food items (in terms of energy gained per unit of handling time) in favor of locating less profitable, but larger items that are subsequently carried to cover for consumption. The squirrels' tendency to reject the more profitable items decreases with both an increase in the distance to cover and a decrease in the size of the less profitable

items. Such behavior is contrary to the expectations of "classical" diet theory (see Stephens and Krebs 1986), but it is consistent with a foraging – predation risk trade-off in which the major component of risk is the time spent vulnerable to attack.

Nonclassical diet selection under the risk of predation may also occur when the available food items differ in the degree to which handling and vigilance for predators are mutually exclusive. Lima (1988c) examined diet selection in dark-eyed juncos where handling and vigilance were mutually exclusive for items of high profitability (that must be eaten with the head down), but not for less profitable items (that can be eaten with the head up). Under such conditions, the proportion of the diet consisting of less profitable items may decrease as the need to be vigilant decreases. Such a decrease in the need to be vigilant occurs with an increase in flock size (see below). Accordingly, the juncos exhibit flock size dependent diet selection (Fig. 4), suggesting an important role therein for the predator detection subcomponent of risk (*p* in Fig. 1). Lima (1988d) considers further the implications of vigilance for diet selection.

Desert heteromyid rodents are more selective of seed types in high risk areas, i.e., away from protective cover. For instance, *Perognathus fallax* and *Dipodomys merriami* take preferred seeds to equally available nonpreferred seeds in a ratio of 2.5:1.0 when foraging beneath vegetation, but in a ratio of 7.5:1.0 when in the open (Hay and Fuller 1981). A similar effect was reported for *D. merriami* by Bowers (1988), but in neither case was a behavioral rationale provided for the change in selectivity.

Dill and Fraser (1984) examined a case of decision making under the risk of predation that may have implications for diet selection. They studied juvenile coho salmon, *Oncorhynchus kisutch*, which are sit and wait predators that feed on stream drift. These fish are difficult to detect because of their cryptic coloration (Donnelly and Dill 1984), but only when motionless. Accordingly, after recently sighting a model of a predatory rainbow trout, *Salmo gairdneri*, salmon lower their tendency to move to intercept oncoming prey, and thus reduce their encounter volume, especially for the largest (most profitable) prey. This trade-off, in which prey assess predator encounters but have control over the predator detection subcomponent of risk (*q* in Fig. 1), has obvious implications for diet selection.

In a very similar experiment, Metcalfe *et al.* (1987a) demonstrated that juvenile Atlantic salmon alter their feeding behavior for up to 2 h after a 30-s sighting of a brown trout, *Salmo trutta*, model. Specifically, they are less likely to orient to or attack passing food and consequently suffer reduced food intake (see also Huntingford *et al.* 1988). The salmon also alter their selectivity, more frequently attacking inedible prey after sighting the predator (Metcalfe *et al.* 1987b). Although this could obviously influence diet selection, the authors imply that it results less from changed decisions by the fish than from their inability to attend simultaneously to the two visual tasks of food assessment and vigilance for predators.

How to handle food

Models of feeding behavior have typically treated handling times as a fixed time constraint (Stephens and Krebs 1986). This is a reasonable approximation in many cases, but it appears that handling times are often under the control of an animal; a good example of this is partial prey consumption (e.g., Lucas 1985). Very little work exists concerning the handling of prey items under the risk of predation, but a few studies suggest a role for risk in decision making.

Krebs (1980) suggested that handling times in great tits,

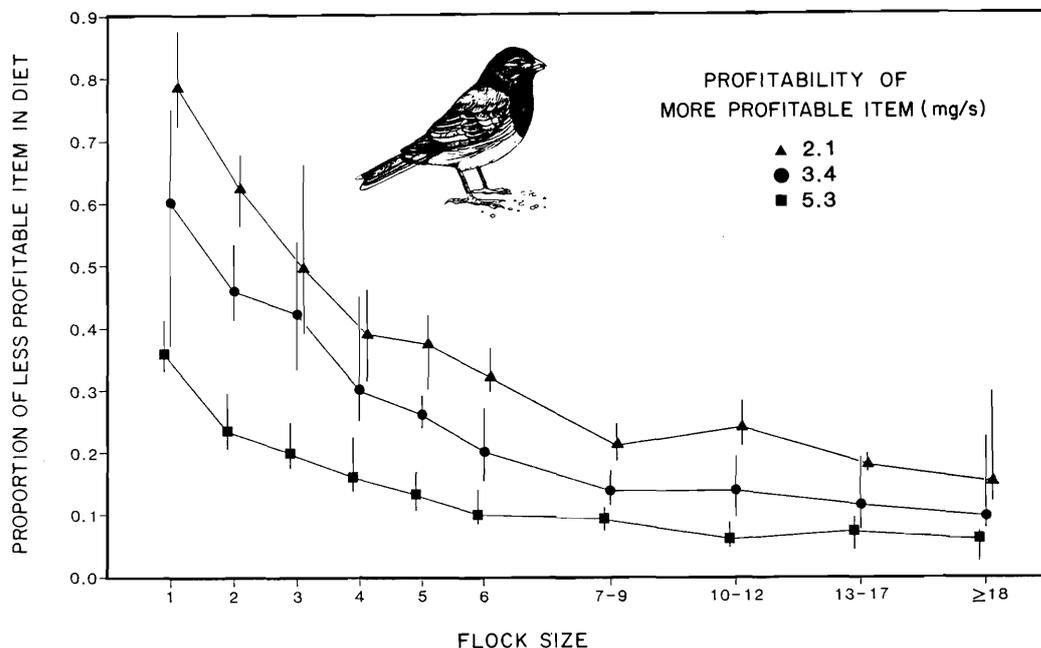


FIG. 4. Diet selection by free-living juncos in simple two-prey environments as a function of flock size. The juncos chose between whole millet seeds (the less profitable item at 1.9 mg/s (kernel mass/handling time)), and a given size class of millet kernel bits (the more profitable item, with the profitability indicated). There was effectively no search time between food items. A junco could be vigilant while husking whole millet seeds, but not while pecking up the bits of millet kernels; the proportion of observed diet consisting of the former item decreased with an increase in both flock size and the profitability of the latter food items. Data are presented as means (and range) of behavior over 4 days of observations. From Lima (1988c).

Parus major, are determined by an energy – predation risk trade-off where predator detection is the major subcomponent of predation risk under a forager's control. The reason is simple: a great tit must keep its head down while breaking up a food item and thus might not detect an attacking predator. To detect a predator, it must regularly interrupt the food handling process to scan its environment. Because scanning detracts from energy intake rate, Krebs reasoned that food-deprived birds might scan less while handling food items (i.e., have shorter handling times) than more satiated birds; this is what was observed (Fig. 5).

Valone and Lima (1987) reported that several species of birds exhibit shorter handling times when in the open than in protective cover. This reflects the fact that birds in cover break up food items to a much greater extent before consumption than those away from cover. By breaking up food items before consumption, it is likely that a bird can increase the efficiency and (or) the speed of digestion; birds consuming food away from cover apparently waived this benefit in an attempt to decrease the time they spent exposed to predators. Analogous reasoning may explain quantitatively similar cover–open tendencies in the handling times of gray squirrels (see Lima *et al.*, 1985, and Lima and Valone, 1986). Newman *et al.* (1988) found that gray squirrel seed handling time depends on distance to cover *per se*, being shorter at 15 m than at 5 m from trees (cf. Dill and Houtman 1989); travel speeds between adjacent patches, another assumed “constraint” on foraging, also depended on distance to cover in this study.

Decisions not necessarily related to feeding

As noted in the Introduction, we are concerned with studies analysing decisions made under the risk of predation that require an animal to assess its environment and respond appropriately. Relatively few studies of this nature exist outside of the context of feeding behavior, and thus we have grouped all of them under

the above self-explanatory, but deliberately vague, subheading. Even though we will not be dealing with decisions traditionally within the realm of feeding behavior, the reader will nonetheless find a strong influence of energy in decision making, be it via energy expenditure or acquisition.

Sociality

Predation has long been implicated as a major selective force in the evolution of many patterns of sociality, such as colonial breeding, mating systems, social structures, flocking, roosting, etc. (Crook 1965; Bertram 1978; Pulliam and Caraco 1984; Godin 1986; Pitcher 1986). It is not our intention to provide yet another review of this massive literature. Rather, in keeping with our major theme, we will focus upon those studies which examine social phenomena as an outcome of decisions made by individuals based on their assessment of the prevailing risk of predation and other environmental factors. As we will show, beyond those studies dealing with vigilance, remarkably few can be included here.

Vigilance

Vigilance for predators as a social phenomenon is one of the most studied aspects of behavior under the risk of predation. The common observation is that individuals in a foraging group spend less time being vigilant with an increase in group size. This has been demonstrated in both mammals (Berger 1978; Hoogland 1979; Lipetz and Bekoff 1982; Alados 1985; Monaghan and Metcalfe 1985; Risenhoover and Bailey 1985; Carey and Moore 1986; Dehn 1986; LaGory 1986; Wirtz and Wawra 1986; Wawra 1988) and birds (Dimond and Lazarus 1974; Powell 1974; Lazarus 1978, 1979; Abramson 1979; Caraco 1979a; Barnard 1980; Bertram 1980; Caraco *et al.* 1980a, 1980b; Goldman 1980; Jennings and Evans 1980; Elgar and Catterall 1981; Inglis and Lazarus 1981; Burger 1982; Pulliam *et al.* 1982; Elgar *et al.* 1984; Metcalfe 1984a, 1984b; Sullivan 1984a, 1984b, 1988; Barnard and Thompson 1985;

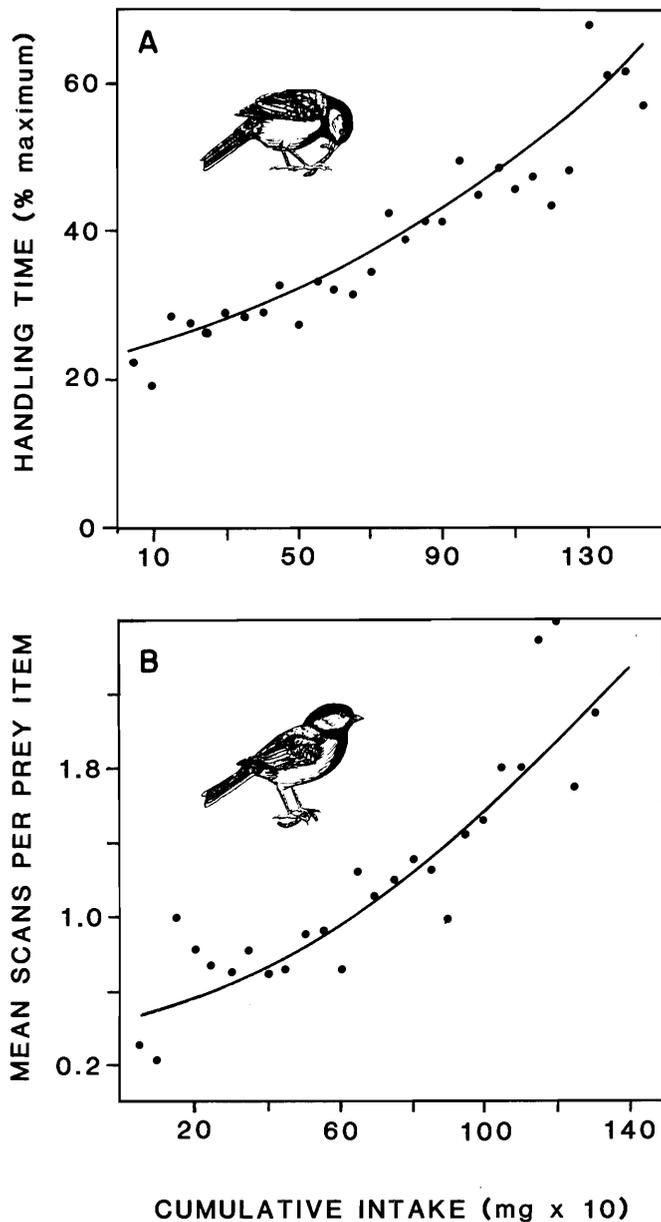


FIG. 5. Prey handling by food-deprived great tits. Data are pooled from five individual birds handling portions of mealworms. Plotted are (A) total handling time (including scanning time, expressed as percentage of maximum observed handling times), and (B) the mean number of scans per prey handled as a function of cumulative food intake in a given session. The increase in handling time with cumulative food intake is a direct result of increased scanning. Redrawn from Krebs (1980).

Elgar 1986*b*, 1987; Glück 1986; Popp 1986; Lima 1987*b*; Ekman 1987; Heinsohn 1987; Hogstad 1988*b*; Redpath 1988, but see Smith, 1977, and Pöysä, 1987). In addition, position within the group (Jenning and Evans 1980; Alados 1985; Phelan 1987) and group composition (Metcalf 1984*b*; Sullivan 1984*a*, 1984*b*; Barnard and Thompson 1985; Thompson and Thompson 1985; Hogstad 1988*b*; Popp 1988) have been shown to be important factors in vigilance. Lendrem (1984) and da Silva and Terhune (1988) also found that vigilance in "sleeping" birds and seals, respectively, declined with group size (see also Ball *et al.* 1984); however, Redpath (1988) found no effect of group size in preening birds.

The bias toward avian studies reflects the ease with which vigilance may be distinguished from other activities in birds, and probably not a lack of generality of the basic result; some data for fish are suggestive (Magurran *et al.* 1985; Godin *et al.* 1988; but see Godin and Morgan 1985). We also note that subcomponents of risk other than predator detection (e.g., distance away from threat (Lendrem 1983)), many under an animal's control, combine to influence vigilance in feeding animals (see Lima 1987*a* and Elgar 1989 for reviews).

The trade-off commonly thought to underlie the above "group size effect" is straightforward: the act of being vigilant detracts from energy intake; thus, a change in any factor that lessens the need to be vigilant should lead to a decrease in vigilance. Since an increase in group size leads to more eyes able to scan for predators, a given group member can be less vigilant while the overall vigilance of the group suffers little (assuming that all group members are somehow alerted to a predator once it has been detected). This explanation seems relatively sound, but there may be some problems with its details. For instance, factors such as the benefit of being the first to detect and (or) respond to an attack (cf. Elgar 1986*a*) and competition for readily depletable food may alter this conventional explanation. Inglis and Lazarus (1981) suggest that the decrease in vigilance in flocks of geese is due mainly to the fact that the highly vigilant geese on the edge of the flock comprise a smaller proportion of the flock as its size increases. Dehn (1986) suggests that "false alarms" are a major factor in determining vigilance. Further problems with the interpretation of the group size effect, such as the object of vigilance (e.g., predators vs. conspecifics (Knight and Knight 1986; Waite 1987*a*, 1987*b*; Roberts 1988)) and evolutionary stability in vigilance patterns, are examined more fully in Elgar (1989) and Lima (1990*a*).

A relatively unstudied area in social vigilance is the phenomenon of sentinels: animals that completely forego feeding and stand guard while the remainder of the group forages (e.g., Rasa 1986, 1987; Ferguson 1987). As in "conventional" social vigilance discussed above, the existence of sentinels raises questions about the evolutionary stability of apparent cooperation, i.e., who does the guarding and what is the guarantee that others will reciprocate and take their turn as guard? This is more problematic given the potential risk in being a sentinel (Rasa 1987). Following Axelrod and Hamilton (1981), it is probably no coincidence that sentinels are often observed in stable, family-based groups in birds (e.g., Ferguson, 1987) and mammals (e.g., Rasa, 1986).

Group size

Despite the great interest in vigilance as a function of group size, little empirical work exists that directly examines group size as a function of the decisions made by individual members to join or leave groups given their assessment of predation risk and other factors.

Caraco (1979*a*) found that group size in yellow-eyed juncos, *Junco phaeonotus*, increases with a decrease in both temperature and food abundance. Subsequent work with these juncos showed that group size also increases with the distance to cover (Caraco *et al.* 1980*a*) and in the presence of a potential predator (Caraco *et al.* 1980*b*). After explicitly considering several aspects (subcomponents) of predation risk, Caraco (1979*b*, 1980) developed a cogent argument that these patterns reflect the outcome of energy and predation risk dependent decisions made both by dominant individuals attempting to control group size and subordinate individuals deciding whether to remain in a group given the behavior of the more dominant individuals (see

also Caraco *et al.* 1989). Similarly, Elgar (1987) found that a house sparrow's decision to join a given flock is aggression and predation risk dependent. Furthermore, Elgar (1986b) found that solitary house sparrows may seek to establish flocks around themselves, but only when the food resource is divisible among potential flock members. Additional work with this system showed that a house sparrow's tendency to establish flocks increases in high-risk situations (Fig. 6; Elgar 1986c). In a related study, Ekman (1987) found that willow tits increase group size after alarm calls.

An apparent trade-off between safety and competition for food affects choice of group size in shoaling threespine sticklebacks. Van Havre and FitzGerald (1988) found that hungry sticklebacks are more likely to associate with small ($n = 15$) than large ($n = 25$) shoals; the reverse holds for satiated fish.

There is an intuitive appeal to greater safety in numbers, but the precise benefit of being in a larger group is not always clear. In the presence of a predator, increased group size may reflect a social escape tactic (*e*, Fig. 1), the benefits of social vigilance (*p*), and (or) diluted risk (*e*). To make matters more complicated, some animals may reduce group size under an increased risk of predation. For instance, teal (*Anas crecca*) group size varies inversely with raptor flyover frequency, and average group size after a flyover is smaller than that before (Pöysä 1987a). Caldwell (1986) similarly found flock size in various herons to decrease with increasing attacks by hawks (*Buteo* spp). Savino and Stein (1989) found that bluegill shoaling may initially increase and then decrease with increasing density of vegetation, but only in the presence of predators. The reason for these group size decreases are even less clear.

Finally, individuals may be especially vulnerable to predation if they appear different from other group members (the "odddity effect"). It is therefore of interest that both marine (Wolf 1985) and freshwater fish (Allan and Pitcher 1986) tend to leave schools comprised largely of another species when these are threatened by predators.

Group structure

Abrahams and Colgan (1985) found that schooling shiners, *Notropis heterodon*, swim in the same horizontal plane in the absence of a predator, but stagger themselves into a more three-dimensional arrangement in the presence of a predator. These authors provide evidence that shiners swimming in formation in a monolayer gain an energy-saving hydrodynamic benefit, but argue that the cost of such a schooling formation is a decreased ability to detect predators; adjacent individuals obstruct a fish's view of its surroundings. Thus, the shiners may stagger themselves in the presence of a predator to better monitor the latter's movements, at the cost of less efficient locomotion.

In contrast, social groups of other species become more compact in the presence of predators, probably because the advantages of group defense and avoidance outweigh the cost of obstructed vision. Thus, nearest neighbor distances in flocks of turnstone, *Arenaria interpres*, decrease in the presence of sparrowhawks, and redshank, *Tringa totanus*, abandon their territories and form flocks in response to the same predator (Whitfield 1988). Buff-breasted sandpipers, *Tryngites subruficollis*, similarly abandon their territories and begin to flock with the appearance of predators (Myers 1980); flocking in shorebirds is an integral part of their escape tactic (*e.g.*, Dekker, 1988). In addition, schools of some fish species become more concentrated in the presence of predators (*Leucaspius delineatus* (Andörfer 1980; various minnows, Allan and Pitcher

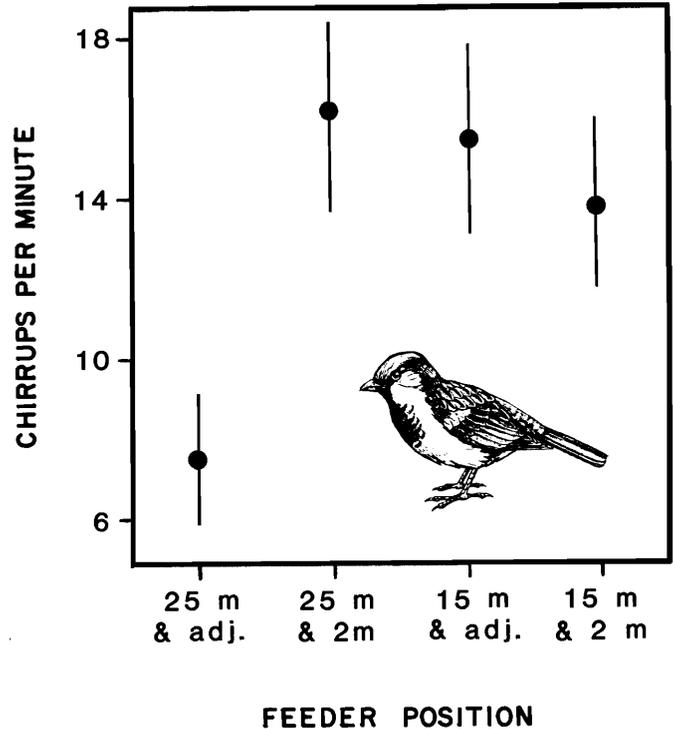


FIG. 6. Flock-establishing behavior of solitary house sparrows, which use "chirrup" calls to establish flocks around themselves. Data are given as mean chirrup rates as a function of feeder position (perceived risk). The feeder, supplied with seeds, was placed either 15 or 25 m from an observer, and either adjacent (adj.) to or 2 m from a low wall to which they flew when alarmed. The chirruping rate was significantly lower in the safest feeder position (25 m and adj.) than at the others (*t*-tests, $P < 0.001$). Redrawn from Elgar (1986c).

1986; Magurran and Pitcher 1987; Morgan 1988a, 1988b)). This may be the result of individuals reducing the frequency or duration of straggling from schools when predators are present. The latter effect has been demonstrated in the banded killifish, *Fundulus diaphanus*, by Morgan and Godin (1985), who also provide evidence that stragglers experience an increased risk of capture by predatory white perch, *Morone americana*.

Certain areas within a group are undoubtedly safer than others, but surprisingly few studies address the implications of this for individual behavior. Ekman (1987) and Ekman and Askenmo (1984) found that subordinate members of titmice flocks (*Parus* spp.) were forced by the dominants to feed in the less safe (open) portions of trees; here, components of risk concerning both attack frequency and escape may be in operation. Similarly, Schneider (1984) found that subordinate white-throated sparrows are relegated by dominants to positions in the flock most distant from protective cover. In an experimental study of the social organization of a colonial web-building spider, *Metepeira incrassata*, L. S. Rayor and G. W. Uetz (manuscript in preparation) showed that larger individuals actively seek the central position of the colony where attacks from predatory wasps are much reduced, relegating the smaller individuals to the outer colony. This central location, however, is less profitable from a foraging viewpoint.

Behavior after an encounter

General activity

Several examples have been reported of animals altering their general activity levels in the presence (or odor) of predators. In

most cases, the animals are observed to reduce their spontaneous activity levels. This has been reported for various species of zooplankton in the presence of the predatory copepod *Acanthocyclops vernalis* (Li and Li 1979), the stream isopod *Lirceus fontinalis* in the presence of green sunfish, *Lepomis cyanellus* (Holomuzki and Short 1988), the shrimp *Tozeuma* in the presence of pinfish (Main 1987), crayfish *Astacus astacus* in the presence of perch, *Perca fluviatilis* (Hamrin 1987), larval odonates, *Coenagrion puella* and *Ischnura verticalis*, in the presence of fish predators (Convey 1988, and Dixon and Baker 1988, respectively), the velid bug *Microvelia australis* in the presence of green sunfish (Sih 1988), the stonefly *Phasganophora capitata* exposed to trout skin mucus (Williams 1986), the marine gastropod *Thais lamellosa* exposed to waterborne stimuli from crabs or damaged conspecifics (Appleton and Palmer 1988), and threespine sticklebacks exposed to model herons (Godin and Sproul 1988).

In some cases, reduction in activity results from the increased use of refuges. The Florida harvester ant, *Pogonomyrmex badius*, ceases aboveground activity in response to high removal rates simulating the presence of predators (Gentry 1974). Larval tree frogs, *Hyla chrysocelis*, and smallmouth salamanders, *Ambystoma texanum*, spend more time in a refuge in the presence of the odor of green sunfish than in its absence (Petranka *et al.* 1987, and Kats 1988, respectively), as do johnny darters, *Etheostoma nigrum*, in the presence of smallmouth bass (Rahel and Stein 1988). Several additional examples are reviewed in Dill (1987).

Given that moving prey are often more easily detected by predators, reduced activity may be an attempt by prey to increase the value of a in Fig. 1. In some cases, this is clearly done at some cost to energy intake; for example, guppies decrease their feeding rate in the presence of predatory cichlids (Fraser and Gilliam 1987), and dragonfly larvae do the same when they detect the presence of predatory notonectids (Hedges 1986). Reduced movement may also reduce the rate at which dragonfly larvae are able to find ephemeral food sources (Dixon and Baker 1987).

Less commonly, prey respond to the presence of predators by increasing their activity levels. Examples include the zooplankton *Diaphanosoma leuchtenbergianum* in the presence of a predatory copepod (Li and Li 1979), and the stonefly *Paragnetina media* exposed to trout skin mucus (Williams 1986). Increases in activity may represent either escape or avoidance responses, increasing the values of e or a (Fig. 1), respectively. Whether a prey decreases or increases its spontaneous activity level when predators are nearby (but not yet attacking) may depend on how secure the prey feels against its background: cryptic species may be more likely to restrict movement, compared with more conspicuous prey.

Escaping from predators

We have seen that an animal's ability to control the escape subcomponents of predation risk (e_1 and e_2), manifested as a choice of distance to safety, has a strong influence on where it feeds. However, control of the escape subcomponents extends to decisions about whether or when to attempt escape given an encounter. An animal clearly has control over this decision, but why would it choose not to attempt escape? The answer is simple: not all encounters with a predator, or all moments during an encounter, are equally dangerous. Since the decision to escape has costs (energy expenditure and lost opportunity to engage in other activities), then it should depend on the animal's assessment of risk (see Ydenberg and Dill 1986).

The risk in a predator-prey encounter depends, among other things, on the time it would take the prey to reach safety once it begins to flee. Dill and Houtman (1989) have shown that the flight-initiation distance of gray squirrels attacked with a remote-control predator increases as distance to safety (the nearest tree) increases. A similar result has been obtained in a rock-dwelling African cichlid fish, *Melanochromis chipokae*. When a predator appears, fish farther from safety (rocks) begin their flight back to the rocks sooner than those nearby. Flight-initiation distance and speed seem to be chosen such that a fish reaches the rocks a constant length of time before the predator: the fish seem to maintain a constant "margin of safety" (Dill 1990). McLean and Godin (1989) report similar behavior in banded killifish, but not in more heavily armored (less vulnerable) sticklebacks (*Gasterosteus* and *Pungitius* spp.).

Some field observations also support a relationship between flight initiation and the distance to cover or predators. Grant and Noakes (1987) found an inverse relationship between flight-initiation distance and cover density (inversely correlated with distance to nearest cover) in the brook trout, *Salvelinus fontinalis*. The likelihood that white-tailed deer, *Odocoileus virginianus*, will flee from a human detected at long distances depends on habitat: flight is more likely in forests than in pastures, perhaps because forests are perceived as more dangerous (LaGory 1986, 1987).

Risk also depends on the number of individuals in a feeding group. The flight-initiation distance of juvenile waterstriders, *Gerris remigis*, to an approaching cannibalistic adult is shorter in large groups than in those of intermediate size, and can be described by a model incorporating both constraints on predator detection, the dilution effect, and energy - predation risk trade-offs (Dill and Ydenberg 1987).

Heatwole (1968) has shown that cryptic *Anolis* lizards have shorter flight-initiation distances than do less well camouflaged ones. This can be explained by assuming that risk depends in part on the probability that the predator has sighted the prey (q); cryptic animals are at lower risk and therefore should have a shorter flight-initiation distance. Unfortunately, such observations alone provide no evidence for risk assessment, which would require placing lizards on different backgrounds and studying their flight behavior. More convincing is the observation that flight-initiation distance in *Anolis lineatopus* is inversely correlated with body temperature, which constrains running ability (Rand 1964). Regarding crypticity and escape, it would be interesting to determine whether some lizards change coloration (increase crypticity) in the presence of predators. Such changes in crypticity have been noted in other creatures. For example, two species of hermit crabs increase the number of anemones placed on their shells (thus becoming more cryptic) when they sense the odor of octopus (Brooks and Mariscal 1986). Similarly, the spider crab, *Acanthonyx petiveri*, decorates itself with algae when it finds itself on a substrate against which its body contrasts, thereby reducing its visibility to potential predators (Wilson 1987).

Aspects of escape behavior other than flight-initiation distance are also influenced by risk. For example, Helfman (1989) has shown that the strength of predator avoidance/escape in the threespot damselfish, *Stegastes planifrons*, varies directly with the size and threatening posture of predatory Atlantic trumpetfish, *Aulostomus maculatus*. The zebra-tailed lizard, *Callisaurus draconoides*, gives apparent pursuit deterrence signals to predators only when the former are at intermediate distances from cover, the situation in which the net benefit of such signals is expected to be greatest (Hasson *et al.* 1989).

Few, if any, studies in behavioral ecology have considered the e_3 escape subcomponent of d (escape after capture, Fig. 1) to be assessable and under the prey's control; a nonzero e_3 might occur only if predators sometimes mishandle prey. However, tonic immobility after capture, or "death feigning," appears to be a behavioral adaptation for increasing e_3 , and Suarez and Gallup (1983) review evidence which strongly suggests such behavioral responses to capture vary with a prey's assessment of risk. Further work in this area may prove interesting.

Inspecting predators

Rather than immediately attempting escape upon encountering a potential predator, some prey actually approach and "inspect" it. Predator inspection may be fairly widespread in vertebrates (see Pitcher *et al.* 1986), but it has been examined in detail only in fish.

Magurran and Girling (1986) showed that predator inspection functions, at least in part, in predator recognition; predatory and nonpredatory fish may be similar in appearance and the minnow *Phoxinus phoxinus* can make the distinction only after a close-range examination of potential predators. Of course, this can be a risky affair, and several lines of evidence suggest that predator inspection in these minnows is strongly influenced by their assessment of risk. Pitcher *et al.* (1986) found that feeding minnows (i) increase predator inspections as a predator (pike, *Esox lucius*) approaches, (ii) inspect a stationary predator more than a more dangerous, moving one, and (iii) approach a predator more closely when inspecting in a group (see also Magurran 1986). Magurran and Pitcher (1987) also found inspections to cease after a successful attack.

Beyond predator recognition, "inspectors" may gain information concerning the state (or motivation) of the predator (Magurran and Girling 1986) and (or) the risk of impending attack (Pitcher *et al.* 1986). Predator inspection may also function in pursuit deterrence (Magurran and Pitcher 1987). This uncertainty concerning the precise function(s) of predator inspection, however, clouds the exact nature of the cost-benefit trade-offs involved. Furthermore, Pitcher *et al.* (1986) and Magurran and Higham (1988) demonstrated that information gained by the inspecting minnows may be transferred to other group members, thus raising the question of stability in apparent cooperation within groups of minnows; i.e., why should some minnows voluntarily incur an increased risk of predation to gain information that can be shared by others? Magurran and Higham (1988) suggested that inspectors may actually "manipulate" other group members, while Milinski (1987) suggests that sticklebacks inspecting a predator engage in evolutionarily stable reciprocity (cf. Axelrod and Hamilton 1981).

Mobbing predators

Birds defending eggs or young may carry out attacks against (or mob) potential predators. These predators may pose little threat to the parents themselves, but this need not be the case. Curio *et al.* (1983) showed that mobbing great tits will approach owls more closely than sparrowhawks (*Accipiter nisus*). The sparrowhawks present not only a greater overall risk (great tits form a larger proportion of their diet), but also a greater momentary risk (danger); these two factors are not likely to be independent, however. In a later paper, Curio and Regelman (1985) showed that the tits' mobbing behavior changes (move lengths get shorter and calling rates increase) as they get closer to the owl, where risk presumably is greater. They also reviewed anecdotal evidence that mobbing is less likely to be performed by birds more prone to capture. Several animals other than tits mob predators, but no other workers provide

quantitative data on the effect of risk level on the mobbers' behavior.

The mobbing phenomenon does not fit neatly into our discussion of the components of predation risk because mobbers, like predator inspectors, actually seek encounters with potential predators. It is clear from the above work, however, that mobbers may be assessing several aspects of risk in their decision making, particularly the likelihood of an attack from the predator. Another important subcomponent may be related to escape as a function of the distance to the predator (should it decide to attack).

Respiration

Several fish species inhabiting waters prone to oxygen depletion are able to gulp air to ensure adequate respiration. Their tendency to "breathe" air increases with a decrease in the dissolved oxygen content of the water (see Kramer 1983). This may appear to have a strictly physiological interpretation, but such would be incomplete because rising to the surface to "breathe" entails a considerable risk of predation from both aerial and aquatic predators. Several studies have shown that the perception of predation risk alters air breathing.

In an early study, Kramer and Graham (1976) found that grouped fish tend to breathe synchronously after a predator-mimicking disturbance. Gee (1980) also found synchrony in air breathing in other fish species, and Baird (1983) made similar observations in a frog, *Xenopus laevis*. Although not clear, synchronous breathing may be an attempt to control the escape subcomponent of predation risk (e_1 and e_2 in Fig. 1), perhaps via risk dilution. A role for the avoidance subcomponent a in decision making is also indicated by the tendency of several air-breathing fish species to decrease their rate of air breathing and spend more time in deeper portions of test aquaria in the presence of green-backed herons, *Butorides virescens* (Kramer *et al.* 1983; see also Smith and Kramer 1986). Dwarf gouramis, *Colisa lalia*, in the presence of a predatory fish, *Channa micropeltes*, also decrease their rate of air breathing as well as increase their use of cover (Fig. 7; Wolf and Kramer 1987).

The respiratory behavior of non-air-breathing fish may also be influenced by the risk of predation. Kramer *et al.* (1983) showed that several non-air-breathers spend more time in the relatively oxygen-rich surface layer of water ("aquatic surface respiration") when dissolved oxygen decreases, and that their tendency to do so decreases in the presence of a predatory heron. However, Poulin *et al.* (1987) found that the risk experienced by surface-respiring fish may actually be relatively low (under low oxygen levels) if the predator is a non-air-breathing fish that is negatively affected by low oxygen levels.

There is little doubt that both air breathing and aquatic surface respiration are influenced by a fish's ability to assess and control its risk of predation. Behavioral modifications, such as a decreased rate of air breathing in the presence of a predator, are presumably done at some physiological cost, although its nature has not been considered in detail.

We have focused on respiration in fish because of a lack of such studies in other creatures. However, Gilliam *et al.* (1989) present evidence that tubificid oligochaete worms are increasingly reluctant to expose their external gills in the water column (for respiration) as the density of predatory fish increases. We suspect that similar situations are common in invertebrates.

Discussion and prospectus

The information reviewed above strongly suggests that many aspects of decision making in animals are sensitive to the risk of

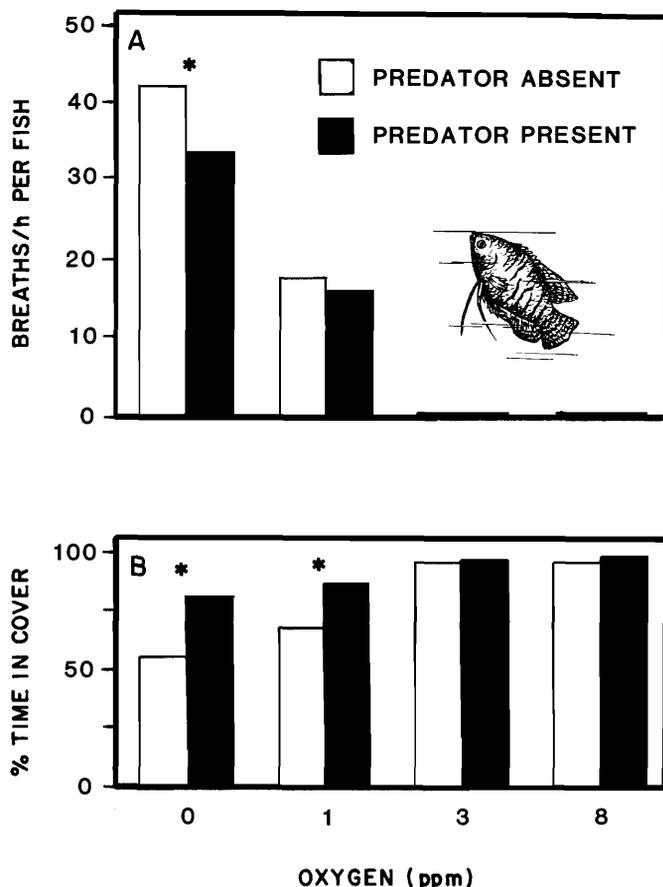


FIG. 7. Breathing behavior of dwarf gouramis in the presence or absence of a predator: (A) breaths/h per fish and (B) % time in cover as a function of the water's dissolved oxygen content. Data are pooled estimates from 14 or 15 trials, each consisting of data from three gouramis. The fish breathed less frequently and spent more time in cover in the presence of a predator (*, $P < 0.05$ by t -tests). In addition, breathing decreased and the use of cover increased with increasing oxygen level. Redrawn from Wolf and Kramer (1987).

predation. In many cases, decision making appears to reflect an adaptive trade-off between the need to avoid predation and various other needs. Although there is a scarcity of work in many of the areas discussed above, we feel that this basic result will be very general, since most animals are potential prey for others.

We wish to stress that the risk of predation is an integral part of the decision-making process. Consider, for example, an animal that has been observed to locate and consume several prey items. We might say that we have observed foraging behavior. To be sure, the animal did ingest food, but was it just "foraging"? Our review strongly suggests that this animal was "considering" not only its options as they relate to efficient food intake, but also how those options influence its risk of being preyed upon. To the extent that the term "foraging behavior" is associated strictly with the act of food intake, its use in describing behavior is misleading because it detracts attention from important determinants of behavior that are unrelated to energy. The same can be said concerning any behavior, not just foraging.

It is also important to note that the risk of predation does not "constrain" behavior. Although it is often stated that the risk of predation acts as a constraint on foraging behavior (e.g., Milinski 1986), one could just as easily argue that foraging is a

major constraint on predator avoidance. The fact is that neither foraging nor predation act as constraints. The behavioral options open to a feeding animal lie on a continuum between energy maximization (at the complete expense of predator avoidance) and minimization of risk (at the complete expense of feeding). Clearly, neither extreme option is desirable and optimal behavior will lie somewhere in between; however, there is nothing "constraining" the animal from choosing one of the extremes. We suggest that the term "constraint" be reserved for factors such as gut size, day length, or feeding anatomy, which are not under the individual's control and therefore actually constrain the animal to a particular set of behavioral options (cf. Belovsky 1978).

Given the evidence gathered thus far, we strongly suggest that future studies on decision making in animals should consider the risk of predation as a determinant of behavior from the outset. To not do so may be misleading. For example, in a study of feeding behavior, simply demonstrating behavioral responses to changes in the foraging environment that are in accord with the predictions of an energy-based model does not confirm energy as an adequate currency of fitness; we suspect that such studies actually examine behavior against a background of behavioral responses to the risk of predation and other factors. We also stress that researchers should strive to achieve as much rigor as possible in defining the components of predation risk that are (i) relevant, (ii) assessable, and (iii) under an animal's control.

We expect that the future will see more work on the role of predation risk in animal behavior and behavioral ecology in general. We now wish to identify some potentially fruitful areas of research and note some problems that may be encountered.

Behavior of feeding animals

Although decision making in animals feeding under the risk of predation has been an active area of research, much work remains concerning the scope and generality of the results obtained so far. In fact, our review reveals several areas that have received virtually no attention from a predation risk perspective. We suspect that predation-related research in such areas as central-place foraging, patch-leaving rules, sampling/information gathering (e.g., exploration), risk sensitivity (where "risk" refers to the risk of starvation), and food hoarding will prove quite fruitful.

For instance, patch-leaving rules may be strongly influenced by the need to be vigilant while feeding; the same holds for central-place foraging decisions (e.g., Covich 1976), which might also be strongly influenced by the risk of predation on dependent young at the central place (Freed 1981; Martindale 1982). Sampling of the environment to gain information may entail significantly increased exposure to predators, thus the extent of sampling (or exploration) may depend on predation risk. Decisions concerning the hoarding of food should also be sensitive to predation because such activity will require significant exposure to predators. Studies of starvation-risk sensitivity may benefit from a predation perspective because behavioral options which lessen the risk of starvation (such as feeding faster) may entail an increased risk of predation (see McNamara and Houston 1986, and Weissburg 1986). In short, virtually any foraging decision that must be made under the risk of predation may differ from one based upon energetic considerations alone.

Reproduction

There is a considerable body of evidence suggesting that

TABLE 1. Examples of male reproductive activity leading to increased risk of predation

Species	Activity and effect	Reference
Firefly (<i>Photinus</i>)	Response to mimetic female call leads to predation by <i>Photuris</i> females	Lloyd 1965
Field cricket (<i>Gryllus integer</i>)	Calling leads to tachinid fly parasitism	Cade 1975
Cicada (<i>Okanagana rimosa</i>)	Song attracts female dipteran parasite	Soper <i>et al.</i> 1976
Noctuid moth (<i>Spodoptera frugiperda</i>)	Response to mimetic female pheromone leads to predation by bolas spider	Eberhard 1977
Hanging fly (<i>Hylobittacus apicalis</i>)	Searching for nuptial gift for female leads to spider predation	Thornhill 1980
Southern stink bug (<i>Nezara viridula</i>)	Sex pheromone attracts female tachinid fly parasite	Harris and Todd 1980
Digger wasps (<i>Philanthus</i> sp.)	Territorial flights lead to robberfly predation	Gwynne and O'Neill 1980
Frog (<i>Physalaemus pustulosus</i>)	Calling attracts predatory bats	Tuttle and Ryan 1981; Ryan 1985
Katydid (<i>Neoconocephalus tripos</i>)	Song attracts tachinid fly parasite	Burk 1982
Waterbug (<i>Belostoma flumineum</i>)	Male parental care (egg carrying) leads to raft spider predation	Kruse 1986
Tick-tock cicada (<i>Cicadetta quadricincta</i>)	Movement towards answering female leads to spider predation	Gwynne 1987
Cock-of-the-rock (<i>Rupicola rupicola</i>)	Displaying males attacked at leks	Trail 1987
Guppy (<i>Poecilia reticulata</i>)	Displays attract predator's attention	Endler 1987
Pipefish (<i>Nerophis ophidian</i>)	Male parental care (egg carrying) leads to increased predation	Svensson 1988

TABLE 2. Examples of female reproductive activity leading to increased risk of predation

Species	Activity and effect	Reference
<i>Daphnia galeata</i> and <i>D. pulex</i>	Carrying of eggs leads to predation by fish and newts	Mellors 1975
Scincid lizards	Egg carrying decreases running speed and probably leads to increased predation	Shine 1980
Copepod (<i>Cyclops vicinus</i>)	Egg carrying leads to predation by fish	Winfield and Townsend 1983
Marine copepod (<i>Eurytemora hirundoides</i>)	Egg carrying leads to predation by sticklebacks	Vuorinen <i>et al.</i> 1983
Mormon cricket (<i>Anabrus simplex</i>)	Competition for male spermatophores increases vulnerability to digger wasps	Gwynne and Dodson 1983
Decorated cricket (<i>Gryllodes supplicans</i>)	Attraction to calling male leads to gecko predation	Sakaluk and Belwood 1984
Deer mouse (<i>Peromyscus maniculatus bairdi</i>)	Estrous increases predation by weasels	Cushing 1985
Prawn (<i>Palaemon adspersus</i>)	Egg carrying leads to fish predation	Berglund and Rosenqvist 1986
Firefly (<i>Photinus collustrans</i>)	Mating (leaving burrows) exposes females to increased predation	Wing 1988

reproductive activity places animals under increased risk of predation (or fatal parasitism). The risk experienced by males may be increased in several ways, especially by calling and display behaviors conspicuous to both females and predators (Table 1). Although most such cases reported to date deal with insects, the effect is undoubtedly more general. In the case of females, egg carrying may increase predation risk by increasing visibility to predators or decreasing speed and manoeuvrability, but several other effects have also been reported (Table 2). One or both sexes may also pay a cost in terms of the increased vulnerability to predation often associated with parental duties (e.g., Ainley and DeMaster 1980). For all these reasons, the

reproductive period is often a time of greatly increased predation; this is part of the "cost of reproduction" which influences the evolution of life-history strategies (Stearns 1976).

Given that reproductive activities increase the risk of predation and that animals have made mortality-reproduction trade-offs in evolutionary time, it would be surprising if they did not do so in ecological time as well, i.e., base certain reproductive decisions on estimates of the prevailing risk of predation. However, we have found very few convincing examples of it in the voluminous literature on animal reproduction. One simple example is provided by Ryan (1985) (see also Tuttle *et al.*

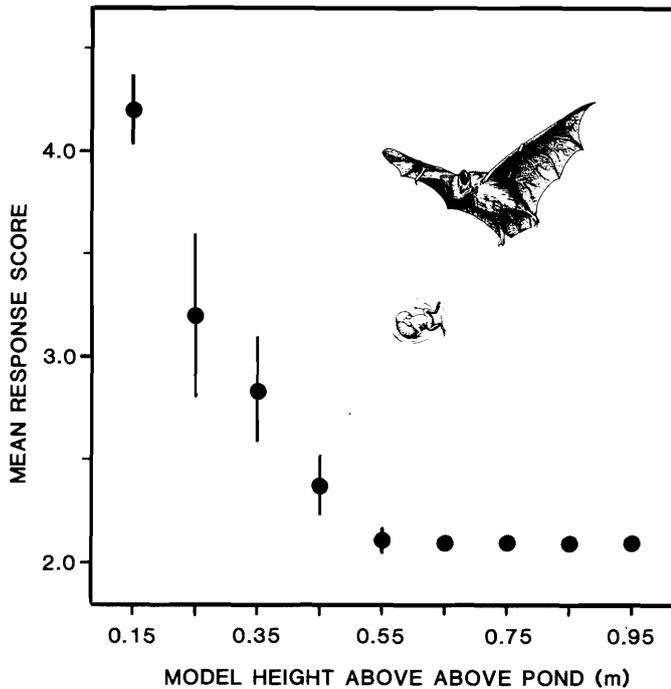


FIG. 8. Escape tactics of chorusing male tungara frogs as a function of perceived risk. Perceived risk was manipulated by varying the height that a model bat was flown over the pond. Observed escape responses were scored on a scale from 1 to 5 and the values given are means \pm SE: 1, continued calling; 2, stopped calling but remained inflated; 3, stopped calling and deflated; 4, deflated and lowered body into water; 5, dived. Above a height of 0.6 m, the bat model invariably elicited a score of 2. Data from Ryan (1985).

1982), who studied the behavior of male tungara frogs, *Physalaemus pustulosus*, chorusing under the risk of predation by a bat, *Trachops cirrhosus*: frog escape tactics in response to simulated bat attacks were directly related to the distance between the model bat and the frog (Fig. 8), and the length of time that chorusing was "shut down" after an attack was influenced both by the type of bat (predatory or nonpredatory) flown over the frogs and ambient light levels. The paucity of such studies probably reflects the strong evolutionary emphasis in the study of reproduction rather than a general lack of decision making in ecological time. Research on such decision making will likely be an area of much activity in the near future. At this point, we sketch a few of the questions which can be posed. As was the case for foraging decisions, reproductive decisions may be broadly placed in three categories: when, where, and how.

Animals may alter their reproductive effort at times when they assess predation risk to be particularly high. For instance, some animals may reduce predation risk via synchronous breeding, but this has potential costs as well, particularly increased competition for food. Consequently, animals should reproduce more synchronously when they judge risk to be high. Caraco and Pulliam (1984) have considered breeding synchrony in a game-theory framework and predicted that the ESS (evolutionarily stable strategy) distribution of births should vary with the intensity of predation on offspring. However, their argument is entirely evolutionary and does not seem to allow for the assessment of predation risk on individual parents or offspring at the start of the breeding season.

Some "where" decisions can be considered in much the same

way. Animals should choose where to breed based upon their estimate of local predation risk to themselves. Again, this may be lower where others are mating (e.g., in leks; Trail 1987) or caring for eggs or young (e.g., in colonies). This effect may even be interspecific. For example, some passerine birds appear to prefer to breed inside rather than outside lapwing (*Vanellus vanellus*) territories (Eriksson and Götmark 1983), probably because predation rate on eggs is lower there (Goransson *et al.* 1975). Although there is mounting evidence that birds choose nest sites to minimize predation risk to their offspring (Martin 1988), it is not especially relevant to our present discussion unless parent and offspring risks are correlated, which they might be.

Another "where" decision has been considered by Iwasa *et al.* (1984), who demonstrate mathematically that host selection by parasitoids should depend on the likelihood of predation while ovipositing on the available host types. A female who can assess changes in prevailing risk level should benefit from such an ability.

"How" decisions are still more diverse and many could be made more efficiently via an assessment of risk. In the interests of brevity, we confine our speculation to two issues of considerable current interest: clutch size and alternative male reproductive tactics. Several authors have shown that optimal clutch size (or reproductive effort) in a variety of circumstances should depend on the rate of predation on the parent (Abrams 1983; Weis *et al.* 1983; Charnov and Skinner 1985; Houston and McNamara 1986; Lima 1987c). All of these arguments have been evolutionary ones and none have implied assessment strategies by the female. However, females capable of a flexible clutch size should outcompete those whose clutch size has been adjusted evolutionarily to some average level of risk. Even if clutch size is fixed in ecological time, decisions about how much foraging effort, etc., to devote to offspring are probably under a parent's control and thus subject to its assessment of predation risk (see Lima 1987c); parent-offspring conflict may be a particularly interesting area of study in this regard (cf. Lazarus and Inglis 1986).

It is now recognized that there exist in many species two (or more) types of male reproductive tactics (e.g., Gross 1984). In at least some of these cases the tactics are not genetically fixed, but are part of a conditional strategy: males decide which tactic to adopt based upon their current assessment of the environment (e.g., Waltz and Wolf 1988). Since predation risk influences the relative costs of many behavioral alternatives (e.g., calling for mates vs. satellite behavior; see Table 1), predation risk assessment should be well developed in the males of such species.

Perhaps because evolutionary trade-offs between risk and reproduction are so widely appreciated, some authors seem to have ignored completely the possibility of trade-offs in ecological time. To take one example, the widely quoted study of Farr (1975) showed that male guppies court at a lower rate in streams containing predators. Farr interprets this as an evolutionary response and does not mention the possibility that male guppies might simply assess predation risk and adjust their courtship intensity accordingly. Indeed, Endler (1987) has recently reported evidence for just such an effect. Similarly, Strong (1973) found that the length of amplexus of the amphipod *Hyallela azteca* is shorter in lakes where fish predation is more intense (amplexus pairs are more vulnerable to predation; but see Gwynne 1989). Although this is considered to be an evolutionary response, the possibility of assessment cannot be ex-

cluded. Sih (1988) has recently reported that the presence of predatory fish reduces the proportion of a semiaquatic bug, *Microvelia australina*, found in tandem (this is considered to be primarily a postcopulatory mate-guarding behavior). The mechanism underlying this effect is uncertain, but A. Sih (personal communication) suggests that males are reducing their guarding duration because the attack rate is higher on pairs than on singletons. It is therefore increasingly likely that mating behaviors may vary depending upon each individual's assessment of risk in ecological time. To exclude such a possibility would require manipulation of predation risk, perhaps by transplantation experiments.

Modeling

We have not yet discussed the various mathematical models of behavior under the risk of predation. Such models are actually in their infancy and a complete treatment of them is outside the scope of this paper. Our goal here is to examine some limitations of a common mathematical treatment of the risk of predation.

The most prevalent way of incorporating predation risk into a model is via the assumption of a constant death rate. The basic mathematical treatment is simple. First, it is assumed that the probability of death during any small time interval is constant and independent of time. Under this assumption, the time until death occurs is an exponential random variable; the probability of death during some time period $(0, T)$ is

$$[3] P(\text{death}) = 1 - \exp(-\mu T)$$

where μ is the death rate and T is the time spent vulnerable to predators.

This depiction of risk is most commonly used in analyses of habitat (or patch) selection (Gilliam 1982; Werner and Gilliam 1984; Iwasa *et al.* 1984; Mangel and Clark 1986; Werner 1986; Gilliam and Fraser 1987; Houston *et al.* 1988). In such studies, μ is taken as a habitat-specific constant, and an animal's ability to control its level of risk is limited to its choice of habitat (each differing in μ). However, reference to eq. 1 shows that μ is equivalent to αd and, as seen in the above review, an animal has several options in influencing d (the probability of death, given an encounter) and perhaps even α (the rate of encounter with predators). In other words, the death rate itself is under an animal's control to some extent and not a given habitat-specific constant. Only some models (mainly those concerning vigilance in feeding animals) explicitly consider the behavioral control of μ (e.g., Covich 1976, Pulliam *et al.* 1982, McNamara and Houston 1986, and Lima 1987a).

More work in this area is needed, particularly because one may more readily appreciate the potential complexity in behavioral responses to risk by developing such models. One may also appreciate the fact that the prey's decisions may influence many of the subcomponents of d under the predator's control (see Fig. 1), such as its decision about whether to attack or ignore encountered prey (cf. Hart and Lendrem 1984, and Sih 1984). In fact, game-theoretical analyses of this behavioral interaction will prove useful in analyzing decision making (cf. Iwasa 1982).

We expect that mathematical models will continue to play an important role in the elucidation of predation risk related trade-offs in decision making. Virtually all of the areas discussed above will require more theoretical analysis. In particular, many areas, such as respiration, group structure, and the mobbing of predators, are in need of theoretical attention that may help focus research. Perhaps most of all, much more

theoretical work is needed on the behavior of reproducing animals in the present context of decision making. In any case, we hope that modelers will strive to consider the relevant components of the risk of predation and the fact that many may be under the behavioral control of both prey and predator.

Perceptions and problems

The risk of predation is clearly important in many aspects of animal decision making. We have already mentioned some areas needing further work, but a major question still remains: how is the risk of predation actually perceived by animals? To put it another way, how are the various components of predation risk "measured" by an animal?

Some components are probably relatively easily measured by an animal, including its distance to safety, the maximum speed at which it can travel, the time it spends exposed to predators, etc., but others are not so easily assessed. For instance, it is not clear how an animal might estimate its probability of escape; direct sampling has clear drawbacks.

In short, several aspects of risk will be the subject of much uncertainty. We strongly suspect that animals deal with this uncertainty by using relatively simple "rules" that reflect their evolutionary history of predation. One such simple rule might be: assume attack is likely until experience allows for a more detailed assessment of risk. Rules of this nature may be modified according to the degree of risk assessed via the distance to cover, the openness of the habitat, etc. Many such rules can be envisioned, but there is very little evidence available to assess their actual importance.

Work on the perception of predation risk will likely be very rewarding, but it may also illustrate some problems for researchers. For instance, when studying an animal which "assumes" that "when in the open, there is substantial risk," one may never achieve an experimental situation with no perceived risk. This may be a particular problem with species that have evolved under ambush predation where there is little prior information about impending attack. With such animals, one may at best achieve only a perception of a constant risk. A minimal perception of predation risk may be achievable in those animals that can detect predators via reliable chemical cues (see examples discussed by Dill 1987), but we cannot presently assess this possibility.

There are other potential problems concerning such perceptions and the study of behavior under the risk of predation. For instance, consider the common experimental protocol of comparing the behavior of prey in the presence or absence of a predator. The prey undoubtedly perceive a risk of predation in the presence of a predator, but for the reasons outlined above, they may not perceive zero risk in its absence. In other words, one should not take such experiments as comparisons of behavior in a risky versus a risk-free environment. In addition, one must always be concerned with the spatial scale of experiments when examining behavior in the presence of predators. For example, in a relatively small experimental arena, the predator and prey may be in such close proximity or encounter each other at such high frequency that the prey's behavior is abnormally influenced by escape and avoidance tactics, to the point where meaningful results concerning patch choice, etc., cannot be obtained. When using this protocol, one must be sure that the prey in question actually spend much of their time in close proximity to potential predators. This may be the case in some aquatic systems (e.g., Pitcher 1980), but it is not so for most mammal and bird species.

Another potential problem concerns the presence of observers. It seems likely that observers may be perceived as potential predators; in fact, many studies have used observers as the source of risk (e.g., Elgar 1986c). The fact that experimental subjects do not overtly respond to observers does not necessarily mean that an effect is lacking. For instance, in the diet selection – vigilance interaction study described earlier (Lima 1988c), the juncos consumed a greater proportion of large items in the presence of an observer, in an apparent effort to keep him under surveillance (S.L. Lima, personal observation), but the birds did not appear unusually “anxious.” Suarez and Gallup (1983) describe a more subtle effect where birds may behave differently depending upon whether an exposed observer is actually watching them.

A final problem stemming from the perception of risk concerns how researchers actually measure the risk of predation. An intuitive measure of risk is the observed mortality rate in a prey population (e.g., Ryan 1985). It should be clear, however, that an animal’s perception of risk may grossly exceed its actual risk (see also Lima 1990b); thus, mortality rates *per se* may, for many creatures, be most useful only as indices of relative risk. Gilliam and Fraser (1987) successfully used observed mortality rates to predict habitat shifts in juvenile creek chubs, but even here it is clear that the fish’s short-term perception of risk was an important determinant of habitat use. Overall, measuring perceived predation risk will be a challenge for future research.

Mortality and behavioral sensitivity to the risk of predation

Some recent comparative studies demonstrate that a lack of predators over evolutionary time may lead to reduced behavioral sensitivity to predators (Giles and Huntingford 1984; Magurran 1986; Sih 1986). However, it does not follow that one may discount potential behavioral sensitivity to risk in those animals suffering from little predation in ecological time (e.g., Miller and Gass 1985, and Hennessy 1986). For instance, in many areas, animals may still perceive a risk of predation even though humans have largely extirpated local predators (see above). More importantly, antipredator behavior may be so effective that predators are rarely successful.

Consider the behavior of people crossing a busy street. One might observe their behavior for many days without ever witnessing a person being struck by an automobile. Could it therefore be concluded that the risk of being “preyed upon” by an automobile is unimportant in determining the behavior of pedestrians? The answer is obviously in the negative. Of course, people carefully assess the potential for “predation” before crossing the street; if done properly, no one would ever be struck. Reasoning analogously, Hennessy’s (1986) statement that the mobbing of predators is not risky because mobbing animals are rarely seen to be killed, must be viewed cautiously (see also Curio and Regelmann 1986). As reviewed earlier, the available evidence suggests that the risk of predation is a determinant of some aspects of mobbing behavior. Apparently, a proper assessment of risk by the mobber leaves it relatively safe. Similar reasoning can be applied to other statements concerning mortality and behavioral sensitivity to risk.

Thus, a lack of observed predation does not necessarily imply a lack of behavioral sensitivity to the risk of predation. Only by a careful analysis of behavioral responses to appropriate alterations in the risk of predation can one assess the importance of predation risk in those animals which suffer little or no predation; Morse (1986) provides an example of such an

analysis, which suggests a real lack of sensitivity to the risk of predation in bumblebees (*Bombus* spp.).

Conclusions

Practically all animals are potential prey for some other animal. This ecological/evolutionary truism may at first hardly seem worth mentioning. Few would deny that predation has been a strong selection pressure in producing morphological antipredator adaptations, such as spines and armor, but we have argued that the influence of predation extends all the way to decision making. Indeed, we have argued that the risk of being preyed upon in ecological time is fundamental to a wide variety of decision-making processes. We have reviewed much of the evidence to this effect, encompassing a wide range of topics and taxa, but the studies to date represent only a small proportion of the work in their respective fields; some areas in the study of behavior (e.g., reproduction) remain almost completely unexplored from a predation perspective. Future work in these, and indeed all areas, which considers the role of predation in decision making will provide greater insights into the nature of animal behavior.

Acknowledgements

We wish to thank J.-G. J. Godin and two anonymous reviewers for several useful suggestions and comments on the manuscript. This work was supported in part by a North Atlantic Treaty Organization – National Science Foundation Postdoctoral Fellowship to S.L.L. and a Natural Sciences and Engineering Research Council of Canada grant (No. A6869) to L.M.D.

- ABRAHAMS, M. V., and COLGAN, P. W. 1985. Risk of predation, hydrodynamic efficiency and their influence on school structure. *Environ. Biol. Fishes.* **13**: 195–202.
- ABRAHAMS, M. V., and DILL, L. M. 1989. A determination of the energetic equivalence of the risk of predation. *Ecology*, **70**: 999–1007.
- ABRAMS, P. 1983. Life-history strategies of optimal foragers. *Theor. Popul. Biol.* **24**: 22–38.
- ABRAMSON, M. 1979. Vigilance as a factor influencing flock formation among curlews *Numenius arquata*. *Ibis*, **121**: 213–216.
- AINLEY, D. G., and DEMASTER, D. P. 1980. Survival and mortality in a population of Adelie penguins. *Ecology*, **61**: 522–530.
- ALADOS, C. L. 1985. An analysis of vigilance in the Spanish ibex (*Capra pyrenaica*). *Z. Tierpsychol.* **68**: 58–64.
- ALLAN, J. R., and PITCHER, T. J. 1986. Species segregation during predator evasion in cyprinid fish shoals. *Freshwater Biol.* **16**: 653–659.
- ANDERSON, P. K. 1986. Foraging range in mice and voles: the role of risk. *Can. J. Zool.* **64**: 2645–2653.
- ANDÖRFER, B. 1980. The school behavior of *Leucaspius delineatus* (Heckel) in relation to ambient space and the presence of a pike (*Esox lucius*). *Oecologia*, **47**: 127–140.
- APPLETON, R. D., and PALMER, A. R. 1988. Water-borne stimuli released by predatory crabs and damaged prey induce more predator-resistant shells in marine gastropods. *Proc. Natl. Acad. Sci. U.S.A.* **85**: 4387–4391.
- AXELROD, R., and HAMILTON, W. D. 1981. The evolution of cooperation. *Science (Washington, D.C.)*, **211**: 1390–1396.
- BAIRD, T. A. 1983. Influence of social and predatory stimuli on the air-breathing of the African clawed frog, *Xenopus laevis*. *Copeia*, **1983**: 411–420.
- BALL, N., SHAFFERY, J. P., and AMLANER, C. J., JR. 1984. Sleeping gulls and predator avoidance. *Anim. Behav.* **32**: 1253–1266.
- BARNARD, C. J. 1980. Flock feeding and time budgets in the house sparrow (*Passer domesticus* L.). *Anim. Behav.* **28**: 295–309.
- BARNARD, C. J., and THOMPSON, D. B. A. 1985. Gulls and plovers. Columbia University Press, New York.

- BELOVSKY, G. E. 1978. Diet optimization in a generalist herbivore: the moose. *Theor. Popul. Biol.* **14**: 105–134.
- BERGER, J. 1978. Group size, foraging, and antipredator ploys: an analysis of bighorn sheep decisions. *Behav. Ecol. Sociobiol.* **4**: 91–99.
- BERGLUND, A., and ROSENQVIST, G. 1986. Reproductive costs in the prawn *Palaemon adspersus*: effects on growth and predator vulnerability. *Oikos*, **46**: 349–354.
- BERTRAM, B. C. R. 1978. Living in groups: predators and prey. *In* Behavioural ecology: an evolutionary approach. Edited by J. R. Krebs, and N. B. Davies. Blackwell Scientific Publications, Oxford. pp. 279–309.
- 1980. Vigilance and group size in ostriches. *Anim. Behav.* **28**: 278–286.
- BOWERS, M. A. 1988. Seed removal experiments on desert rodents: the microhabitat by moonlight effect. *J. Mammal.* **69**: 201–204.
- BRIETWISCH, R., and HUDAK, J. 1989. Sex differences in risk-taking behavior in foraging flocks of sparrows. *Auk*, **106**: 150–153.
- BROOKS, W. R., and MARISCAL, R. N. 1986. Population variation and behavioral changes in two pagurids in association with the sea anemone *Calliactis tricolor* (Lesuer). *J. Exp. Mar. Biol. Ecol.* **103**: 275–289.
- BROWN, J. S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. *Behav. Ecol. Sociobiol.* **22**: 37–47.
- 1989. Desert rodent community structure: a test of four mechanisms of coexistence. *Ecol. Monogr.* **59**: 1–20.
- BROWN, J. S., KOTLER, B. P., SMITH, R. J., and WIRTZ, W. O. 1988. The effects of owl predation on the foraging behavior of heteromyid rodents. *Oecologia*, **76**: 408–415.
- BURGER, A. 1982. Foraging behaviour of lesser sheathbills *Chionis minor* exploiting invertebrates on a sub-Antarctic Island. *Oecologia*, **52**: 236–245.
- BURK, T. 1982. Evolutionary significance of predation on sexually signalling males. *Fla. Entomol.* **65**: 90–104.
- CADE, W. 1975. Acoustically orienting parasitoids: fly phonotaxis to cricket song. *Science* (Washington, D.C.), **190**: 1312–1313.
- CALDWELL, G. S. 1986. Predation as a selective force on foraging herons: effects of plumage color and flocking. *Auk*, **103**: 494–505.
- CARACO, T. 1979a. Time budgeting and group size: a test of theory. *Ecology*, **60**: 618–627.
- 1979b. Time budgeting and group size: a theory. *Ecology*, **60**: 611–617.
- 1980. Stochastic dynamics of avian foraging flocks. *Am. Nat.* **115**: 262–275.
- CARACO, T., and PULLIAM, H. R. 1984. Sociality and survivorship in animals exposed to predation. *In* A new ecology: novel approaches to interactive systems. Edited by P. W. Price, C. N. Slobodchikoff, and W. S. Gaud. John Wiley and Sons, New York. pp. 279–309.
- CARACO, T., MARTINDALE, S., and PULLIAM, H. R. 1980a. Avian time budgets and distance to cover. *Auk*, **97**: 872–875.
- 1980b. Avian flocking in the presence of a predator. *Nature* (London), **285**: 400–401.
- CARACO, T., BARKAN, C., BEACHAM, J. L., BRISBIN, L., LIMA, S. L., MOHAN, A., NEWMAN, J. A., WEBB, W., and WITHIAM, M. L. 1989. Dominance and social foraging: a laboratory study. *Anim. Behav.* **38**: 41–58.
- CAREY, H. V. 1985. The use of foraging areas by yellow-bellied marmots. *Oikos*, **44**: 273–279.
- CAREY, H. V., and MOORE, P. 1986. Foraging and predation risk in yellow-bellied marmots. *Am. Midl. Nat.* **116**: 267–275.
- CERRI, R. D., and FRASER, D. F. 1983. Predation and risk in foraging minnows: balancing conflicting demands. *Am. Nat.* **121**: 552–561.
- CHARNOV, E. L., and SKINNER, S. W. 1985. Complementary approaches to the understanding of parasitoid oviposition decisions. *Environ. Entomol.* **14**: 383–391.
- CLARK, C. W., and LEVY, D. A. 1988. Diel vertical migrations by pelagic planktivorous fishes and the antipredator window. *Am. Nat.* **131**: 271–290.
- CLARKE, J. A. 1983. Moonlight's influence on predator/prey interactions between short-eared owls (*Asio flammeus*) and deermice (*Peromyscus maniculatus*). *Behav. Ecol. Sociobiol.* **13**: 205–209.
- CONVEY, P. 1988. Competition for perches between larvae damselflies: the influence of perch use on feeding efficiency, growth rate and predator avoidance. *Freshwater Biol.* **19**: 15–28.
- COVICH, A. P. 1976. Analyzing shapes of foraging areas: some ecological and economic theories. *Annu. Rev. Ecol. Syst.* **7**: 235–257.
- CROOK, J. H. 1965. The adaptive significance of avian social organizations. *Symp. Zool. Soc. Lond.* **14**: 181–218.
- CURIO, E., and REGELMANN, K. 1985. The behavioural dynamics of great tits (*Parus major*) approaching a predator. *Z. Tierpsychol.* **69**: 3–18.
- 1986. Predator harassment implies a real deadly risk: a reply to Hennessy. *Ethology*, **72**: 75–78.
- CURIO, E., KLUMP, G., and REGELMANN, K. 1983. An anti-predator response in the great tit (*Parus major*): is it tuned to predation risk? *Oecologia*, **60**: 83–88.
- CUSHING, B. S. 1985. Estrous mice and vulnerability to weasel predation. *Ecology*, **66**: 1976–1978.
- DA SILVA, J., and TERHUNE, J. M. 1988. Harbour seal grouping as an anti-predator strategy. *Anim. Behav.* **36**: 1309–1316.
- DEHN, M. 1986. Vigilance, group size, and security in Rocky Mountain Elk (*Cervus elaphus nelsoni*). M.Sc. thesis (Environmental Design), University of Calgary, Alta.
- DEKKER, D. 1988. Peregrine falcon and merlin predation on small shorebirds and passerines in Alberta. *Can. J. Zool.* **66**: 925–928.
- DE LAET, J. F. 1985. Dominance and anti-predator behaviour of great tits *Parus major*: a field study. *Ibis*, **127**: 372–377.
- DILL, L. M. 1987. Animal decision making and its ecological consequences: the future of aquatic ecology and behaviour. *Can. J. Zool.* **65**: 803–811.
- 1990. Distance-to-cover and the escape decisions of an African cichlid fish, *Melanochromis chipokae*. *Environ. Biol. Fishes*. In Press.
- DILL, L. M., and FRASER, A. H. G. 1984. Risk of predation and the feeding behavior of juvenile coho salmon (*Oncorhynchus kisutch*). *Behav. Ecol. Sociobiol.* **16**: 65–71.
- DILL, L. M., and HOUTMAN, R. 1989. The influence of distance to refuge on flight-initiation distance in the gray squirrel (*Sciurus carolinensis*). *Can. J. Zool.* **67**: 232–235.
- DILL, L. M., and YDENBERG, R. C. 1987. The group size – flight distance relationship in waterstriders (*Gerris remigis*). *Can. J. Zool.* **65**: 223–226.
- DIMOND, S., and LAZARUS, J. 1974. The problem of vigilance in animal life. *Brain Behav. Evol.* **9**: 60–79.
- DIXON, S. M., and BAKER, R. L. 1987. Effects of fish on feeding and growth of larval *Ischnura verticalis* (Coenagrionidae: Odonata). *Can. J. Zool.* **65**: 2276–2279.
- 1988. Effects of size on predation risk, behavioural response to fish, and cost of reduced feeding in larval *Ischnura verticalis* (Coenagrionidae: Odonata). *Oecologia*, **76**: 200–205.
- DONNELLY, W. A., and DILL, L. M. 1984. Evidence for crypsis in coho salmon, *Oncorhynchus kisutch* (Walbaum), parr: substrate colour preference and achromatic reflectance. *J. Fish Biol.* **25**: 183–195.
- EBERHARD, W. G. 1977. Aggressive chemical mimicry by a bolas spider. *Science* (Washington, D.C.), **198**: 1173–1175.
- EDMUNDS, M. 1974. Defence in animals. Longman Inc., New York.
- EKMANN, J. 1987. Exposure and time use in willow tit flocks: the cost of subordination. *Anim. Behav.* **35**: 445–452.
- EKMANN, J., and C. ASKENMO. 1984. Social rank and habitat use in willow tit groups. *Anim. Behav.* **32**: 508–514.
- ELGAR, M. A. 1986a. Scanning, pecking, and alarm flights in house sparrows. *Anim. Behav.* **34**: 1892–1894.
- 1986b. House sparrows establish foraging flocks by giving chirrup calls if resources are divisible. *Anim. Behav.* **34**: 169–174.
- 1986c. The establishment of foraging flocks in house spar-

- rows: risk of predation and daily temperature. *Behav. Ecol. Sociobiol.* **19**: 433–438.
- 1987. Food intake and resource availability: flocking decisions in house sparrows. *Anim. Behav.* **35**: 1168–1176.
- 1989. Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biol. Rev.* **64**: 13–33.
- ELGAR, M. A., and CATTERALL, C. P. 1981. Flocking and predator surveillance in house sparrows: test of an hypothesis. *Anim. Behav.* **29**: 868–872.
- ELGAR, M. A., BURREN, P. J., and POSEN, M. 1984. Vigilance and perception of flock size in foraging house sparrows (*Passer domesticus* L.). *Behaviour*, **90**: 215–223.
- ENDLER, J. A. 1987. Predation, light intensity, and courtship behaviour in *Poecilia reticulata* (Pisces: Poeciliidae). *Anim. Behav.* **35**: 1376–1385.
- ERIKSSON, M. O. G., and GÖTMARK, F. 1983. Habitat selection: do passerines nest in association with Lapwings *Vanellus vanellus* as defence against predators? *Ornis Scand.* **13**: 189–192.
- FARR, J. A. 1975. The role of predation in the evolution of social behavior of natural populations of the guppy, *Poecilia reticulata* (Pisces: Poeciliidae). *Evolution* (Lawrence, Kans.), **29**: 151–158.
- FEENER, D. H., JR. 1988. Effects of parasite on foraging and defense behavior of a termitophagus ant, *Pheidole titanus* Wheeler (Hymenoptera: Formicidae). *Behav. Ecol. Sociobiol.* **22**: 421–427.
- FELTMATE, B. W. 1987. Predator-prey interactions in a stream: combined field-laboratory study of *Paragnetina media* (Plecoptera) and *Hydropsyche sparna* (Trichoptera). *Can. J. Zool.* **65**: 448–451.
- FELTMATE, B. W., BAKER, R. L., and POINTING, P. J. 1986. Distribution of the stonefly nymph *Paragnetina media* (Plecoptera: Perlidae): influence of prey, predators, current speed, and substrate composition. *Can. J. Fish. Aquat. Sci.* **43**: 1582–1587.
- FERGUSON, J. W. H. 1987. Vigilance behavior in white-browed sparrow-weavers, *Plocepasser mahali*. *Ethology*, **76**: 223–235.
- FERGUSON, S. H., BERGERUD, A. T., and FERGUSON, R. 1988. Predation risk and habitat selection in the persistence of a remnant caribou population. *Oecologia*, **76**: 236–245.
- FISCHER, R. U., JR., STANDORA, E. A., and SPOTILA, J. R. 1987. Predator-induced changes in thermoregulation of bluegill, *Lepomis macrochirus*, from a thermally altered reservoir. *Can. J. Fish. Aquat. Sci.* **44**: 1629–1634.
- FOSTER, S. A., GARCIA, V. B., and TOWN, M. Y. 1988. Cannibalism as the cause of an ontogenetic shift in habitat use by fry of the threespine stickleback. *Oecologia*, **74**: 577–585.
- FRASER, D. F., and GILLIAM, J. F. 1987. Feeding under predation hazard: response of the guppy and Hart's rivulus from sites with contrasting predation hazard. *Behav. Ecol. Sociobiol.* **21**: 203–209.
- FRASER, D. F., and HUNTINGFORD, F. A. 1986. Feeding and avoiding predation hazard: the behavioral response of the prey. *Ethology*, **73**: 56–68.
- FREED, L. A. 1981. Breeding biology of house wrens: new views of avian life history phenomena. Ph.D. dissertation, University of Iowa, Iowa City.
- GEE, J. H. 1980. Respiratory patterns and antipredator responses in the central mudminnow, *Umbra limi*, a continuous, facultative, air-breathing fish. *Can. J. Zool.* **58**: 819–827.
- GENTRY, J. B. 1974. Response to predation by colonies of the Florida harvester ant, *Pogonomyrmex badius*. *Ecology*, **55**: 1328–1338.
- GILES, N., and HUNTINGFORD, F. A. 1984. Predation risk and inter-population variation in anti-predator behaviour in the three-spined stickleback *Gasterosteus aculeatus* L. *Anim. Behav.* **32**: 264–275.
- GILLIAM, J. F. 1982. Habitat use and competitive bottlenecks in size-structured fish populations. Ph.D. thesis, Michigan State University, East Lansing.
- GILLIAM, J. F., and FRASER, D. F. 1987. Habitat selection when foraging under predation hazard: a model and a test with stream-dwelling minnows. *Ecology*, **68**: 1856–1862.
- GILLIAM, J. F., FRASER, D. F., and SABAT, A. M. 1989. Strong effects of foraging minnows on a stream benthic invertebrate community. *Ecology*, **70**: 445–452.
- GLÜCK, E. 1986. Flock size and habitat-dependent food and energy intake of foraging goldfinches. *Oecologia*, **71**: 149–155.
- GODIN, J.-G. J. 1986. Antipredator function of shoaling in teleost fishes: a selective review. *Nat. Can. (Québec)*, **113**: 241–250.
- GODIN, J.-G. J., and MORGAN, M. J. 1985. Predator avoidance and school size in a cyprinodontid fish, the banded killifish (*Fundulus diaphanus* Lesueur). *Behav. Ecol. Sociobiol.* **16**: 105–110.
- GODIN, J.-G. J., and SMITH, S. A. 1988. A fitness cost of foraging in the guppy. *Nature* (London), **333**: 69–71.
- GODIN, J.-G. J., and SPROUL, C. D. 1988. Risk taking in parasitized sticklebacks under threat of predation: effects of energetic need and food availability. *Can. J. Zool.* **66**: 2360–2367.
- GODIN, J.-G. J., CLASSON, L. J., and ABRAHAMS, M. V. 1988. Group vigilance and shoal size in a small characin fish. *Behaviour*, **104**: 29–40.
- GOLDMAN, P. 1980. Flocking as a possible predator defense in dark-eyed juncos. *Wilson Bull.* **92**: 85–95.
- GORANSSON, G., KARLSSON, J., NILSSON, S. G., and ULFSTRAND, S. 1975. Predation on birds' nests in relation to antipredator aggression and nest density: an experimental study. *Oikos*, **26**: 117–120.
- GRANT, J. W. A., and 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.* **44**: 1390–1396.
- GROSS, M. R. 1984. Sunfish, salmon, and the evolution of alternative reproductive strategies and tactics in fishes. In *Fish reproduction: strategies and tactics*. Edited by R. Wootton and G. Potts. Academic Press, London. pp. 55–75.
- GRUBB, T. C., JR., and GREENWALD, L. 1982. Sparrows and a brushpile: foraging responses to different combinations of predation risk and energy cost. *Anim. Behav.* **30**: 637–640.
- GWYNNE, D. T. 1987. Sex-biased predation and the risky mate-locating behaviour of male tick-tock cicadas (Homoptera: Cicadidae). *Anim. Behav.* **35**: 571–576.
- 1989. Does copulation increase risk of predation? *Trends Ecol. Evol.* **4**: 54–56.
- GWYNNE, D. T., and DODSON, G. N. 1983. Nonrandom provisioning by the digger wasp, *Palmodus laevis* (Hymenoptera: Sphecidae). *Ann. Entomol. Soc. Am.* **76**: 434–436.
- GWYNNE, D. T., and O'NEILL, K. M. 1980. Territoriality in digger wasps results in sex biased predation on males (Hymenoptera: Sphecidae, Philanthus). *J. Kans. Entomol. Soc.* **53**: 220–224.
- HAMRIN, S. F. 1987. Seasonal crayfish activity as influenced by fluctuating water levels and presence of a fish predator. *Holarct. Ecol.* **10**: 45–51.
- HARRIS, V. E., and TODD, J. W. 1980. Male-mediated aggregation of male, female and 5-th-instar southern green stink bugs and concomitant attraction of a tachinid parasite, *Trichopoda pennipes*. *Entomol. Exp. Appl.* **27**: 117–126.
- HART, A., and LENDREM, D. W. 1984. Vigilance and scanning patterns in birds. *Anim. Behav.* **32**: 1216–1224.
- HARVEY, B. C., CASHNER, R. C., and MATTHEWS, W. J. 1988. Differential effects of largemouth and smallmouth bass on habitat use by stoneroller minnows in stream pools. *J. Fish Biol.* **33**: 481–487.
- HARVEY, P. H., and GREENWOOD, P. J. 1978. Anti-predator defense strategies: some evolutionary problems. In *Behavioral ecology: an evolutionary approach*. Edited by J. R. Krebs and N. B. Davies. Sinauer Associates, Sunderland, MA. pp. 129–151.
- HASSON, O., HIBBARD, R., and CEBALLOS, G. 1989. Pursuit deterrent function of tail-wagging of the zebra-tailed lizard (*Callisaurus draconoides*). *Can. J. Zool.* **67**: 1203–1209.
- HAY, M. E., and FULLER, P. J. 1981. Seed escape from heteromyid rodents: the importance of microhabitat and seed preference. *Ecology*, **62**: 1395–1399.
- HEADS, P. A. 1985. The effect of invertebrate and vertebrate predators on foraging movements of *Ischnura elegans* larvae (Odonata: Zygoptera). *Freshwater Biol.* **15**: 559–571.
- 1986. The costs of reduced feeding due to predator avoidance: potential effects on growth and fitness in *Ischnura elegans* larvae (Odonata: Zygoptera). *Ecol. Entomol.* **11**: 369–377.

- HEATWOLE, H. 1968. Relationship of escape behavior and camouflage in anoline lizards. *Copeia*, 1968: 109–113.
- HEGNER, R. E. 1985. Dominance and anti-predator behaviour in blue tits (*Parus caeruleus*). *Anim. Behav.* **33**: 762–768.
- HEINSOHN, R. G. 1987. Age-dependent vigilance in winter aggregations of cooperatively breeding white-winged choughs (*Corcorax melanorhamphos*). *Behav. Ecol. Sociobiol.* **20**: 303–306.
- HELFMAN, G. S. 1986. Behavioral responses of prey fishes during predator–prey interactions. In *Predator–prey relationships: perspectives and approaches from the study of lower vertebrates*. Edited by M. E. Feder and G. V. Lauder, University of Chicago Press, Chicago. pp.135–156.
- 1989. Threat-sensitive predator avoidance in damselfish–trumpetfish interactions. *Behav. Ecol. Sociobiol.* **24**: 47–58.
- HELLER, R., and MILINSKI, M. 1979. Optimal foraging of sticklebacks on swarming prey. *Anim. Behav.* **27**: 1127–1141.
- HENNESSY, D. F. 1986. On the deadly risk of predator harassment. *Ethology*, **72**: 72–74.
- HOGSTAD, O. 1988a. Social rank and antipredator behavior of willow tits *Parus montanus* in winter flocks. *Ibis*, **130**: 45–56.
- 1988b. Advantages of social foraging of willow tits *Parus montanus*. *Ibis*, **130**: 275–283.
- HOLBROOK, S. J., and SCHMITT, R. J. 1988a. The combined effects of predation risk and food reward on patch selection. *Ecology*, **69**: 125–134.
- 1988b. Effects of predation risk on foraging behavior: mechanisms altering patch choice. *J. Exp. Mar. Biol. Ecol.* **121**: 151–163.
- HOLLING, C. S. 1959. The components of predation as revealed by a study of small mammal predation on the European pine sawfly. *Can. Entomol.* **91**: 293–320.
- HOLOMUZKI, J. R. 1986. Predator avoidance and diel patterns of microhabitat use by larval tiger salamanders. *Ecology*, **67**: 737–748.
- HOLOMUZKI, J. R., and SHORT, T. M. 1988. Habitat use and fish avoidance behaviors by the stream-dwelling isopod *Lirceus fontinalis*. *Oikos*, **52**: 79–86.
- HOOGLAND, J. L. 1979. The effect of colony size on individual alertness of prairie dogs (Sciuridae: *Cynomys* spp.). *Anim. Behav.* **27**: 394–407.
- HOUSTON, A. I., and MCNAMARA, J. M. 1986. The influence of mortality on the behavior that maximizes reproductive success in a patchy environment. *Oikos*, **47**: 267–274.
- HOUSTON A., CLARK, C., MCNAMARA, J., and MANGEL, M. 1988. Dynamic models in behavioural and evolutionary ecology. *Nature* (London), **332**: 29–34.
- HUNTINGFORD, F. A., METCALFE, N. B., and THORPE, J. E. 1988. Feeding motivation and response to predation risk in Atlantic salmon parr adopting different life history strategies. *J. Fish Biol.* **32**: 777–782.
- INGLIS, I. R., and LAZARUS, J. 1981. Vigilance and flock size in brent geese: the edge effect. *Z. Tierpsychol.* **57**: 193–200.
- IWASA, Y. 1982. Vertical migration of zooplankton: a game between predator and prey. *Am. Nat.* **120**: 171–180.
- IWASA, Y., SUZUKI, Y., and MATSUDA, H. 1984. Theory of oviposition strategy of parasitoids. I. Effect of mortality and limited egg number. *Theor. Popul. Biol.* **26**: 205–227.
- JAKOBSEN, P. J., JOHNSEN, G. H., and LARRSON, P. 1988. Effects of predation risk and parasitism on the feeding ecology, habitat use, and abundance of lacustrine threespine stickleback (*Gasterosteus aculeatus*). *Can. J. Fish. Aquat. Sci.* **45**: 426–431.
- JENNINGS, T., and EVANS, S. M. 1980. Influence of position in the flock and flock size on vigilance in the starling *Sturnus vulgaris*. *Anim. Behav.* **28**: 634–635.
- KATS, L. B. 1988. The detection of certain predators via olfaction by small-mouthed salamander larvae (*Ambystoma texanum*). *Behav. Neural Biol.* **50**: 126–131.
- KNIGHT, S. K., and KNIGHT, R. L. 1986. Vigilance patterns in bald eagles feeding in groups. *Auk*, **103**: 263–272.
- KOTLER, B. P. 1984a. Effects of illumination on the rate of resource harvesting in a community of desert rodents. *Am. Midl. Nat.* **111**: 383–389.
- 1984b. Risk of predation and the structure of desert rodent communities. *Ecology*, **65**: 689–701.
- 1984c. Harvesting rates and predatory risk in desert rodents: a comparison of two communities on different continents. *J. Mammal.* **65**: 91–96.
- KRAMER, D. L. 1983. The evolutionary ecology of respiratory mode in fishes: an analysis based on the costs of breathing. *Environ. Biol. Fishes*, **9**: 145–158.
- KRAMER, D. L., and GRAHAM, J. B. 1976. Synchronous air breathing, a social component of respiration in fishes. *Copeia*, 1976: 689–697.
- KRAMER, D. L., MANLEY, D., and BOURGEOIS, R. 1983. The effect of respiratory mode and oxygen concentration on the risk of aerial predation in fishes. *Can. J. Zool.* **61**: 653–665.
- KREBS, J. R. 1980. Optimal foraging, predation risk, and territory defence. *Ardea*, **68**: 83–90.
- KRUSE, K. C. 1986. Male parental care increases predation vulnerability in waterbugs (*Belostoma flumineum*). Paper presented at the Animal Behavior Society Meeting, June 1986, Tucson, AZ.
- LAGORY, K. E. 1986. Habitat, group size, and the behaviour of white-tailed deer. *Behaviour*, **98**: 168–179.
- 1987. The influence of habitat and group characteristics on the alarm and flight response of white-tailed deer. *Anim. Behav.* **35**: 20–25.
- LAZARUS, J. 1978. Vigilance, flock size and domain of danger size in the white-fronted goose. *Wildfowl*, **29**: 135–145.
- 1979. The early warning function of flocking in birds: an experimental study with captive quelea. *Anim. Behav.* **27**: 855–865.
- LAZARUS, J., and INGLIS, I. R. 1986. Shared and unshared parental investment, parent–offspring conflict and brood size. *Anim. Behav.* **34**: 1791–1804.
- LENDREM, D. W. 1983. Predation risk and vigilance in the blue tit (*Parus caeruleus*). *Behav. Ecol. Sociobiol.* **14**: 9–13.
- 1984. Sleeping and vigilance in birds. II. An experimental study of the Barbary dove (*Streptopelia risoria*). *Anim. Behav.* **32**: 243–248.
- LI, J. L., and LI, H. W. 1979. Species-specific factors affecting predator–prey interactions of the copepod *Acanthocyclops vernalis* with its natural prey. *Limnol. Oceanogr.* **24**: 613–626.
- LIMA, S. L. 1985. Maximizing feeding efficiency and minimizing time exposed to predators: a trade-off in the black-capped chickadee. *Oecologia*, **66**: 60–67.
- 1987a. Vigilance while feeding and its relation to the risk of predation. *J. Theor. Biol.* **124**: 303–316.
- 1987b. Distance to cover, visual obstructions, and vigilance in house sparrows. *Behaviour*, **102**: 231–238.
- 1987c. Clutch size in birds: a predation perspective. *Ecology*, **68**: 1062–1070.
- 1988a. Initiation and termination of daily feeding in dark-eyed juncos: influences of predation risk and energy reserves. *Oikos*, **53**: 3–11.
- 1988b. Vigilance during the initiation of daily feeding in dark-eyed juncos. *Oikos*, **53**: 12–16.
- 1988c. Vigilance and diet selection: a simple example in the dark-eyed junco. *Can. J. Zool.* **66**: 593–596.
- 1988d. Vigilance and diet selection: the classical diet model reconsidered. *J. Theor. Biol.* **132**: 127–143.
- 1990a. On the interpretation of vigilance. In *Interpretation and explanation in the study of animal behavior: comparative perspectives*. Edited by M. Bekoff and D. Jamieson. Westview Press, Boulder, CO. In press.
- 1990b. Evolutionarily stable antipredator behavior in isolated foragers: on the consequences of successful escape. *J. Theor. Biol.* In press.
- LIMA, S. L., and VALONE, T. J. 1986. Influence of predation risk on diet selection: a simple example in the grey squirrel. *Anim. Behav.* **34**: 536–544.
- LIMA, S. L., VALONE, T. J., and CARACO, T. 1985. Foraging efficiency – predation risk trade-off in the grey squirrel. *Anim. Behav.* **33**: 155–165.

- LIMA, S. L., WIEBE, K. L., and DILL, L. M. 1987. Protective cover and the use of space by finches: is closer better? *Oikos*, **50**: 225–230.
- LIPETZ, V. E., and BEKOFF, M. 1982. Group size and vigilance in pronghorns. *Z. Tierpsychol.* **58**: 203–216.
- LLOYD, J. E. 1965. Aggressive mimicry in *Photuris*: firefly femmes fatales. *Science* (Washington, D.C.), **149**: 653–654.
- LOCKARD, R. B., and OWINGS, D. H. 1974a. Moon-related surface activity of bannertail (*Dipodomys spectabilis*) and Fresno (*D. nitratoides*) kangaroo rats. *Anim. Behav.* **22**: 262–273.
- 1974b. Seasonal variation in moonlight avoidance by bannertail kangaroo rats. *J. Mammal.* **55**: 189–193.
- LUCAS, J. R. 1985. Partial prey consumption by antlion larvae. *Anim. Behav.* **33**: 945–958.
- MAGNHAGEN, C. 1988a. Predation risk and foraging in juvenile pink (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*). *Can. J. Fish. Aquat. Sci.* **45**: 592–596.
- 1988b. Changes in foraging as a response to predation risk in two gobiid fish species, *Pomatoschistus minutus* and *Gobius niger*. *Mar. Ecol. Prog. Ser.* **49**: 21–26.
- MAGURRAN, A. E. 1986. Predator inspection behavior in minnow shoals: differences between populations and individuals. *Behav. Ecol. Sociobiol.* **19**: 267–273.
- MAGURRAN, A. E., and GIRLING, S. L. 1986. Predator recognition and response habituation in shoaling minnows. *Anim. Behav.* **34**: 510–518.
- MAGURRAN, A. E., and HIGHAM, A. 1988. Information transfer across fish shoals under predation threat. *Ethology*, **78**: 153–158.
- MAGURRAN, A. E., and PITCHER, T. J. 1987. Provenance, shoal size and the sociobiology of predator evasion in minnow shoals. *Proc. R. Soc. London Ser. B*, **229**: 439–465.
- MAGURRAN, A. E., OULTON, W. J., and PITCHER, T. J. 1985. Vigilant behaviour and shoal size in minnows. *Z. Tierpsychol.* **67**: 167–178.
- MAIN, K. L. 1987. Predator avoidance in seagrass meadows: prey behavior, microhabitat selection, and cryptic coloration. *Ecology*, **68**: 170–180.
- MANGEL, M., and CLARK, C. W. 1986. Towards a unified foraging theory. *Ecology*, **67**: 1127–1138.
- MARTIN, T. E. 1988. On the advantage of being different: nest predation and the coexistence of bird species. *Proc. Natl. Acad. Sci., U.S.A.* **85**: 2196–2199.
- MARTINDALE, S. 1982. Nest defense and central place foraging: a model and experiment. *Behav. Ecol. Sociobiol.* **10**: 85–89.
- MCLEAN, E. B., and GODIN, J.-G.J. 1989. Distance to cover and fleeing from predators in fish with different amounts of defensive armour. *Oikos*, **55**: 281–290.
- MCMANARA, J. M., and HOUSTON, A. I. 1986. The common currency for behavioral decisions. *Am. Nat.* **127**: 358–378.
- MELLORS, W. K. 1975. Selective predation on ephippial *Daphnia* and the resistance of ephippial eggs to digestion. *Ecology*, **56**: 974–980.
- METCALFE, N. B. 1984a. The effects of habitat on the vigilance of shorebirds: is visibility important? *Anim. Behav.* **32**: 981–985.
- 1984b. The effects of mixed-species flocking on the vigilance of shorebirds. Who do they trust? *Anim. Behav.* **32**: 986–993.
- METCALFE, N. B., HUNTINGFORD, F. A., and THORPE, J. E. 1987a. The influence of predation risk on the feeding motivation and foraging strategy of juvenile Atlantic salmon. *Anim. Behav.* **35**: 901–911.
- 1987b. Predation risk impairs diet selection in juvenile salmon. *Anim. Behav.* **35**: 931–933.
- MILINSKI, M. 1984. A predator's cost of overcoming the confusion effect of swarming prey. *Anim. Behav.* **32**: 1157–1162.
- 1985. Risk of predation of parasitized sticklebacks (*Gasterosteus aculeatus* L.) under competition for food. *Behaviour*, **93**: 203–216.
- 1986. Constraints placed by predators on feeding behaviour. *In* The behaviour of teleost fishes. Edited by T. Pitcher. Croom Helm, Ltd., London. pp. 236–252.
- 1987. Tit for tat in sticklebacks and the evolution of cooperation. *Nature* (London), **325**: 433–435.
- MILINSKI, M., and HELLER, R. 1978. Influence of a predator on the optimal foraging behaviour of sticklebacks (*Gasterosteus aculeatus* L.). *Nature* (London), **275**: 642–644.
- MILLER, R. S., and GASS, C. L. 1985. Survivorship in hummingbirds: is predation important? *Auk*, **102**: 175–178.
- MITTELBAUGH, G. G. 1984. Predation and resource partitioning in two sunfishes (Centrarchidae). *Ecology*, **65**: 499–513.
- 1986. Predator-mediated habitat use: some consequences for species interactions. *Environ. Biol. Fishes*, **16**: 159–169.
- MØLLER, A. P. 1988. False alarm calls as a means of resource usurpation in the great tit *Parus major*. *Ethology*, **79**: 25–30.
- MONAGHAN, P., and METCALFE, N. B. 1985. Group foraging in wild brown hares: effects of resource distribution and social status. *Anim. Behav.* **33**: 993–999.
- MORGAN, M. J. 1988a. The effect of hunger, shoal size and the presence of a predator on shoal cohesiveness in bluntnose minnows, *Pimephales notatus* Rafinesque. *J. Fish Biol.* **32**: 963–971.
- 1988b. The influence of hunger, shoal size, and predator presence on foraging in bluntnose minnows. *Anim. Behav.* **36**: 1317–1322.
- MORGAN, M. J., and GODIN, J.-G.J. 1985. Antipredator benefits of schooling behaviour in a cyprinodontid fish, the banded killifish (*Fundulus diaphanus*). *Z. Tierpsychol.* **70**: 236–246.
- MORIN, P. J. 1986. Interactions between intraspecific competition and predation in an amphibian predator-prey system. *Ecology*, **67**: 713–720.
- MORRISON, D. W. 1978. Lunar phobia in a neotropical fruit bat, *Artibeus jamaicensis* (Chiroptera: Phyllostomidae). *Anim. Behav.* **26**: 852–855.
- MORSE, D. H. 1986. Predatory risk to insects foraging at flowers. *Oikos*, **46**: 223–238.
- MYERS, J. P. 1980. Territoriality and flocking by buff-breasted sandpipers: variations in nonbreeding dispersion. *Condor*, **82**: 241–250.
- NEWMAN, J. A., and CARACO, T. 1987. Foraging, predation hazard and patch use in grey squirrels. *Anim. Behav.* **35**: 1804–1813.
- NEWMAN, J. A., RECER, G. M., ZWICKER, S. M., and CARACO, T. 1988. Effects of predation hazard on foraging "constraints": patch use strategies in grey squirrels. *Oikos*, **53**: 93–97.
- NONACS, P., and DILL, L. M. 1990a. Mortality risk versus food quality trade-offs in common currency: patch preferences in *Lasius palliarsis* ants. *Ecology*. In press.
- 1990b. Mortality risk versus food quality trade-offs in ants: patch use over time. *Ecol. Entomol.* In press.
- PETRANKA, J. W., KATS, L. B., and SIH, A. 1987. Predator-prey interactions among fish and larval amphibians: use of chemical cues to detect predatory fish. *Anim. Behav.* **35**: 420–425.
- PHELAN, J. P. 1987. Some components of flocking behavior in the rock dove (*Columba livia*). *J. Field Ornithol.* **58**: 135–143.
- PHELPS, M. T., and ROBERTS, W. A. 1989. Central-place foraging on a radial maze. *J. Comp. Psychol.* **103**: 326–338.
- PIERCE, C. L. 1988. Predator avoidance, microhabitat shift, and risk-sensitive foraging in larval dragonflies. *Oecologia*, **77**: 81–90.
- PITCHER, T. J. 1980. Some ecological consequences of fish school volumes. *Freshwater Biol.* **10**: 539–544.
- 1986. The function of shoaling behaviour. *In* The behaviour of teleost fishes. Edited by T. J. Pitcher. Croom Helm, Ltd., London. pp. 294–337.
- PITCHER, T. J., GREEN, D. A., and MAGURRAN, A. E. 1986. Dicing with death: predator inspection behaviour in minnow shoals. *J. Fish Biol.* **28**: 439–448.
- PITCHER, T. J., LANG, S. H., and TURNER, J. A. 1988. A risk-balancing trade off between foraging rewards and predation hazard in a shoaling fish. *Behav. Ecol. Sociobiol.* **22**: 225–228.
- POPP, J. W. 1986. Changes in scanning and feeding rates with group size among American goldfinches. *Bird Behav.* **6**: 97–98.
- 1988. Scanning behavior of finches in mixed-species groups. *Condor*, **90**: 510–512.
- POULIN, R., and FITZGERALD, G. J. 1989. Risk of parasitism and microhabitat selection in juvenile sticklebacks. *Can. J. Zool.* **67**: 14–18.

- POULIN, R., WOLF, N. G., and KRAMER, D. L. 1987. The effect of hypoxia on the vulnerability of guppies (*Poecilia reticulata*, Poeciliidae) to an aquatic predator (*Astronotus ocellatus*, Cichlidae). *Environ. Biol. Fishes*, **20**: 285–292.
- POWELL, G. V. N. 1974. Experimental analysis of the social value of flocking by starlings (*Sturnus vulgaris*) in relation to predation and foraging. *Anim. Behav.* **22**: 501–505.
- POWER, M. E., and MATTHEWS, W. J. 1983. Algae-grazing minnows (*Camptostoma anomalum*), piscivorous bass (*Micropterus* spp.), and the distribution of attached algae in a small prairie-margin stream. *Oecologia*, **60**: 328–332.
- POWER, M. E., MATTHEWS, W. J., and STEWART, A. J. 1985. Grazing minnows, piscivorous bass, and stream algae: dynamics of a strong interaction. *Ecology*, **66**: 1448–1456.
- PÖYSÄ, H. 1987. Numerical and escape responses of foraging teals *Anas crecca* to predation risk. *Bird Behav.* **7**: 87–92.
- PRICE, M. V., WASER, N. M., and BASS, T. A. 1984. Effects of moonlight on microhabitat use by desert rodents. *J. Mammal.* **65**: 353–356.
- PULLIAM, H. R., and CARACO, T. 1984. Living in groups: is there an optimal group size? In *Behavioural ecology: an evolutionary approach*. Edited by J. R. Krebs and N. B. Davies. Sinauer Associates, Sunderland, MA. pp. 127–147.
- PULLIAM, H. R., PYKE, G. H., and CARACO, T. 1982. The scanning behavior of juncos: a game-theoretical approach. *J. Theor. Biol.* **95**: 89–103.
- RAESS, F., and MALY, E. J. 1986. The short-term effects of perch predation on a zooplankton prey community. *Hydrobiologia*, **140**: 155–160.
- RAHEL, F. J., and STEIN, R. A. 1988. Complex predator-prey interactions and predator intimidation among crayfish, piscivorous fish, and small benthic fish. *Oecologia*, **75**: 94–98.
- RAND, A. S. 1964. Inverse relationship between temperature and shyness in the lizard *Anolis lineatopus*. *Ecology*, **45**: 863–864.
- RASA, O. A. E. 1986. Coordinated vigilance in dwarf mongoose family groups: the watchman's song hypothesis and the costs of guarding. *Ethology*, **71**: 340–344.
- 1987. Vigilance behavior in dwarf mongooses: selfish or altruistic? *S. Afr. J. Sci.* **83**: 587–590.
- REDPATH, S. 1988. Vigilance levels in preening Dunlin *Calidris alpina*. *Ibis*, **130**: 555–557.
- RISEHOOVER, K. L., and BAILEY, J. A. 1985. Relationships between group size, feeding time, and agonistic behavior of mountain goats. *Can. J. Zool.* **63**: 2501–2506.
- ROBERTS, S. C. 1988. Social influences on vigilance in rabbits. *Anim. Behav.* **36**: 905–913.
- RYAN, M. J. 1985. The Tungara frog: a study in sexual selection and communication. University of Chicago Press, Chicago, IL.
- SAKALUK, S. K., and BELWOOD, J. J. 1984. Gecko phonotaxis to cricket calling song: a case of satellite predation. *Anim. Behav.* **32**: 659–662.
- SAVINO, J. F., and STEIN, R. A. 1989. Behavioral interactions between fish predators and their prey: effects of plant density. *Anim. Behav.* **37**: 311–321.
- SCHLOSSER, I. J. 1987. The role of predation in age- and size-related habitat use by stream fishes. *Ecology*, **68**: 651–659.
- 1988a. Predation risk and habitat selection by two size classes of a stream cyprinid: experimental test of a hypothesis. *Oikos*, **52**: 36–40.
- 1988b. Predation rates and the behavioral response of adult brassy minnows (*Hybognathus hankinsoni*) to creek chub and smallmouth bass predators. *Copeia*, 1988: 691–698.
- SCHMITT, R. J., and HOLBROOK, S. J. 1985. Patch selection by juvenile black surfperch (Embiotocidae) under variable risk: interactive influence of food quality and structural complexity. *J. Exp. Mar. Biol. Ecol.* **85**: 269–285.
- SCHNEIDER, K. J. 1984. Dominance, predation, and optimal foraging in white-throated sparrow flocks. *Ecology*, **65**: 1820–1827.
- SCHOENER, T. W. 1971. Theory of feeding strategies. *Annu. Rev. Ecol. Syst.* **2**: 369–404.
- SEMLITSCH, R. D. 1987. Interactions between fish and salamander larvae: costs of predator avoidance or competition? *Oecologia*, **72**: 481–486.
- SHINE, R. 1980. "Costs" of reproduction in reptiles. *Oecologia*, **46**: 92–100.
- SIH, A. 1980. Optimal behavior: can foragers balance two conflicting demands? *Science (Washington, D.C.)*, **210**: 1041–1043.
- 1982. Foraging strategies and the avoidance of predation by an aquatic insect, *Notonecta hoffmanni*. *Ecology*, **63**: 786–796.
- 1984. The behavioral response rate between predator and prey. *Am. Nat.* **123**: 143–150.
- 1986. Antipredator responses and the perception of danger by mosquito larvae. *Ecology*, **67**: 434–441.
- 1987. Predators and prey lifestyles: an evolutionary and ecological overview. In *Predation: direct and indirect impacts on aquatic communities*. Edited by W. C. Kerfoot and A. Sih. University Press of New England, Hanover, NH.
- 1988. The effects of predators on habitat use, activity and mating behaviour of a semi-aquatic bug. *Anim. Behav.* **36**: 1846–1848.
- SMITH, J. N. M. 1977. Feeding rates, search paths, and surveillance for predators in great-tailed grackle flocks. *Can. J. Zool.* **55**: 891–898.
- SMITH, R. S., and KRAMER, D. L. 1986. The effect of apparent predation risk on the respiratory behavior of the Florida gar (*Lepisosteus platyrhincus*). *Can. J. Zool.* **64**: 2133–2136.
- SOLUK, D. A., and COLLINS, N. C. 1988. Balancing risks? Responses and nonresponses of mayfly larvae to fish and stonefly predators. *Oecologia*, **77**: 370–374.
- SONERUD, G. A. 1985. Brood movements in grouse and waders as defense against win-stay search in their predators. *Oikos*, **44**: 287–300.
- SOPER, R. S., SHEWELL, G. E., and TYRELL, D. 1976. *Colcondamyia auditrix* Nov. Sp. (Diptera: Sarcophagidae), a parasite which is attracted by the mating song of its host, *Okanagana rimosa* (Homoptera: Cicadidae). *Can. Entomol.* **108**: 61–68.
- STANGEL, P. W., and SEMLITSCH, R. D. 1987. Experimental analysis of predation on the diel vertical migrations of a larval salamander. *Can. J. Zool.* **65**: 1554–1558.
- STEARNS, S. C. 1976. Life-history tactics: a review of the ideas. *Q. Rev. Biol.* **51**: 3–47.
- STEIN, R. A., and MAGNUSON, J. J. 1976. Behavioral response of crayfish to a fish predator. *Ecology*, **57**: 751–761.
- STEPHENS, D. W., and KREBS, J. R. 1986. *Foraging theory*. Princeton University Press, Princeton, NJ.
- STRONG, D. R., JR. 1973. Amphipod amplexus, the significance of ecotypic variation. *Ecology*, **54**: 1383–1388.
- SUAREZ, S. D., and GALLUP, G. G., JR. 1983. Emotionality and fear in birds: a selected review and reinterpretation. *Bird Behav.* **5**: 22–30.
- SULLIVAN, K. A. 1984a. Information exploitation by downy woodpeckers in mixed-species flocks. *Behaviour*, **91**: 294–311.
- 1984b. The advantages of social foraging in downy woodpeckers. *Anim. Behav.* **32**: 16–22.
- 1988. Ontogeny of time budgets in yellow-eyed juncos: adaptation to ecological constraints. *Ecology*, **69**: 118–124.
- SVENSSON, I. 1988. Reproductive costs in two sex-role reversed pipefish species. *J. Anim. Ecol.* **57**: 929–942.
- THOMPSON, D. B. A., and THOMPSON, M. L. P. 1985. Early warning and mixed species association: the "plover's page" revisited. *Ibis*, **127**: 559–562.
- THORNHILL, R. 1980. Mate choice in *Hylobittacus apicalis* (Insecta: Mecoptera) and its relation to some models of female choice. *Evolution (Lawrence, Kans.)*, **34**: 519–538.
- TRAIL, P. W. 1987. Predation and antipredator behavior at Guianan cock-of-the-rock leks. *Auk*, **104**: 496–507.
- TRAVERS, S. E., KAUFMAN, D. W., and KAUFMAN, G. A. 1988. Differential use of experimental habitat patches by foraging *Peromyscus maniculatus* on dark and bright nights. *J. Mammal.* **69**: 869–871.
- TUTTLE, M. D., and RYAN, M. J. 1981. Bat predation and the evolu-

- tion of frog vocalizations in the Neotropics. *Science* (Washington, D.C.), **214**: 677–678.
- TUTTLE, M. D., TAFT, L. K., and RYAN, M. J. 1982. Evasive behaviour of a frog in response to bat predation. *Anim. Behav.* **30**: 393–397.
- UNDERWOOD, R. 1982. Vigilance behaviour in grazing African antelopes. *Behaviour*, **79**: 81–107.
- VALONE, T. J., and LIMA, S. L. 1987. Carrying food items to cover for consumption: the behavior of ten bird species feeding under the risk of predation. *Oecologia*, **71**: 286–294.
- VAN HAVRE, N., and FITZGERALD, G. J. 1988. Shoaling and kin recognition in the threespine stickleback (*Gasterosteus aculeatus* L.). *Biol. Behav.* **13**: 190–201.
- VUORINEN, I., RAJASILTA, M., and SALO, J. 1983. Selective predation and habitat shift in a copepod species — support for the predation hypothesis. *Oecologia*, **59**: 62–64.
- WAITE, T. A. 1987a. Dominance-specific vigilance in the tufted titmouse: effects of social context. *Condor*, **89**: 932–935.
- 1987b. Vigilance in the white-breasted nuthatch: effects of dominance and sociality. *Auk*, **104**: 429–434.
- WAITE, T. A., and GRUBB, T. C., JR. 1987. Dominance, foraging and predation risk in the tufted titmouse. *Condor*, **89**: 936–940.
- WALTZ, E. C., and WOLF, L. L. 1988. Alternative mating tactics in male white-faced dragonflies (*Leucorrhinia intacta*): plasticity of tactical options and consequences for reproductive success. *Evol. Ecol.* **2**: 205–231.
- WATANUKI, Y. 1986. Moonlight avoidance behavior in Leach's storm-petrels as a defense against slaty-backed gulls. *Auk*, **103**: 14–22.
- WAWRA, M. 1988. Vigilance patterns in humans. *Behaviour*, **107**: 61–71.
- WEIS, A. E., PRICE, P. W., and LYNCH, M. 1983. Selective pressures on clutch size in the gall maker *Asteromyia carbonifera*. *Ecology*, **64**: 688–695.
- WEISSBURG, M. 1986. Risky business: on the ecological relevance of risk-sensitive foraging. *Oikos*, **46**: 261–262.
- WELLBORN, G. A., and ROBINSON, J. V. 1987. Microhabitat selection as an antipredator strategy in the aquatic insect *Pachydiplax longipennis* Burmeister (Odonata: Libellulidae). *Oecologia*, **71**: 185–189.
- WERNER, E. E. 1986. Amphibian metamorphosis: growth rate, predation risk, and the optimal size at transformation. *Am. Nat.* **128**: 319–341.
- WERNER, E. E., and GILLIAM, J. F. 1984. The ontogenetic niche and species interactions in size-structured populations. *Annu. Rev. Ecol. Syst.* **15**: 393–425.
- WERNER, E. E., GILLIAM, J. F., HALL, D. J., and MITTELBACH, G. G. 1983. An experimental test of the effects of predation risk on habitat use in fish. *Ecology*, **64**: 1540–1548.
- WHITFIELD, D. P. 1988. Sparrowhawks *Accipiter nisus* affect the spacing behaviour of wintering Turnstone *Arenaria interpres* and Redshank *Tringa totanus*. *Ibis*, **130**: 284–287.
- WILLIAMS, D. D. 1986. Factors influencing the microdistribution of two sympatric species of Plecoptera: an experimental study. *Can. J. Fish. Aquat. Sci.* **43**: 1005–1009.
- WILSON, P. 1987. Substrate selection and decorating behavior in *Acanthonyx petiveri* related to exoskeleton color (Brachyura, Majidae). *Crustaceana*, **52**: 135–140.
- WINFIELD, I. J., and TOWNSEND, C. R. 1983. The cost of copepod reproduction: increased susceptibility to fish predation. *Oecologia*, **60**: 406–411.
- WING, S. R. 1988. Cost of mating for female insects: risk of predation in *Photinus collustrans* (Coleoptera: Lampyridae). *Am. Nat.* **131**: 139–142.
- WIRTZ, P., and WAWRA, M. 1986. Vigilance and group size in *Homo sapiens*. *Ethology*, **71**: 283–286.
- WOLF, N. G. 1985. Odd fish abandon mixed-species groups when threatened. *Behav. Ecol. Sociobiol.* **17**: 47–52.
- WOLF, N. G., and KRAMER, D. L. 1987. Use of cover and the need to breathe: the effects of hypoxia on vulnerability of dwarf gouramis to predatory snakeheads. *Oecologia*, **73**: 127–132.
- WOLFE, J. L., and SUMMERLIN, C. T. 1989. The influence of lunar light on nocturnal activity of the old-field mouse. *Anim. Behav.* **37**: 410–414.
- WONG, C. K., RAMCHARAN, C. W., and SPRULES, W. G. 1986. Behavioral responses of a herbivorous calanoid copepod to the presence of other zooplankton. *Can. J. Zool.* **64**: 1422–1425.
- YDENBERG, R. C., and DILL, L. M. 1986. The economics of fleeing from predators. *Adv. Study Behav.* **16**: 229–249.