
Stress and Decision Making under the Risk of Predation: Recent Developments from Behavioral, Reproductive, and Ecological Perspectives

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I. INTRODUCTION

My objective here is to provide a comprehensive review of recent empirical and theoretical work on antipredator decision making. The ways in which predators influence the behavioral decisions made by their prey is now the subject of a large and growing literature. This sustained interest in the behavioral aspects of predator-prey interactions is readily traced to the fact that virtually all animals are subjected to some form of predation, and many biological and ecological insights can be gained from an understanding of the ways in which predators influence their prey's behavior.

Prey decision making under the risk of predation essentially allows an animal to manage predator-induced stress. Stress is not a term commonly associated with the study of antipredator decision making, but this is largely a matter of semantics, and one can relate stress to such decision making in several contexts. If one defines stress as an environmental condition that diminishes Darwinian fitness through either reproduction or survival (e.g., Sibly and Calow, 1989), then few aspects of an environment would lead to more stress than predators. Note that death due to predation is not the sort of stress that I consider here; observable predator-induced stress in animals is (in part) a result of prey decision making itself, such as the energetic stress caused by choosing to feed less in the presence of predators. One might thus consider the adaptive management of this sort of predator-induced stress as a main function of antipredator decision making. Forms of non-predator-induced stress, such as energetic stress caused by food shortages, will also influence such decision making. This view of stress is

ecological or evolutionary in perspective, and most of the existing literature deals with stress in this context.

A more classical definition of stress concerns the rapid increase in certain hormones (e.g., glucocorticoids) in response to some threatening situation (Weiner, 1992). This hormonal response is considered to be a biological marker of fear (Boissy, 1995), and there exists a substantial literature on fear and the physiological (neuroendocrine) stress response (for a review, see Boissy, 1995). However, relatively few studies on physiological stress have worked with predators, and research relating such stress to antipredator behavior is still in its infancy (Bercovitch *et al.*, 1995; Boissy, 1995). Further research into these physiological aspects of stress may ultimately have several important implications for how we view antipredator decision making, several of which I summarize in a closing section.

Regardless of the topic being addressed, all of the published works included in this review share certain characteristics. First, the behaviors/decisions in question respond *in ecological time* to changes in some component of the risk of predation (*sensu* Lima and Dill, 1990). That is, this review concerns plastic behavioral traits that respond to short-term perceived changes in the risk of predation. Thus, I do not consider in detail those aspects of behavior that respond to predation over evolutionary time (see Edmunds, 1974; Endler, 1991). Second, figuring prominently in most studies included herein is the inevitable trade-off between the benefits of avoiding possible predation and the costs of doing so, in terms of feeding, survival, or reproduction (i.e., stresses as defined earlier). Third, for reasons of manageability, I include work published primarily during the last 7–8 years. This covers roughly the time period since the publication of several relevant reviews that were written in the late 1980s (Dill, 1987; Sih, 1987; Lima and Dill, 1990). The present review nevertheless encompasses about twice the number of papers covered by Lima and Dill (1990), whose comprehensive coverage extended over almost a 15-year period!

I have strived to provide perspectives on antipredator decision making that encompass several levels of biological organization. I thus cover the spectrum from short-term decision making by individuals to the consequences of such decision making for long-term fitness, population dynamics, and species interactions. Work on short-term decision making under the risk of predation has a relatively long history of study (Milinski, 1986; Sih, 1987; Lima and Dill, 1990), whereas most of the work on its consequences has appeared in recent years. My choices for the topics organizing this review reflect an attempt to provide a representative perspective on the current state of the field—I hope they succeed. In the hope of synthesizing available studies as much as possible, I have also classified studies across several topics to the extent warranted.

II. BEHAVIOR OF FEEDING ANIMALS: CLASSICAL MOTIVATIONS

It is appropriate to begin with an examination of recent empirical and theoretical work on foraging behavior. By "classical," I refer to studies motivated directly or historically by optimal foraging theory (Stephens and Krebs, 1986). Work in this area still forms the main empirical, theoretical, and philosophical basis for the study of decision making under the risk of predation. Note that while this section focuses mainly on classical issues, subsequent sections often deal with the behavior of feeding animals to one degree or another.

A. ENERGETIC STRESS AND STATE-DEPENDENT RISK TAKING

1. *Empirical Studies*

One of the best ways to demonstrate that animals trade off safety against feeding is to manipulate their internal (energetic) state (Milinski, 1993). Such a manipulation is usually accomplished via a period of food deprivation. Provided that riskier behavioral options are also those that allow for a higher rate of energy intake, then an energetically stressed animal should accept a relatively high risk of predation while feeding. This idea goes back to the very earliest of studies on anti predator trade-offs (Milinski and Heller, 1978; Dill and Fraser, 1984). Work on state-dependent risk taking began in earnest during the late 1980s, and the pace of research has accelerated in recent years (Table I).

Recent demonstrations of state-dependent risk taking make clear that such behavior is widespread. Almost without exception, over a wide range of decision making and taxa (Table I), energetically stressed animals will accept relatively great risk to obtain food. Most studies manipulated an animal's energetic state (hunger), with a few exceptions addressing issues such as the effects of reproductive or migratory state. Moore's (1994) study is particularly interesting in this regard; warblers in a migratory state (and thus in need of large energetic reserves for long-distance flight) took greater risks than control birds even though the former had higher energetic reserves than the latter. Another unusual result concerns the demonstration that bumblebee workers accept greater risks for increased food intake when their colony is experiencing energetic stress (Cartar, 1991). In related work, Weary *et al.* (1996) found that slower growing piglets accept a higher risk of maternal crushing to secure increased milk intake.

2. *Theory: The Rise of Stochastic Dynamic Programming*

State-dependent decision making under the risk of predation is at the heart of stochastic dynamic programming (SDP). The introduction of SDP

TABLE I
RECENT STUDIES EXAMINING STATE-DEPENDENT RISK-TAKING IN ANIMALS

	Animal	State/Stress	Context and result	Source
Invertebrates				
	Bumble bee (<i>Bombus occidentalis</i>)	Energetic	Foraging workers are reluctant to flee from predator when colony's reserves are low	Cartar (1991)
	Barnacle (<i>Balanus glandula</i>)	Energetic	Poorly fed barnacles resume feeding faster following encounter with predator	Dill and Gillett (1991)
	Stonefly larvae (<i>Paragnetina media</i>)	Energetic	No apparent effect of hunger on use of space	Feltmate and Williams (1989a)
	Mayfly larvae (<i>Baetis tricaudatus</i>)	Energetic	Hungry larvae increase feeding by spending less time in refuges	Kohler and McPeek (1989)
	Stonefly larvae (<i>Acroneuria</i> and <i>Paragnetina</i> , 2 spp.)	Energetic	No effect of hunger on tendency to enter drift	Rader and McArthur (1995)
	Whirligig beetle (<i>Dineutes assimilis</i>)	Energetic	Hungry beetles occupy profitable but risky outer portion of group	Romey (1995)
	Whirligig beetle (<i>D. assimilis</i>)	Energetic	Hungry beetles adopt solitary foraging to increase energetic gain	Romey and Rossman (1995)
	Backswimmer (<i>Notonecta hoffmani</i>)	Energetic	Hungry individuals resume feeding faster following encounter with predator	Sih (1992a)
	Dogwhelk (<i>Nucella lapillus</i>)	Energetic	Hungry individuals move more and spend less time in aerial refuges	Vadas <i>et al.</i> (1994)
Vertebrates				
	Ground squirrel (<i>Spermophilus beldingi</i>)	Body mass	Individuals with low body mass show reduced vigilance following alarm calls	Bachman (1993)

<i>Stickleback (<i>Spinachia spinachia</i>)</i>	Energetic	Hungry fish choose riskier but more profitable patches	Croy and Hughes (1991)
<i>Stickleback (<i>Gasterosteus aculeatus</i>)</i>	Energetic	Hungry fish choose increasingly safer but less profitable prey as they satiate	Godin (1990)
<i>Stickleback (<i>G. aculeatus</i>)</i>	Energetic	Hungry fish increase predator inspection, reflecting a greater need for information (?)	Godin and Crossman (1994)
<i>Atlantic salmon (<i>Salmo salar</i>)</i>	Energetic	Hungry fish resume feeding faster following encounter with predator	Gotceitas and Godin (1991)
<i>Pika (<i>Ochotona collaris</i>)</i>	Reproductive	Lactating females feed in riskier but more profitable microhabitats	Holmes (1991)
<i>Frog larvae (2 <i>Rana</i> spp.)</i>	Energetic	Hungry tadpoles increase activity under all levels of risk	Horat and Semlitsch (1994)
<i>Stickleback (<i>G. aculeatus</i>)</i>	Energetic	Hungry fish feed on dense but dangerous portions of prey swarms	Jakobsen <i>et al.</i> (1994)
<i>Willow tit (<i>Parus montanus</i>)</i>	Energetic	Hungry birds resume feeding faster following encounter with predator	Koivula <i>et al.</i> (1995)
<i>Roach (<i>Rutilus rutilus</i>)</i>	Energetic	Hungry fish occupy profitable but risky periphery of the group	Krause <i>et al.</i> (1992); Krause (1993a)
<i>Dark-eyed junco (<i>Junco hyemalis</i>)</i>	Energetic	Hungry birds increase rate of energy intake by reducing vigilance	Lima (1995)
<i>Coho salmon (<i>Oncorhynchus kisutch</i>)</i>	Energetic	Hungry fish are more willing to attack distant prey following recent exposure to predator	Martel and Dill (1993)
<i>Yellow-rumped warbler (<i>Dendroica coronata</i>)</i>	Migratory	Birds in migratory state resume feeding faster following encounter with predator	Moore (1994)
<i>Crucian carp (<i>Carassius carassius</i>)</i>	Energetic	Hungry fish feed in riskier but more profitable microhabitats	Petterson and Brönmark (1993)
<i>Porcupine (<i>Erethizon dorsatum</i>)</i>	Body mass	Individuals with low body mass feed in risky but profitable microhabitats	Sweitzer and Berger (1992)

to behavioral ecology was spurred by the need to combine disparate quantities like predator avoidance and food intake into a common framework for making predictions about state-dependent behavior (McNamara and Houston, 1986; Mangel and Clark, 1988). SDP models use the numerical technique of backward induction to develop an optimal behavioral "program" in which optimal behavior is specified for all possible internal states and environmental contingencies. The intuitive and conceptual appeal of such behavioral programs, and the relative accessibility of SDP modeling to biologists (via Mangel and Clark, 1988), have led to much recent interest in SDP.

Published SDP models cover a wide range of behavioral issues in decision making under the risk of predation. The more "classically" oriented models examine issues of state dependence (typically energetic stress) in diet selection (Godin, 1990; Burrows and Hughes, 1991) or patch use (Newman, 1991; see also Houston *et al.*, 1993; McNamara and Houston, 1994), while others have explored state-dependent foraging activity/effort (Werner and Anholt, 1993; Crowley and Hopper, 1994). Rosland and Giske (1994) and Fiksen and Giske (1995) have developed models of optimal diel vertical migration in aquatic animals. Houston and McNamara (1989) have used SDP to explore the issue of foraging effort in closed versus open experimental systems. The use of rules of thumb regarding uncertainty about predation risk has also been addressed with SDP (Bouskila and Blumstein, 1992). In addition, a series of SDP models incorporating body-mass-dependent predation in birds addresses issues of optimal body mass (McNamara and Houston, 1990; Houston and McNamara, 1993; Bednekoff and Houston, 1994; see also Bull *et al.*, 1996, for related work with fish), the decision to hoard food (Lucas and Walter, 1991), and the temporal patterning of daily foraging behavior (Bednekoff and Houston, 1994; McNamara *et al.*, 1994). McNamara and Houston (1992), Houston *et al.* (1993), and Bednekoff (1997) have used SDP to explore several issues surrounding the trade-off between feeding and antipredatory vigilance. SDP models have also addressed the influence of predation risk on optimal sociality (Szekely *et al.*, 1991; Paveri-Fontana and Focardi, 1994), parental behavior (Clark and Ydenberg, 1990a,b), and various aspects of mating behavior (Sargent, 1990; Crowley *et al.*, 1991; Kålås *et al.*, 1995; Lucas and Howard, 1995; Lucas *et al.*, 1996).

This interest in SDP modeling has not yet produced a corresponding increase in empirical tests of such models. Few SDP models are even accompanied by much empirical information (but see Godin, 1990; Burrows and Hughes, 1991; Lucas and Walter, 1991; Rosland and Giske, 1994; Bull *et al.*, 1996). Furthermore, most studies demonstrating state-dependent antipredatory decision making (Table I) do not directly address SDP theory.

The problem here may lie in (1) the sometimes extremely complex nature of SDP models (e.g., Burrows and Hughes, 1991; Crowley and Hopper, 1994; Rosland and Giske, 1994; Fiksen and Giske, 1995; Lucas and Howard, 1995), which may have outstripped the empiricist's ability to provide even qualitative tests of theory, and (2) the fact that qualitative predictions regarding state-dependent behavior often do not require SDP modeling. The value of SDP models is nonetheless clear and important, especially with regard to the link between short-term decision making and life-history phenomena (Clark, 1994; McNamara *et al.*, 1995). I return to the issue of testability and the importance of models later in this section.

B. THE μ/g RULE FOR OPTIMAL BEHAVIOR

The μ/g rule specifies that an animal can maximize its fitness, or optimally manage its predator-induced stress, by choosing the behavioral option that minimizes the rate of mortality (μ) per unit increase in growth rate (g). Gilliam (1982; see also Werner and Gilliam, 1984) derived this rule for animals that experience continuous growth up to some reproductive size, but it has since been broadened to other animals in the form the μ/f rule, where f represents feeding rate (Gilliam and Fraser, 1988; Gilliam, 1990). In all of its guises, the μ/g rule has undeniable appeal. It has been applied to the question of patch choice (Gilliam and Fraser, 1987, 1988; Moody *et al.*, 1996; Sih, 1998), diet choice (Gilliam, 1990), foraging effort (Werner and Anholt, 1993), avian migration (Lindström, 1990), and life-history evolution (Werner, 1986; Aksnes and Giske, 1990). Furthermore, the μ/g rule has been derived in several contexts (Clark and Levy, 1988; McNamara and Houston, 1992, 1994; Houston *et al.*, 1993) and without the dynamical theory used in its original formulation (Aksnes and Giske, 1990; Leonardsson, 1991; Brown, 1992; Clark, 1994; Clark and Dukas, 1994; Hugie and Dill, 1994; Dukas and Clark, 1995).

Several recent papers caution that the μ/g rule has its limitations (many of which were noted in Gilliam, 1982). Ludwig and Rowe (1990) and Rowe and Ludwig (1991) show that time constraints in reaching reproductive size can negate the simple μ/g rule. Clark (1994) adds that the μ/g rule implies an unlikely scenario in which reproductive value does not change over time. McNamara and Houston (1994; see also Houston *et al.*, 1993) show further that the μ/g rule requires no stochasticity or state dependency in μ or g (or f). Most importantly, McNamara and Houston show that the μ/g rule applies only when long-term foraging options are not subject to change. Such an environment is unlike that in which the μ/g rule might be tested experimentally.

Despite these apparent limitations, the μ/g rule can perform well even when some of the above conditions are clearly violated (Werner and Anholt, 1993; Crowley and Hopper, 1994). This suggests that animals might actually use some μ/g -like rule in their decision making. However, only Gilliam and Fraser (1987) provide quantitative empirical support for such a rule. Gotceitas (1990) claims empirical support for the μ/g rule, but his results suggest a more simple alternative explanation (see McNamara and Houston, 1994) in which the fish studied simply acted to minimize μ . Other tests (Bowers, 1990; Turner and Mittelbach, 1990) provide only qualitative support that appears consistent with the general expectations of several different models. In any case, the μ/g rule remains a powerful heuristic tool in the study of decision making under the risk of predation.

C. FORAGING IN A PATCHY ENVIRONMENT

Here, I address primarily the relatively abstract theoretical and empirical aspects of foraging in a patchy environment, typically a laboratory or “mathematical” environment. I address the more ecologically motivated studies of habitat use in a later section. This distinction is not always easily made, but it is a useful one.

1. Patch Choice

Recent theoretical developments in this area concern the Ideal Free Distribution (IFD) model of patch choice. This model posits that animals with perfect (ideal) information are free to choose patches such that they maximize their fitness, subject to the choices made by other animals. A common prediction is that the distribution of animals among patches will eventually stabilize (at the IFD) and match the distribution of food resources among patches (Milinski and Parker, 1991). Predators can certainly disrupt the IFD, and Moody *et al.* (1996) provide a much-needed theoretical perspective on this phenomenon. They show that (1) undermatching of food resources is a universal expectation when resource-rich patches are also the riskier patches (e.g., Abrahams and Dill, 1989), and that (2) multiple stable distributions are possible under some circumstances. Other recent IFD-based models examine situations in which predators respond to the distribution of prey, and prey, in turn, respond to the distribution of both their food resources and predators (Schwinning and Rosenzweig, 1990; Hugie and Dill, 1994; Sih, 1998; see also van Baalen and Sabelis, 1992). The overall results indicate that stable distributions across patches of both predator and prey are possible outcomes in many situations (but see Schwinning and Rosenzweig, 1990). These multi-trophic-level models also make the counterintuitive predictions that (1) the distribution of predators should

tend to match their prey's resource distribution (Hugie and Dill, 1994; Sih, 1998), and (2) the prey distribution may not closely match the distribution of prey resources (Hugie and Dill, 1994; but see Sih, 1998). Empirical tests of these predictions ought to be feasible, but none has been reported (but for related empirical studies, see Sih, 1984; Formanowicz and Bobka, 1989).

Empirically, predator-induced deviations from the Ideal Free Distribution have been used to assess the "energetic equivalence" of predator avoidance in predation-risk-dependent patch choice (Abrahams and Dill, 1989; Todd and Cowie, 1990; Utne *et al.*, 1993); the ultimate goal here is to express food intake and predator avoidance in the common currency of energy (see also Kotler and Blaustein, 1995, for a different perspective on this matter). Kennedy *et al.* (1994) criticized such IFD-based studies for assuming an IFD rather than assessing the possibility of systematic deviations from the IFD. Kennedy *et al.* also present a non-IFD-based alternative to assessing the energetic equivalence of predator avoidance, but Moody *et al.* (1996) warn that this alternative has no functional basis. Moody *et al.* caution further that the entire enterprise of determining such energetic equivalencies may rest on shaky conceptual ground.

There have been relatively few non-IFD-related developments regarding patch choice under the risk of predation. Theoretically, Gilliam and Fraser (1988) extend the μ/g rule to patch choice with depleting resources. Houston *et al.* (1993) provide a cogent discussion and review of the relationships among models of optimal patch choice under the risk of predation. Empirically, there have been several recent demonstrations that patch choice represents an energy-predation trade-off when dangerous patches are also energetically profitable (e.g., Gotceitas, 1990; Gotceitas and Colgan, 1990a,b; Brown *et al.*, 1992a,b; Pettersson and Brönmark, 1993; Scrimgeour and Culp, 1994a; Scrimgeour *et al.*, 1994). These studies complement many similar studies reviewed in Lima and Dill (1990). Nonacs and Dill (1990) provide the unique result that a worker ant's decision to feed in a risky patch reflects the contribution that its efforts make to colony growth.

2. Time in Patches

Recent theoretical treatments of patch use differ considerably in their predictions. Newman (1991) indicates that optimal patch residence time may be influenced little by the risk of predation. In contrast, Brown (1992) develops several models in which optimal patch residence times are highly predation-risk dependent. This discrepancy may reflect disparate assumptions about whether patches vary in predation risk or energetic quality. Empirically, there is much evidence that the degree to which small mammals exploit patches is predation-risk dependent (see Section VIII,A).

3. *Choice of Foraging Location*

Several recent (and somewhat difficult to categorize) papers come under this general heading, which addresses within-patch decisions about where to feed. For instance, Jakobsen *et al.* (1994) found that sticklebacks forage on denser portions of zooplanktonic swarms only when energetically stressed or safe from attack; this reflects a trade-off between predator detection and feeding rate (see also Milinski and Heller, 1978; Godin and Smith, 1988). Vásquez (1994) found that a small cricetid rodent becomes a refuge-seeking, central-place consumer of food when feeding under a threat of predation. Peterson and Skilleter (1994) found that clams shift feeding location from substrate (risky but profitable option) to water column (safe but less profitable option) after suffering partial siphon loss to foraging fish. This shift is consistent with an energy-predation trade-off, but it is not clear whether clams can assess the risk of (partial) predation independent of the act itself, or whether they could effectively employ both foraging options after partial siphon loss (see also Lindsay and Woodin, 1995).

D. DIET SELECTION

Recent work provides much-needed theoretical perspectives on diet selection under the risk of predation. Gilliam (1990) describes a particularly insightful extension of the μ/g rule to the question of diet selection. This model exhibits quasi-classical behavior (see Stephens and Krebs, 1986) in which prey-specific predation risks are a determinant of prey ranking. Godin (1990) developed an SDP model that predicted that profitable but risky prey (large prey whose consumption interferes with predator detection) should be consumed preferentially only by energetically stressed animals. Burrows and Hughes (1991) presented an ambitious SDP model in which mortality and digestive constraints combine to cause a general contraction of the diet with increasing risk of predation.

Empirical work on diet selection has been limited. Godin (1990) provided empirical evidence that diet selection in guppies is predation-risk and state dependent as predicted (qualitatively) by his SDP model; further support for this model lies in the observation that fish may prefer large, profitable items only under low predation risk (Ibrahim and Huntingford, 1989). Phelan and Baker (1992) suggested that predation-risk-related travel costs influence diet selection in mice, but their test suffered from a lack of any manipulation of risk. Brown and Morgan (1995) showed that a squirrel's apparent preference for certain food types can be predation-risk dependent, even though one food type may be inherently preferred over others.

E. TESTABILITY AND THE ROLE OF THEORETICAL MODELS

It is appropriate at this point to address some important issues regarding the role of modeling in the study of predator-induced stress and antipredator decision making, as "classically motivated" work is the most theory-rich area that I consider in this review. The following discussion, however, applies generally to subsequent sections.

These issues regarding the role of modeling concern the virtual absence of quantitative tests of theory. Besides the efforts of Gilliam and Fraser (1987) and Gotceitas (1990), few attempts at quantitative tests have been reported. There are probably several reasons for this phenomenon. First, many simple models are obviously caricatures of reality that demand no quantitative test. At the opposite extreme, some ambitious SDP models may outstrip the ability of empiricists to provide even qualitative tests of predictions. A more fundamental problem concerns our inability to measure the risk of predation itself (or its various components). Only a few field studies have much quantitative information on the risk of predation (e.g., Watts, 1990; Harfenist and Ydenberg, 1995), and none provides information that relates an animal's conceivable behavioral options to particular risks of predation. This sort of information is critical to making quantitative behavioral predictions about the adaptive management of predator-induced stress.

To what extent are we limited by our inability to provide quantitative tests of theory? Two lines of argument suggest that this limitation is not too severe. First, qualitative tests of carefully reasoned predictions should prove enlightening in most situations. Second, even without quantitative tests, there has been an invaluable interplay between theory and empiricism in the study of decision making under the risk of predation, and I see no reason why this will not continue. On the other hand, Brown (1992) argues that models with rather disparate fitness formulations can yield similar qualitative predictions. Quantitative tests may ultimately be needed to determine which fitness formulation is superior.

Given our ongoing inability to provide quantitative tests of theory, modelers have little choice but to strive for qualitative predictions that distinguish among various hypotheses. I personally prefer relatively simple models with broad heuristic value, but Abrams (1993a) argues that simple models can also be misleading. In any case, a pluralism of modeling approaches should continue to provide a strong conceptual basis for further empirical and theoretical progress.

III. PATTERNS OF ACTIVITY

"Activity" studies examine the influence of predators on both the level and the temporal patterning of prey activity. I consider each of these areas

in turn. These studies on prey activity provide some of the best documented behavioral responses by prey to the presence of predators, and form the foundation for much behaviorally explicit ecological research on predator-prey interactions (e.g., Werner, 1992; Wooster and Sih, 1995).

A. LEVELS OF ACTIVITY

I distinguish between two types of activity, movement and refuging. An animal can in principle vary these two types of activity independently in response to the risk of predation (Sih and Kats, 1991; Werner and Anholt, 1993). By movement, I refer to things like speed of movement, length of moves, frequency of movement, and so on. Refuging refers to a situation in which an animal retreats to a refuge and emerges infrequently and for only brief periods; a refuge is, for example, a burrow or rock crevice (as opposed to a safe habitat) in which an animal cannot readily feed, locate mates, and so on (e.g., Sih *et al.*, 1988). Categorizing a given activity as either movement or refuging is usually straightforward, although many studies do not define in detail the behaviors under examination.

A decrease in prey activity following a heightened threat of predation has been a reasonably well established result for some time (Sih, 1987; Lima and Dill, 1990; Kolar and Rahel, 1993; Wooster and Sih, 1995), one that also figures prominently in studies related to physiological (neuroendocrine) stress (Boissy, 1995). Work in recent years indicates that such a response is indeed ubiquitous across diverse taxa (Table II). Almost all species studied exhibit decreased movement, increased refuging, or both (if both types of behavior were examined) in response to an increase in the risk of predation. Several studies indicate that many aquatic (and even some terrestrial) animals respond to the chemical evidence of predators as well as the actual presence of predators (for an extensive review, see Kats and Dill, 1998).

There were exceptions to the general result of decreased activity with increasing risk (Table II). Some cases with no response to predator manipulation may have involved prey large enough to be invulnerable to predators (e.g., Willman *et al.*, 1994), while in others a nonsignificant effect was in the typical direction (e.g., Walls, 1995). Houtman and Dill (1994) found a decrease in movement by marine sculpins only if the background provided some degree of crypticity. Larval *Ambystoma* salamanders decreased movement only in the absence of a refuge; otherwise, movement increased in an effort to reach a refuge (Sih and Kats, 1991). The case of increased movement in toad larvae in response to an alarm substance (Hews, 1988) may also represent refuge-seeking behavior. Sih and Krupa (1992) argued that female water striders take advantage of a predator-induced decrease

TABLE II
RECENT STUDIES EXAMINING CHANGES IN PREY ACTIVITY IN RESPONSE TO PREDATOR PRESENCE OR PERCEPTION THEREOF

Species	Predator ^a	Activity ^b	Change in activity ^c with			Source
			Risk ↑	Food ↑	Hunger ↑	
Invertebrates						
Aquatic snail (<i>Physella</i> and <i>Planorbella</i> , 2 spp.)	Alarm substance	R	Inc ^d	NP	—	Alexander and Covich (1991a,b)
Crayfish (<i>Pacifastacus leniusculus</i>)	Fish C	M	Dec	—	—	Blake and Hart (1993)
		R	Inc	—	—	
Damselfly larvae (2 <i>Enallagma</i> spp.)	Fish P, larval odonate P	M	Dec (1 sp.), NR (1 sp.)	—	—	Blois-Heulin <i>et al.</i> (1990)
Shrimp (<i>Atya lanipes</i>)	Large shrimp P	M	Dec	NP	—	Crowl and Covich (1994)
		R	Inc	NP	—	
Larval mayfly (<i>Paraleptophlebia heteronea</i>)	Fish P	R	Inc	NP	—	Culp <i>et al.</i> (1991)
Grass shrimp (<i>Palaemonetes pugio</i>)	Fish P	R	Inc	NP	—	Everett and Ruiz (1993)
Stonefly larvae (<i>Paragnetina media</i>)	Fish P	M	Dec	NP	—	Feltmate <i>et al.</i> (1992)
Crayfish (<i>Orconectes virilis</i>)	Alarm substance	M	Dec	NP	—	Hazlett (1994)
Crayfish (3 <i>Orconectes</i> spp.)	Fish P	R	Inc	—	—	Hill and Lodge (1994)
Isopod (<i>Lirceus fontinalis</i>)	Fish P	M	Dec	—	—	Holomuzki and Short (1990)
Amphipod (<i>Gammarus minus</i>)	Fish C	M	Dec	NP	—	Holomuzki and Hoyle (1990)
Isopod (<i>L. fontinalis</i>)	Fish P	M	Dec	—	—	Huang and Sih (1990, 1991)
Damselfly larvae (2 <i>Enallagma</i> spp.)	Larval dragonfly P	M	Dec	Inc	—	Jeffries (1990)
Damselfly larvae (<i>Coenagrion hastulatum</i>)	Larval dragonfly P	M	Dec	NR	—	Johansson (1993)
Mayfly larvae (<i>Baetis tricaudatus</i>)	Fish P	M	Dec	NR	Inc	Kohler and McPeek (1989)
		R	Inc	Dec	Dec	

(continued)

TABLE II (Continued)

Species	Predator ^a	Activity ^b	Change in activity ^c with			Source
			Risk ↑	Food ↑	Hunger ↑	
Chironomid larvae (<i>Chironomus tentans</i>)	Fish P	R	Inc ^d	NP	-	Macchiusi and Baker (1991)
Chironomid larvae (<i>C. tentans</i>)	Fish P	R	Inc	Dec	-	Macchiusi and Baker (1992)
Damselfly larvae (4 <i>Enallagma</i> spp.)	Fish P, larval dragonfly P	M	Dec	-	-	McPeek (1990)
Worker ants (<i>Lasius pallitarsis</i>)	Large ant P	M	Dec	Inc	-	Nonacs (1990)
Caddis larvae (<i>Rhyacophila nubila</i>)	None	R	-	NP	Dec	Otto (1993)
Water flea (2 <i>Daphnia</i> spp.)	Copepod P	M	Dec (1 sp.), inc (1 sp.)	-	-	Ramcharan and Sprules (1991)
Marine snail (<i>Stramonita haemastoma</i>)	Crab P	R	Inc	-	-	Richardson and Brown (1992)
Ostracod (<i>Cypridopsis vidua</i>)	Fish C	R	Inc	-	-	Roca <i>et al.</i> (1993)
Mayfly larvae (<i>Baetis</i> , <i>Ephemerella</i> , <i>Calessenia</i> spp.)	Fish P, stonefly P	R	Inc	NP	-	Scrimgeour <i>et al.</i> (1994)
Isopod (<i>L. fontinalis</i>)	Fish C	M	Dec	-	-	Short and Holomuzki (1992)
Water strider (<i>Aquarius remigis</i>)	Fish P	M	Dec (male), inc (female)	-	Inc	Sih and Krupa (1992, 1995)
Isopod (<i>Saduria entomon</i>)	Larger isopod P	R	Inc	NP	-	Sparrevik and Leonardsson (1995)
Mayfly larvae (2 <i>Baetis</i> spp.)	Fish P	M	NR	-	-	Tikkanen <i>et al.</i> (1994)
		R	Inc ^d	-	-	
Aquatic snail (<i>Physella gyrina</i>)	Alarm substance	R	Inc	-	-	Turner (1996)
Dogwhelk (<i>Nucella lapillus</i>)	Crab C, alarm substance	M	Dec	-	Inc	Vadas <i>et al.</i> (1994)
		R	Inc	-	Dec	
Lobster (<i>Homarus americanus</i>)	Fish P	R	Inc	-	-	Wahle (1992)
Crayfish (3 <i>Orconectes</i> spp.)	Fish P	R	Dec, 1 sp., NR, 2 spp. ^d	Dec	-	Willman <i>et al.</i> (1994)

Fish						
Fathead minnow (<i>Pimephales promelas</i>)	Alarm substance	R	Inc	NP	-	Brown <i>et al.</i> (1995)
		M	Dec	NP	-	
Fathead minnow (<i>P. promelas</i>)	Alarm substance, fish P	R	Inc	NP	-	Chivers and Smith (1994, 1995)
Brook stickleback (<i>Culaea inconstans</i>)	Alarm substance, fish C	M	Dec	NP	-	Gelowitz <i>et al.</i> (1993)
Marine sculpin (<i>Oligocottus maculosus</i>)	Alarm substance	M	Dec ^e	NP	-	Houtman and Dill (1994)
Coho salmon (<i>Oncorhynchus kisutch</i>)	Duck C	M	Dec	-	-	Martel and Dill (1993)
Coho salmon (<i>O. kisutch</i>)	Duck P	M	Dec	NP	-	Martel and Dill (1995)
Fathead minnow (<i>P. promelas</i>)	Alarm substance, fish P	M	Dec	NP	-	Mathis and Smith (1993a);
		R	Inc	NP	-	Mathis <i>et al.</i> (1993)
Brook stickleback (<i>C. inconstans</i>)	Alarm substance	M	Dec	NP	-	Mathis and Smith (1993b)
Darter (3 <i>Etheostoma</i> spp.)	Fish P	M	Dec ^e	NP	-	Radabaugh (1989)
Lumpfish larvae (<i>Cyclopterus lumpus</i>)	Fish P	M	Dec ^d	Dec ^d	-	Williams and Brown (1991)
Amphibians						
Frog larvae (<i>Rana catesbeiana</i>)	Larval dragonfly P	M	-	Dec	-	Anholt and Werner (1995)
Newt larvae (<i>Taricha torosa</i>)	Adult newt C	R	Inc	NP	-	Elliott <i>et al.</i> (1993)
Salamander larvae (<i>Ambystoma maculatum</i>)	Fish P	R	Inc	-	-	Figiel and Semlitsch (1990)
Frog larvae (<i>Ascaphus truei</i>)	Fish and salamander C	R	Inc	-	-	Feminella and Hawkins (1994)
Toad (<i>Bufo americanus</i>)	Snake P	M	Dec	-	-	Hayes (1989)
Toad (<i>B. americanus</i>)	Snake P	M	Dec	NP	Inc	Heinen (1994a,b)
Toad larvae (<i>B. americanus</i>)	Alarm substance	M	Inc	NP	-	Hews (1988)
Frog larvae (2 <i>Rana</i> spp.)	Fish C	M	Dec	Dec or NR	Inc	Horat and Semlitsch (1994)
		R	NR	NR	NR	
Salamander larvae (<i>A. texanum</i>)	Fish P	R	Inc	-	-	Huang and Sih (1990, 1991)
Frog, toad larvae (<i>Hyla</i> and <i>Bufo</i> , 4 spp.)	Fish, newt, dragonfly P	M	Dec	-	-	Lawler (1989)

(continued)

TABLE II (Continued)

Species	Predator ^a	Activity ^b	Change in activity ^c with			Source
			Risk ↑	Food ↑	Hunger ↑	
Frog larvae (<i>R. temporaria</i>)	Fish, crayfish C	M	Dec	NP	-	Manteifel (1995)
Salamander larvae (<i>A. babouri</i>)	Fish P	R	Inc	-	Dec	Sih <i>et al.</i> (1988)
Salamander larvae (<i>A. babouri</i>)	Fish C	M	Dec	NP	-	Sih and Kats (1991)
Salamander larvae (<i>A. babouri</i>)	Fish P	R	Inc	-	-	Sih <i>et al.</i> (1992)
Toad larvae (<i>B. americanus</i>)	Larval dragonfly	M	Dec	NR	-	Skelly and Werner (1990)
Frog larvae (<i>Hyla versicolor</i>)	Salamander P	M	Dec	-	-	Skelly (1992)
Frog larvae (2 <i>Pseudacris</i> spp.)	Dragonfly larva P	M	Dec ^d	Dec ^d	-	Skelly (1995)
Frog larvae (2 <i>Rana</i> spp.)	Fish P,C	M	Dec	NP	-	Stauffer and Semlitsch (1993)
Salamander larvae (2 <i>Ambystoma</i> spp.)	Large salamander P	R	Inc (1 sp.), NR (1 sp.)	NP	-	Walls (1995)
Frog larvae (<i>R. aurora</i>)	Alarm substance	M	Dec	NP	-	Wilson and Lefort (1993)
Other Vertebrates						
Gerbils (2 <i>Gerbilus</i> spp.)	Owl P	M	Dec	-	-	Abramsky <i>et al.</i> (1996)
Rat (<i>Rattus</i> sp.)	Cat P	M	Dec	-	-	Blanchard and Blanchard (1989)
		R	Inc	-	-	
Bank voles (<i>Clethrionomys glareolus</i>)	Mammals C	M	Dec	-	-	Jedrzejewska and Jedrzejewski (1990); Jedrzejewska <i>et al.</i> (1993)
Field vole (<i>Microtus agrestis</i>)	Falcon P	M	Dec	-	-	Korpimäki <i>et al.</i> (1996)
Desert rodents (4 heteromyids, 1 cricetid)	Owls P	M	Dec	-	-	Longland and Price (1991)
Lizard (<i>Lacerta vivipara</i>)	Snake C	M	Dec	NP	-	Van Damme <i>et al.</i> (1990)

^a P, Predator present; C, chemical scent of predator; "alarm substance" usually refers to a chemical emanating from a killed or injured conspecific.

^b R, Refuging; M, movement.

^c NR, No response; Dec and Inc, decrease or increase, respectively, in the activity in question; -, no manipulation; NP, food not present.

^d Response varied according to body size; some size classes may have been invulnerable to predators.

^e May see only under cryptic conditions.

in male activity to pursue their own activities free from male harassment, hence their atypical response to predator presence.

Surprisingly few studies have examined an animal's level of activity in the context of managing stress caused by a lower rate of feeding. In fact, food (or an identifiable impetus for nonzero activity) was not present in approximately 40% of the studies in Table II. Food was present but unmanipulated in an additional 40% of studies; presumably, under these circumstances, a reduction in activity led to a decreased feeding rate. Studies manipulating food levels show mainly a decrease in activity with increasing food availability. Such a decrease is consistent with theoretical expectations (Abrams, 1991; Werner and Anholt, 1993), provided that risk increases with activity. The few studies manipulating an animal's state show a consistent increase in activity (increased movement, decreased refuging) in energetically stressed animals. Such a state-dependent response is indicative of a trade-off between activity and the risk of predation (see Section II,A).

Underlying any functional explanation for a predator-induced decrease in activity is the assumption that increased activity raises the risk of predation. Presumably, increased activity raises the probability of being detected or encountered by a predator (but see also Houtman and Dill, 1994). This assumption receives support from several recent studies involving diverse predator-prey systems (e.g., Vaughn and Fisher, 1988; Daly *et al.*, 1990; FitzGibbon, 1990; Rahel and Kolar, 1990; Everett and Ruiz, 1993; Otto, 1993; Heinen, 1994a; Anholt and Werner, 1995; Martel and Dill, 1995). Skelly (1994) provides a particularly nice demonstration of this effect by comparing predation on active and partially anesthetized tadpoles. Furthermore, a predator-induced increase in activity in *Daphnia oregonensis* (Ramcharan and Sprules, 1991) actually led to greater mortality. Interspecific patterns in predation linked to differing levels of activity (Hershey, 1987; Lawler, 1989; Chovanec, 1992; Azevedo-Ramos *et al.*, 1992; Juliano *et al.*, 1993; Grill and Juliano, 1996) provide further support for this important assumption.

B. TEMPORAL PATTERNS IN ACTIVITY

1. *Diel Vertical Migration by Zooplankton*

Zooplankton undertaking diel vertical migration (DVM) descend to the depths during the day, and ascend to the surface at night; cases of reverse DVM (the opposite activity pattern) are also known (Ohman, 1990). Gliwicz and Pijanowska (1988) and Lampert (1989) note that, by the mid-1980s, many studies suggested that DVM is an adaptation against visually feeding predators rather than one related to the reduction of energetic stress, as

once thought. Recent work on DVM collectively provides an unusually comprehensive view of predator-induced stress and decision making.

The antipredator hypothesis posits that animals engaged in DVM trade off the energetic benefits of remaining in the warm and food-rich surface layers against the safety of the dark, but relatively cold and food-poor deeper water (Lampert, 1989; Fiksen and Giske, 1995). Accordingly, the addition of a predatory stimulus to experimental test chambers induces or enhances DVM in many cladocerans (primarily *Daphnia* spp.; Dodson, 1988; Leibold, 1990; Dawidowicz and Loose, 1992; Dini and Carpenter, 1992; Young and Watt, 1993; Loose and Dawidowicz, 1994), copepods (Bollens and Frost, 1989b; Neill, 1992), and *Chaoborus* midges (Dawidowicz *et al.*, 1990; Leibold, 1990; Tjossem, 1990). Similar effects occur upon whole-lake additions or removals of planktivorous fish (Dini *et al.*, 1993). These experimental results have been corroborated by field work showing that changes in DVM correspond closely to behavioral and distributional changes in planktivorous fish (Dini and Carpenter, 1988; Bollens and Frost, 1989a, 1991; Dodson, 1990; Levy, 1990a; Ohman, 1990; Ringelberg *et al.*, 1991; Frost and Bollens, 1992).

The way in which predation risk interacts with nonpredatory factors (e.g., food abundance, water temperature) to influence DVM is relatively unexplored territory. However, recent work suggests that DVM can be enhanced with the addition of food near the water's surface (Leibold, 1990) or can be diminished with food addition to deeper water (Dini and Carpenter, 1992); observational evidence also suggests a strong effect of resource depth distribution on DVM (Gliwicz and Pijanowska, 1988). Fiksen and Giske (1995) suggest further that the effects of food abundance on optimal DVM may be markedly nonlinear and circumstance dependent. Theory also suggests that factors such as light transmission and water temperature may be important determinants of the optimal depth of DVM (Aksnes and Giske, 1990; Levy, 1990b; Fiksen and Giske, 1995), but there appears to be relatively little experimental work in this area.

Gabriel and Thomas (1988) present a game-theoretical model of DVM suggesting that at evolutionary stability some members of a population may not engage in DVM. There is no strong evidence for such an effect (but see Guisande *et al.*, 1991), although clonal (genetic) differences in DVM are known to occur (De Meester, 1993; De Meester *et al.*, 1995). It is also known that species or size classes most vulnerable to fish predation tend to be those whose migratory behavior is most affected by changes in the predatory regime (Dodson, 1988; Ohman, 1990; Leibold, 1991; Neill, 1992; Watt and Young, 1994; see also Fiksen and Giske, 1995). Conspicuous, egg-carrying females may also be reluctant to ascend to the surface even under relatively dark conditions (Bollens and Frost, 1991).

The proximate factors influencing DVM have also been examined. Chemicals emitted by predators are sufficient (and perhaps necessary) to induce DVM in most species studied (see Larsson and Dodson, 1993, for a review). Some progress has been made in characterizing the chemical(s) that signal the presence of predators (Parejko and Dodson, 1990; Loose *et al.*, 1993). Rapidly changing light levels may also induce DVM (Ringelberg, 1991a,b; see also Clark and Levy, 1988), but zooplankton may initiate migration well in advance of changing light levels (Young and Watt, 1993).

Studies examining the long-term stress induced by DVM associate slower growth (Dawidowicz and Loose, 1992; Gliwicz, 1994; Loose and Dawidowicz, 1994) and delayed reproduction (Vuorinen, 1987) with descending into the depths during the day. Loose and Dawidowicz (1994) argue that these costs of DVM are due mainly to the colder temperatures of deep water (see also Aksnes and Giske, 1990). Despite these costs, demographic analyses (Ohman, 1990; Bollens and Frost, 1991) suggest that DVM confers a net advantage if it results in even a modest lowering of the risk of predation.

2. *Diel Migration in Fish*

Fish may also engage in diel migrations, both vertical and horizontal (Helfman, 1986; Clark and Levy, 1988; Levy, 1990a,b; Gliwicz and Jachner, 1992). Clark and Levy (1988) outline several hypotheses for such migratory behavior, which parallel those proposed for zooplankton (see earlier discussion). One of these hypotheses suggests that DVM in planktivorous fish reflects little more than the DVM of their prey, but this alone cannot explain DVM in such fish (Clark and Levy, 1988; Levy, 1990b; Rosland and Giske, 1994). Furthermore, these fish may undergo DVM even in the absence of DVM in their prey (Gliwicz and Jachner, 1992; Rosland and Giske, 1994). Theoretical and empirical evidence suggests that DVM in planktivores reflects in part the risk imposed upon them by piscivores (Clark and Levy, 1988; Gliwicz and Jachner, 1992; Rosland and Giske, 1994). In any case, there appears to be little definitive experimental work on diel migration in fish.

3. *Nocturnal versus Diurnal Activity*

Several recent studies show that animals will switch between nocturnal and diurnal activity, depending on the activity patterns of predators. Fenn and Macdonald (1995) showed that normally nocturnal rats may shift to diurnal activity in response to nocturnal activity by foxes. Such flexibility in rat activity was anticipated in recent psychological work on the patterning of rat behavior in response to threatening stimuli (Lester and Fanselow, 1992; Helmstetter and Fanselow, 1993). A literature review by McNeil *et*

al. (1992) suggests further that some birds may shift to nocturnal activity to avoid a strong diurnal risk of predation. Similarly, tiger moth (*Spilosoma congrua*) larvae become more nocturnal after diurnal encounters with wasps (Stamp and Bowers, 1993). On the more aquatic side of things, Culp and Scrimgeour (1993) and Cowan and Peckarsky (1994) showed that mayflies (*Baetis* spp.) switch from largely aperiodic to nocturnal feeding in the presence of visually hunting fish. Juvenile crayfish become more nocturnal in the presence of fish, but more diurnal in the presence of larger (and nocturnal) adult crayfish (Blake *et al.*, 1994).

4. *Diel Drift Periodicity in Stream Insects*

The tendency for large benthic stream insects to enter the nocturnal drift (to move via the current to a downstream site) has long been interpreted as an antipredator response, as these insects would be at risk to size-selective fish predators in the diurnal drift (Allan, 1978). Flecker (1992) found support for this idea in a comparative study of streams with and without fish, and suggested that such nocturnal drift periodicity was a fixed (evolutionary) response to predation (see also Andersson *et al.*, 1986; Malmqvist, 1988). However, much recent work shows clearly that at least some stream insects actively decide to enter the nocturnal drift in response to an increased local risk of predation (Williams, 1990; Poff *et al.*, 1991; Andersen *et al.*, 1993; Douglas *et al.*, 1994; Forrester, 1994a,b; McIntosh and Townsend, 1994; Tikkannen *et al.*, 1994). Rader and McArthur (1995) show further that the tendency of stoneflies to enter the nocturnal drift is reduced in habitats with abundant refuges.

5. *Daily Activity Patterns and Body Mass in Birds*

Bednekoff and Houston (1994) and McNamara *et al.* (1994) argue theoretically that patterns in the daily feeding activity of birds should reflect a trade-off between the costs (reduced speed or maneuverability) and benefits (reduced energetic stress) of carrying high fat reserves. These models suggest that such a trade-off can produce the bimodal daily feeding pattern commonly seen in birds (McNamara *et al.*, 1994) even in the absence of diel cycles in temperature, food availability, and so on. However, the behavioral consequences of such trade-offs have received little experimental attention (but see Witter *et al.*, 1994). Observational evidence nevertheless suggests an important role for fat-reserve-related predatory effects in avian biology (Witter and Cuthill, 1993).

6. *Nondiel Temporal Patterns in Activity*

a. *Activity and the Lunar Cycle.* The brighter portion of a lunar cycle represents a period of elevated risk for animals hunted by predators like

owls. Accordingly, recent studies have demonstrated repeatedly that small, nocturnal mammals are relatively inactive under bright moonlight. This is the case in gerbils (Kotler *et al.*, 1991, 1993a,b; Hughes and Ward, 1993; Hughes *et al.*, 1994), for whom Kotler *et al.* (1991) verify an elevated risk of owl predation under bright conditions. Kotler *et al.* (1994a) also found that gerbils reduce activity in anticipation of moonrise, indicating that the simple avoidance of light is not necessarily the proximate factor controlling lunar-based activity cycles.

Recent work on heteromyid rodents also shows strong moonlight avoidance (Bowers, 1990; Daly *et al.*, 1992; Bouskila, 1995; see also Lockard and Owings, 1974; but see Longland and Price, 1991). Daly *et al.* (1992) found that heteromyid kangaroo rats compensate for the lack of activity during periods of full moon by increased crepuscular activity, which actually makes them more vulnerable to diurnal predators. Work on murid rodents (in addition to gerbils; Wolfe and Summerlin, 1989; Simonetti, 1989; Dickman, 1992; Vásquez, 1994) and Old World porcupines (Brown and Alkon, 1990) indicates the same general trends in moonlight avoidance.

The generality of moonlight avoidance in small nocturnal mammals is clear, but there appears to have been little recent work on nonmammalian species. However, Gliwicz (1986) and Dodson (1990) suggest that the lunar cycle can also affect the strength of diel vertical migration in zooplankton.

b. Activity on Other Time Scales. Nondiel patterns in activity have received relatively little attention outside of the context of the lunar cycle. However, tidal cycles may influence risk taking by refuging barnacles (Dill and Gillett, 1991) and migrating intertidal-feeding fish (Burrows and Gibson, 1995). On a shorter time scale, Speakman *et al.* (1995) suggest that temporal clumping in the nightly emergence of bats from maternity colonies represents an attempt by individuals to dilute the risk of owl predation. Kalcounis and Brigham (1994) nevertheless found that the presence of a vocal owl model had no impact on any aspect of bat emergence patterns.

Activity cycles expressed over an entire season have received almost no attention. Lucas *et al.* (1996) provide an interesting exception in their dynamic game analysis of chorusing behavior in male frogs. Their analysis suggests that an interaction between predation risk, energetic stress, male density, and female behavior may produce pulses (or waves) of chorusing activity over the breeding season.

IV. AFTER AN ENCOUNTER WITH A PREDATOR

Recent work on postencounter decision making covers a variety of topics, such as the resumption of activity, the choice of escape behavior, and flight

initiation distance. In covering these topics, I focus on behavior that is flexible with respect to changes in the predatory environment; papers describing simple evasive behaviors in response to attack are outside the scope of this review.

A. POSTENCOUNTER RESUMPTION OF ACTIVITY

Prey typically reduce activity via reduced movement, increased refuging, or both, upon an encounter with a predator (Table II). An animal must, of course, resume its normal activity at some point. The period of reduced activity may range from a few seconds in hermit crabs (Scarratt and Godin, 1992) to several days in small mammals (Jedrzejewski and Jedrzejewska, 1990; Kotler, 1992; Saarikko, 1992). However, despite the many activity-related studies in Table II, there is relatively little work on the factors affecting an animal's decision to resume activity.

One factor influencing the decision to resume activity is the nature of the predatory threat, with animals remaining inactive for longer periods in riskier situations (Scarratt and Godin, 1992; Sih, 1992a; Gotceitas and Godin, 1993; Johansson and Englund, 1995). Several recent studies also demonstrate that energetically stressed animals resume activity sooner than those well fed (Dill and Gillett, 1991; Gotceitas and Godin, 1991; Sih, 1992a; Koivula *et al.*, 1995). Moore (1994) found that birds in a migratory state (with large energy reserves and a need to acquire even more) were more eager to resume feeding than nonmigratory birds after exposure to a hawk.

Theoretical studies on the resumption of activity are few. However, Sih (1992a) provides a good theoretical discussion of the ways in which energetic stress and information combine to influence the postencounter resumption of activity in refuging prey. Stochastic dynamic programming could also be usefully applied to this temporal phenomenon, but apparently only one such model has been presented (Kålås *et al.*, 1995, dealing with the resumption of lekking following a predatory encounter). Johansson and Englund (1995) present a much-needed (but brief) game-theoretical perspective on the resumption of activity, which suggests that prey will generally outwait all but the most persistent predators.

B. PURSUIT-DETERRENCE SIGNALS

Upon detecting a predator, an animal may signal that (1) the predator has been detected, and (2) it is able to escape; such signals should deter further pursuit. This mutually beneficial form of communication between prey and predator (Hasson, 1991) should be subject to some form of cost-benefit analysis on the part of prey (Caro, 1995), but few studies have taken

such a perspective. Caro (1994) and Caro *et al.* (1995) provide exceptions in their thoughtful consideration of antipredator signaling in ungulates. Caro (1994) argues convincingly that much antipredator behavior in African ungulates is pursuit-deterrence signaling. Similarly, Caro *et al.* (1995) conclude that tail flagging in white-tailed deer (*Odocoileus virginianus*) functions as a pursuit-deterrence signal (see also Smith, 1991). The tail-flicking response of rails (Aves) to various aspects of predation risk also suggests that such behavior functions as a pursuit-deterrence signal (Alvarez, 1993). Furthermore, predator inspection behavior has been implicated as a form of pursuit-deterrence signaling in fish and mammals (see later discussion). On a theoretical note, Vega-Redondo and Hasson (1993) suggest that "honest" antipredator signaling can be evolutionarily stable depending on the processes by which predators and prey encounter each other.

C. FLIGHT INITIATION

Prey often allow a predator to approach up to a certain point (the flight initiation distance, FID) before initiating escape behavior. Several recent studies complement earlier work (see Ydenberg and Dill, 1986; Lima and Dill, 1990), suggesting that FIDs increase in riskier situations, and are thus the outcome of a cost-benefit analysis by prey. A good example of such decision making occurs in woodchucks (*Marmota monax*), which increase FIDs with an increase in the distance to the nearest refuge burrow (Bonenfant and Kramer, 1996) and when the predator approaches from the side opposite such a refuge (Kramer and Bonenfant, 1997); these studies complement similar work on tree squirrels (Dill and Houtman, 1989). Fish may increase their FID when far from a refuge (Dill, 1990) or when in smaller groups (Abrahams, 1995). Bulova (1994) also found a positive relationship between distance to refuge and FID in two iguanid lizards, and (surprisingly) a tendency toward shorter FIDs when approached directly by a predator (as opposed to a more tangential approach).

There are still few studies examining nonpredatory influences on decisions regarding flight initiation. However, Scrimgeour and Culp (1994a) and Scrimgeour *et al.* (1994) found that FIDs in mayflies were shorter in patches with a better food supply. Gravid female lizards may have lower FIDs than nongravid females, perhaps reflecting the former's relative inability to flee from predators (Braña, 1993).

D. CHOICE OF ESCAPE BEHAVIOR

Animals generally have several escape options and may perform various escape maneuvers at differing intensities. Legault and Himmelman (1993)

showed that the intensity of evasive behavior in several molluscs and echinoderms varied positively with the danger posed by an encounter with a starfish; these results imply a cost to escalated escape behavior, but the nature of this cost was not clear. Dill *et al.* (1990) found that alarmed aphids were less likely to drop off high-quality plants than poor-quality plants, and suggested that aphid escape behavior is a function of both lost feeding opportunities (post-escape) and mortality associated with the extreme escape option of dropping off a plant. However, Stadler *et al.* (1994) found that aphids drop off plants *more* readily under better feeding conditions; this contradiction may be related to reproductive considerations. In related work, Cartar (1991) found that threatened worker bumblebees were relatively unlikely to initiate escape maneuvers (i.e., cease feeding) when their colony was under energetic stress. Finally, badgers faced with a dangerous predatory encounter choose the nearest available burrow for escape; they may seek a more distant but safer burrow with a lesser threat (Butler and Roper, 1994).

E. APPROACHING AND INSPECTING PREDATORS

There are many possible benefits and costs associated with the odd behavior of approaching predators, many of which are discussed by Dugatkin and Godin (1992a) in a wide-ranging review. Here, I focus my attention on the phenomenon of "predator inspection" by fish, which has received much attention in recent years.

Predator inspection by fish usually involves one or more fish breaking away from a larger group to approach a predator (Dugatkin and Godin, 1992a). Such inspections may serve to gain information about the type of predator encountered (Magurran and Girling, 1986) or the predator's readiness to attack (Licht, 1989). Dugatkin (1992) demonstrates a mortality cost to such behavior (but see Godin and Davis, 1995), and evidence suggests that inspectors assess these costs when approaching a predator. For instance, inspectors approach more closely when in larger groups, avoid a moving predator, and approach preferentially the tail end of the predator (Pitcher *et al.*, 1986; Magurran and Seghers, 1990a; Dugatkin and Godin, 1992b). Larger fish, with presumably better escape abilities, may inspect more closely (Külling and Milinski, 1992) than smaller individuals. Energetically stressed fish may also inspect more than others, presumably because such fish must feed and thus have a greater need for information on predation risk (Godin and Crossman, 1994; McLeod and Huntingford, 1994). Predator inspection may also serve as a form of pursuit-deterrence signaling (Magurran, 1990; Godin and Davis, 1995; see also FitzGibbon, 1994, for a possible mammalian example).

A great deal of controversy surrounds the related claims that (1) pairs of inspecting fish are caught in the “prisoner’s dilemma,” and (2) such fish engage in a strategy of conditional cooperation resembling the tit-for-tat (TFT) strategy of Axelrod and Hamilton (1981). Evidence in favor of TFT cooperation suggests that inspecting fish exhibit the sort of reciprocation, retaliation, and forgivingness that one might expect in a TFT-like strategy (Milinski, 1987; Dugatkin, 1988; Milinski *et al.*, 1990a,b; Dugatkin and Alfieri, 1991a,b; Huntingford *et al.*, 1994; see also Pitcher, 1992; Chivers *et al.*, 1995b). Evidence against such a strategy suggests that inspectors may not be caught in the prisoner’s dilemma in the first place (and thus the TFT strategy would not apply; Magurran and Nowak, 1991; Murphy and Pitcher, 1991; Magurran and Seghers, 1994; Godin and Davis, 1995; Stephens *et al.*, 1997). I cannot resolve this controversy, but much work clearly remains to be done regarding the nature of predator inspection.

V. SOCIAL SITUATIONS

A. ADAPTIVE SOCIALITY

Decision making by individuals ought to influence the nature of sociality under the risk of predation (e.g., Pulliam and Caraco, 1984). The last few years have seen considerable progress in the study of such decision making, but there are still surprisingly few studies in this area (see also Lima and Dill, 1990; Krause, 1994b). Recent years have also seen advances in the comparative study of predation and sociality (notably in primates; e.g., Boesch, 1991; Cowlishaw, 1994; van Schaik and Hörstermann, 1994; Stanford, 1995), but such work is outside the scope of this review.

1. *Spatial Position in Groups*

Fish may seek out the innermost (safest) area in a group when threatened by predators (Krause, 1993b). However, energetically stressed fish (Krause *et al.*, 1992; Krause, 1993a) and aquatic beetles (Romey, 1995) may seek better feeding opportunities at their group’s (risky) periphery. A similar “spatial conflict” between feeding and safety may influence the location of web-building spiders within the larger colony (Rayor and Uetz, 1990, 1993). Krause (1994b) provides a cogent review of these and related studies on spatial positioning in social animals.

2. *Choice of Group*

Larger groups should provide greater safety from predators than smaller ones, all else being equal. Accordingly, fish given a choice prefer larger

groups, especially when under a heightened risk of predation (Hager and Helfman, 1991; Ashley *et al.*, 1993; Krause and Godin, 1994). Startled fish may also join the largest available group, unless this group is much farther away than a nearby, smaller group (Tegeder and Krause, 1995). A larger group in a risky area may also be avoided (Ashley *et al.*, 1993), and a preference for larger groups may be overridden by a preference for individuals of a similar size (Krause and Godin, 1994; see also later discussion). Krause and Godin (1995) found that large groups of fish may suffer more attacks, but argue that prey are still better off in large groups (see also Wrona and Dixon, 1991; Uetz and Hieber, 1994). Pöysä (1991) suggests that a duck's choice of group may *not* be influenced by the risk of predation, although these ducks may have realized that the predator in question was not much of a threat.

An SDP model by Szekely *et al.* (1991) suggests that energetically stressed birds should be less social (to avoid competitors) than those better fed. I know of no studies testing this prediction in birds, but Romey and Rossman (1995) describe such an effect in aquatic beetles. Paveri-Fontana and Focardi (1994) developed a model of optimal herd size selection in ungulates; they related the results to various ecological processes, but the model's predictions for sociality *per se* were unclear.

3. Size-Assortative Grouping

A small individual in a group of large individuals (or vice versa) may be conspicuous to predators and thus suffer a greater risk of attack (Wolf, 1985; Theodorakis, 1989). Such an effect may explain why fish in a group associate preferentially with others of their size under a heightened risk of predation (Theodorakis, 1989; Ranta *et al.*, 1992a,b; Krause, 1994a; Krause and Godin, 1994). However, under such conditions larger fish may aggressively occupy the group's central position, and thus preclude the intermingling of size classes irrespective of any effect of conspicuousness *per se* (Theodorakis, 1989; Krause, 1994a).

B. VIGILANCE

Many animals face a constant conflict between the need to be alert for attack and the need to feed. A ubiquitous observation is that individuals become progressively less vigilant (alert) as group size increases (see Elgar, 1989, for a benchmark review). This "group size effect" is seen as an outcome of the fact that individual group members can devote less time to vigilance (i.e., more time to feeding) with increasing group size without detracting from the group's collective ability to detect attack (Elgar, 1989).

Interest in antipredatory vigilance has remained high in recent years, and has entered a period of retrospection and reassessment of old ideas. Insightful theory (Packer and Abrams, 1990; McNamara and Houston, 1992) and empirical studies (Krause and Godin, 1996) have elucidated some key issues in the maintenance of social vigilance in selfish animals. Refinements and challenges to the basic concept of collective detection have appeared (Lima and Zollner, 1996; Roberts, 1996). The group size effect itself has received better documentation (e.g., Roberts, 1995). Behavioral sequences involving vigilance have received much needed attention (Desportes *et al.*, 1989; Roberts, 1994). Some exceptional observational studies of predator-prey interactions shed further light on social vigilance (e.g., Cresswell, 1994a). These studies and other developments have been reviewed by Roberts (1996).

VI. REPRODUCTION

Sih (1994) summarizes the current state of affairs with regard to reproductive decision making under the risk of predation: "Although predation risk is often viewed as an important component . . . of the evolution of mating behavior, . . . little effort has gone into gaining a deep, ecologically-rooted understanding of how predation risk influences reproductive behavior." A similar sentiment is expressed in Lima and Dill (1990), Magnhagen (1991, 1993), and Reynolds (1993). Recent years have nonetheless seen considerable progress in understanding such reproductive behavior in many contexts. I review this work below, and in keeping with my overall theme, I focus on the management of predator-induced stress in ecological time. Sih (1994) provides an excellent discussion of the more general evolutionary and ecological aspects of reproductive behavior. I should note that "stress" in this section refers ultimately to a loss of reproductive output, which may or may not reflect a more standard form of stress (e.g., energetic) on the animal in question.

A. MATE CHOICE

Crowley *et al.*'s (1991) ground-breaking model of mate choice suggests that females should become less choosy with an increase in the risk of predation associated with locating mates. In other words, a given class of males will enjoy a diminished mating advantage under a high risk of predation. This prediction is supported by observations of predator-induced random mate choice in fish (Forsgren, 1992; Berglund, 1993). Godin and Briggs (1996) also report a predator-induced lowering of female choosiness in

guppies, but only in females from high-risk streams (but mate choice copying by such guppies may not be influenced by predation risk, Briggs *et al.*, 1996). Similarly, the mating advantage enjoyed by longer-calling male crickets may be overridden if females can approach short-calling males in relative safety (Hedrick and Dill, 1993). On the other hand, large male water striders enjoy an *increased* mating advantage under a high risk of predation (Sih *et al.*, 1990; Sih and Krupa, 1992, 1995, 1996). This unusual result may reflect the female-harassment-based mating system in water striders (Krupa and Sih, 1993). Under a heightened risk of fish predation, males harass females less (i.e., become less active), which may then allow females to be more selective in their choice of mates or avoid mating altogether.

B. ALTERNATIVE MALE MATING TACTICS

Male guppies may court females via conspicuous visual displays, or attempt "sneaky" forced copulations. Endler (1987) found that male guppies attempted more sneaky copulations in the presence of predators. Similar results have been reported in captive (Magurran and Seghers, 1990b) and free-living guppies (Godin, 1995). It is perhaps intuitive that male guppies would adopt the less conspicuous "sneaker" strategy in risky situations (see also Lucas and Howard, 1995; Lucas *et al.*, 1996), but sneaky males may also be taking advantage of a female's preoccupation with predator inspection in the presence of predators (Magurran and Nowak, 1991; Godin, 1995). One might envision other scenarios of predator-induced flexibility in alternative male mating tactics, but there appear to be no other reported cases. However, Magnhagen (1995) found that the riskier tactics used by sneaker and territorial common gobies (*Pomatoschistus microps*) are used less frequently in the presence of predatory fish.

C. MATING DYNAMICS

The act of mating itself may be influenced by the risk of predation. For instance, Travers and Sih (1991) found that male semiaquatic hemipteran insects accept lowered mating success under a high risk of predation by spending less time in tandem (copulating) with a female; tandem pairs make tempting targets for predators (Sih, 1988). Sih and Krupa (1995, 1996) also found a decrease in mating duration and frequency in water striders in the presence of fish, presumably at some reproductive cost to males; tandem pairs once again are at greater risk than singletons (Fairbairn, 1993; Rowe, 1994). Razorfish (*Xyrichtys splendens*) spawn closer to the (safe) sea floor in high-risk situations, which may limit the dispersal success of

resulting zygotes (Nemtzov, 1994). Finally, copulation frequency and number in pipefish (*Syngnathus typhle*) may decrease in the presence of predators (Berglund, 1993; Fuller and Berglund, 1996), but copulation time may increase to compensate (Berglund, 1993).

D. COURTSHIP

Conspicuous activities associated with courtship can lead to a higher risk of predation for males (Lima and Dill, 1990; Magnhagen, 1991). Hence, one might expect lowered courtship activity in the presence of predators. This has been observed in several fish species (Endler, 1987; Berglund, 1993; Forsgren and Magnhagen, 1993; Nemtzov, 1994; Chivers *et al.*, 1995c). Area-specific differences in courtship activity by male fish may also be determined by the local abundance of predators (Hastings, 1991); Lister and Aguayo (1992) suggest that similar effects occur in lizards. Predators may also inhibit courtship and spermatophore deposition by male salamanders (Uzendoski *et al.*, 1993). Following a predatory disturbance, the resumption of courtship chorusing by male frogs is quicker in larger groups, perhaps reflecting a greater dilution of risk in such groups (Jennions and Blackwell, 1992).

E. OVIPOSITIONAL BEHAVIOR

Mating dragonflies are sensitive to the presence of frogs in their choice of oviposition sites (e.g., Michiels and Dhondt, 1990). However, dragonflies appear unable to detect frogs lying in ambush (Rehfeldt, 1992). This inability may explain why dragonflies are attracted to groups of ovipositing pairs, as such groups form only in the absence of frog attacks (Rehfeldt, 1990, 1992).

Regarding theory, Mangel (1989) and Weisser *et al.* (1994) developed models of optimal ovipositional behavior by parasitoids searching in dangerous, patchy environments (see also Iwasa *et al.*, 1984). The results suggest that optimal patch residence times should be sensitive to the risk of mortality experienced by ovipositing females. These models challenge the standard view that parasitoids should act only to maximize their rate of oviposition, but I know of no explicit tests of their predictions.

F. PREGNANCY AND PARENTING

Observational evidence suggests that pregnant or lactating ground squirrels (MacWhirter, 1991) and bighorn sheep (Berger, 1991) take greater risks in order to meet the energetic stresses of mammalian reproduction.

In contrast, egg-carrying marine copepods avoid food-rich surface waters (Bollens and Frost, 1991); their opaque eggs make them vulnerable to detection by surface-feeding fish, even at night.

Nest building and defense by male fish may also be predation-risk dependent. Magnhagen (1990) showed that nest building by male black gobies (*Gobius niger*) diminished in the presence of predators. The lack of such an effect in sand gobies (*Pomatoschistus minutus*) was attributed to their brief life-span (Magnhagen, 1990), which puts a premium on reproducing as soon as possible. Magnhagen and Vestergaard (1991) found that male common gobies took greater risks to defend their broods as their young matured (and presumably became more vulnerable); Magnhagen (1992) provides a general review of brood defense and parental risk taking in fish.

Surprisingly few studies on nestling provisioning in birds consider risk to the parent to be an important determination of parental behavior (Ydenberg, 1994). However, Harfenist and Ydenberg (1995) suggest that rhinoceros auklet (*Cerorhinca monocerata*) chicks fledge younger and at lower body mass in areas frequented by eagles because parents terminate feeding earlier in high-risk areas. Such a decision is in accord with the predictions of Clark and Ydenberg (1990a,b).

G. BREEDING SUPPRESSION

A growing body of work, focused almost exclusively on small boreal mammals (but see Fraser and Gilliam, 1992), addresses the issue of predation risk and the decision to engage in reproduction. Ylönen (1989) first reported that bank voles (*Clethrionomys glareolus*) strongly suppress reproduction upon exposure to mustelid predators. Similar degrees of breeding suppression have been observed in several other laboratory experiments on bank voles (Ylönen *et al.*, 1992; Ronkainen and Ylönen, 1994; Ylönen and Ronkainen, 1994), other *Clethrionomys* voles (Ylönen *et al.*, 1992; Heikkilä *et al.*, 1993), and *Microtus* voles (Koskela and Ylönen, 1995). Korpimäki *et al.* (1994) also demonstrate long-term breeding suppression in bank voles under field conditions.

The mechanism behind this breeding suppression is not well understood. However, female *Clethrionomys* voles aggressively avoid male advances upon exposure to the scent of mustelid predators (Ylönen and Ronkainen, 1994; Ylönen, 1994). Male *Microtus* voles may themselves show less sexual activity in high-risk situations (Koskela and Ylönen, 1995). Energetic stress resulting from reduced feeding under high-risk conditions may also be involved (Heikkilä *et al.*, 1993) in suppressing breeding. Research into the estrous cycle of voles suggests that the mechanism behind breeding suppression has a strong physiological component (Koskela *et al.*, 1996).

This physiological link might conceivably relate to the negative effects of physiological/neuroendocrine stress (caused by exposure to predators) on reproduction (Weiner 1992). Hansson (1995) suggests that reproduction in some boreal voles may be sensitive to physiological stress of any sort, not just that induced by predators.

VII. LONG-TERM CONSEQUENCES OF DECISION MAKING

Most studies on antipredatory decision making accept the idea that any decision has associated with it both a fitness cost (some form of predator-induced stress) and benefit (avoiding an early death). How much do we really know about these issues?

There are now several studies demonstrating that antipredator decision making does indeed lower an animal's risk of predation (as per examples mentioned throughout this review). However, such benefits of antipredator decision making remain a presumption in many research programs, especially those involving terrestrial vertebrates. It is thus perhaps disturbing that a few studies have found antipredator responses to be inadequate in some way. For instance, strong refuging behavior in larval salamanders can be inadequate as a defense against fish predators (Sih *et al.*, 1988; Sih, 1992b); a similar scenario is apparent in an amphipod predator–prey system (Sparrevik and Leonardsson, 1995). McPeek (1990), Werner and McPeek (1994), and Skelly (1995) report cases in which reduced activity in the presence of predators failed to prevent predation; however, these cases involved a lack of coevolutionary history between predator and prey.

Demonstrations of the long-term costs of antipredator behavior are relatively uncommon. Recent years have nevertheless witnessed considerable progress in identifying and quantifying these costs (Table III). A common theme in this work is that antipredator decisions that lower risk (usually habitat shifts or decreased activity) also lead to some form of energetic stress, typically manifest in lower growth rates. Slower growth may lead to a smaller size at maturity (Skelly and Werner, 1990) or prolonged development (Skelly, 1992). Exceptionally complete analyses of such predator-induced stress, covering growth, development, and fecundity, have been possible in mayflies (Peckarsky *et al.*, 1993; Scrimgeour and Culp, 1994b) and chironomids (Ball and Baker, 1995, 1996). These insects have nonfeeding adult life stages, and thus reduced larval growth translates directly into reduced adult fitness (see also Feltmate and Williams, 1991; but see Duvall and Williams, 1995, for a more complicated situation in stoneflies). It is possible that a smaller size at maturity may reflect not only predator-induced stress but also a predator-induced change in life history. There is,

TABLE III
RECENT EXPERIMENTAL DEMONSTRATIONS OF A LONG-TERM COST OF ANTI-PREDATOR DECISION MAKING

Prey	Predator ^a	Prey response	Conditions	Cost	Source
Invertebrates					
Chironomid larvae (<i>Chironomus tentans</i>)	Fish P	Reduced activity	Laboratory	Slower growth and development, lower adult mass at emergence, fewer eggs	Ball and Baker (1995, 1996)
Cladoceran spp.	Copepod P,C	Reduced activity (?)	Laboratory	Slower growth	Gliwicz (1994)
Water flea (<i>Daphnia magna</i>)	Fish C	Vertical migration	Laboratory	Deeper migrants experience slower growth	Dawidowicz and Loose (1992); Loose and Dawidowicz (1994)
Damselfly larvae (<i>Ischnura verticalis</i>)	None	Reduced activity	Laboratory	Simulated predator-induced reduction in feeding slows growth and development	Dixon and Baker (1988)
Ant (<i>Lasius pallitarsis</i>)	Large ant P	Reduced activity	Laboratory	Slower colony growth	Nonacs and Dill (1990)
Dogwhelk (<i>Nucella lapillus</i>)	Crab C	Reduced activity	Laboratory	Slower (or zero) growth	Palmer (1990)
Mayfly larvae (<i>Baetis bicaudatus</i>)	Stonefly P	Escape-induced loss of feeding	Semifield	Adults emerge at lower mass, with fewer eggs (no effect on development time)	Peckarsky <i>et al.</i> (1993)
Marine snail (<i>Stramonita haemastoma</i>)	Crab P	Reduced activity	Laboratory	Slower growth	Richardson and Brown (1992)
Mayfly larvae (<i>B. tricaudatus</i>)	Model fish P	Reduced activity	Laboratory	Slower growth, lower adult mass, longer development, fewer and smaller eggs	Scrimgeour and Culp (1994b)

Buckmoth larvae (<i>Hemileuca lucina</i>)	Wasp P	Microhabitat shift	Semifield	Slower growth	Stamp and Bowers (1991)
Copepod (<i>Eurytemora hirundoides</i>)	None	Vertical migration	Laboratory	Simulated vertical migration leads to longer development	Vourinen (1987)
Vertebrates					
Juvenile perch (<i>Perca fluviatilis</i>)	Fish P	Habitat shift	Semifield	Slower growth (due to increased competition)	Diehl and Eklöv (1995)
Salamander larvae (<i>Ambystoma maculatum</i>)	Fish P	Reduced activity	Laboratory	Slower growth	Figiel and Semlitsch (1990)
Guppy (<i>Poecilia reticulata</i>)	Fish P	Reduced activity, habitat shift	Field	Reduced egg production and growth	Fraser and Gilliam (1992)
Juvenile roach (<i>Rutilus rutilus</i>)	Fish P	Habitat shift	Semifield	Slower growth	Persson and Eklöv (1995)
Toad larvae (<i>Bufo americanus</i>)	Larval odonate P	Reduced activity	Laboratory	Metamorphose at smaller size	Skelly and Werner (1990)
Tree frog larvae (<i>Hyla versicolor</i>)	Salamander P	Reduced activity	Semifield	Slower growth and development	Skelly (1992)
Tree frog larvae (2 <i>Pseudacris</i> spp.)	Larval odonate P	Reduced activity	Laboratory	Slower growth	Skelly (1995)
Crucian carp (<i>Carassius carassius</i>)	Fish P	Habitat shift	Field	Slower growth (due to increased competition)	Tonn <i>et al.</i> (1992)

^a P, predator present; C, chemical scent of predator.

however, no clear evidence for such adaptive life-history changes (Skelly and Werner, 1990; Ball and Baker, 1996).

The current emphasis on predator-induced reductions in growth rates is entirely appropriate as most animals develop as free-living organisms for whom successful reproduction means reaching adult size (cf. Werner and Gilliam, 1984). However, for many birds and mammals, growth is often largely complete before they strike out on their own. For such creatures, the stress resulting from antipredator behavior is probably manifest in decreased body condition (e.g., Hik, 1995; Sinclair and Arcese, 1995), leading ultimately to lower female fecundity or male competitive ability. Such costs may also be manifest in energetic stress experienced by young being provisioned by parents attempting to avoid predation (Harfenist and Ydenberg, 1995).

The survival-growth/reproduction trade-offs apparent in Table III seem adaptive, given that an early death is the likely alternative to incurring some form of predator-induced stress. However, the degree to which "adaptive" approximates "optimal" is unknown. This should come as no surprise, given our inability to quantify many aspects of predation risk (see Section II,E). Perhaps Nonacs and Dill (1990) come closest to making this distinction. They estimated the benefits to an ant colony from extra foraging and the cost of losing workers to predators, and found that the risks taken by workers reflected the potential increase in colony growth as a result of extra foraging.

VIII. ECOLOGICAL INFLUENCES AND IMPLICATIONS

Decision making under the risk of predation can influence the nature of ecological systems. Understanding these influences has long been a major driving force in the study of antipredator decision making (Sih, 1980; Werner *et al.*, 1983). Here, I discuss recent work in this area within three main contexts: the use of space by individuals, population-level consequences, and species interactions. This work involves mostly field or semifield experimentation. Although often not achieving the controlled rigor of laboratory experimentation, this work nevertheless illustrates the potential ecological effects of predator-induced stress and antipredatory decision making.

A. USE OF SPACE

Table IV summarizes studies indicating that predators have a pervasive effect on the use of space by a variety of animals. This work adds to the many (but far fewer) studies on the use of space discussed in Lima and

TABLE IV
RECENT STUDIES EXAMINING THE USE OF SPACE UNDER THE RISK OF PREDATION

Prey	Predator ^a	Scale ^b	Results	Source
Invertebrates				
Chironomid larvae (<i>Chironomus tentans</i>)	Fish	m	No preference for predator-free areas (main response involved lower activity)	Baker and Ball (1995)
Juvenile crayfish (<i>Pacifastacus leniusculus</i>)	Fish, adult crayfish	m	No consistent preference for safer microhabitats	Blake <i>et al.</i> (1994)
Mayfly larvae (<i>Baetis bicaudatus</i>)	Fish C	m	Avoid profitable but risky feeding locations	Cowan and Peckarsky (1994)
Stonefly larvae (<i>Paragnetina media</i>)	Fish	m	Strong preference for color-matching substrate, (undiminished in absence of predator)	Feltmate and Williams (1989b)
Epibenthic invertebrates (several spp.)	Fish	M	Choose areas rich in refuges (woody debris)	Everett and Ruiz (1993)
Mayfly larvae (<i>B. tricaudatus</i>)	Fish	m	Avoid profitable but risky feeding locations	Kohler and McPeek (1989)
Damselfly larvae (<i>Ischnura verticalis</i>)	Fish	m	Strong preference for dark (safe) substrates, which may be enhanced in the presence of predators	Moum and Baker (1990)
Whelk (<i>Buccinum undatum</i>)	Starfish	m, M	m: attracted to feeding starfish M: avoid areas with abundant starfish	Rochette <i>et al.</i> (1995)
Isopod (<i>Saduria entomon</i>)	Large isopod	m	Avoid areas with abundant predators	Sparrevik and Leonardsson (1995)
Juvenile lobster (<i>Homarus americanus</i>)	Fish, crab	m, M	Predator-induced preference for safe, cobble substrate	Wahle and Steneck (1992)
Hermit crabs (<i>Clibanarius</i> , <i>Pagurus</i> spp.)	Crab C, alarm substance	m	Crabs with ill-fitting shells seek areas with recently killed shell occupants; other crabs flee such areas	Rittschoff <i>et al.</i> (1992)
Fish				
Roach (<i>Rutilus rutilus</i>)	Fish	M	Shift from pelagic to littoral zone after predator introduction	Brabrand and Faafeng (1993)
Stream fish (4 spp.)	Fish	m, M	Juveniles and smaller species shift to shallow water at both micro- and macroscales	Brown and Moyle (1991)
Bluegill and shad (<i>Lepomis</i> and <i>Dorosoma</i> spp.)	Fish	m	Only bluegill shift to shallow water in presence of predator	De Vries (1990)

(continued)

TABLE IV (Continued)

Prey	Predator ^a	Scale ^b	Results	Source
Juvenile perch (<i>Perca fluviatilis</i>)	Fish	m, M	m: remain close to refuge in presence of predator M: avoid profitable but risky refuge-poor habitats	Diehl and Eklöv (1995); Eklöv and Diehl (1994); Persson and Eklöv (1995)
Perch and rudd (<i>Perca</i> and <i>Scardinius</i> spp.)	Fish	M	Species segregate into pelagic vs littoral habitats based in part on vulnerability to predator	Eklöv and Hamrin (1989)
Perch and roach (<i>Perca</i> and <i>Rutilus</i> spp.)	Large perch	m, M	m: remain close to refuge in presence of predator M: prefer refuge-rich habitat in presence of predator	Eklöv and Persson (1995); Christensen and Persson (1993); Persson (1991, 1993)
Small stream fish (<i>Rivulus</i> and <i>Poecilia</i> spp.)	Fish	M	Avoid stream pools with predators; move to riffles	Fraser and Gilliam (1992)
Killifish (<i>Rivulus hartii</i>)	Fish	m, M	Fish avoid streams populated by predators	Fraser <i>et al.</i> (1995)
Juvenile salmon (<i>Oncorhynchus tshawytscha</i>)	Bird, fish	m	Prefer deeper water under nonturbid conditions	Gregory (1993)
Juvenile cod (<i>Gadus morhua</i>)	Large cod	m	Predator-induced preference for safe, cobble substrate	Gotceitas and Brown (1993)
Sculpin (<i>Cottus bairdi</i>)	Fish	m	Microhabitat use unaffected by predator presence	Grossman <i>et al.</i> (1995)
Small stream fish (mainly juv. <i>Lepomis</i>)	Fish	m, M	m: shift to shallow water in presence of predator M: avoid pools with predators	Harvey (1991)
Small, soft-rayed fish (4 spp.)	Fish	M	Much emigration from lake (into outlet stream) following predator introduction	He and Kitchell (1990)
Stickleback (<i>Gasterosteus aculeatus</i>)	Fish	m	Stay close to bottom in presence of predator	Ibrahim and Huntingford (1989)
Bleak (<i>Alburnus alburnus</i>)	Fish, alarm substance	m	Preference for vegetated habitats is enhanced by predators and diminished by food in open water	Jachner (1995a,b)
Arctic charr (<i>Salvelinus alpinus</i>)	Fish	M	Ontogenetic shift to pelagic habitat is delayed under risky conditions	L'Abée-Lund <i>et al.</i> (1993)
Fathead minnow (<i>Pimephales promelas</i>)	Alarm substance	m	Avoid areas marked with alarm substance	Mathis and Smith (1992); Chivers <i>et al.</i> (1995a)

Perch (<i>P. fluviatilis</i>)	Fish	M	Choice of littoral (safe) or pelagic zone of lake determined by presence of non-gape-limited predator	Persson <i>et al.</i> (1996)
Small fish (several spp.)	Fish, crab	M	Preference for shallow water reflects risk in deep water	Ruiz <i>et al.</i> (1993)
Juvenile pollock (<i>Theragra chalcogramma</i>)	Large pollock	m	Predator-induced preference for vegetated habitats	Sogard and Olla (1993)
Mosquitofish (<i>Gambusia holbrooki</i>)	Fish	m	Larvae may avoid adult cannibals by associating with predators that are avoided by adults	Winkleman and Aho (1993)
Brook stickleback (<i>Culaea inconstans</i>)	Alarm substance	m	Avoid areas marked with alarm substance	Wisenden <i>et al.</i> (1994)
Amphibians and Reptiles				
Salamander larvae (<i>Ambystoma barbouri</i>)	Fish	m, M	m: predator-induced preference for shallow water M: avoidance of pools with predators	Sih <i>et al.</i> (1992)
Salamander larvae (2 <i>Ambystoma</i> spp.)	Large salamander	m	Shift to deeper water in presence of predator (one species only)	Walls (1995)
Birds				
Himalayan snowcock (<i>Tetraogallus himalayensis</i>)	Eagle	m, M	Escape tactic may constrain birds to steep terrain	Bland and Temple (1990)
Redshank (<i>Tringa totanus</i>)	Raptors	m, M	m: juveniles feed in risky, profitable microhabitats M: prefer less profitable but safe habitat (mussel beds)	Cresswell (1994b)
Titmice (2 <i>Parus</i> spp.)	Raptor	m	Feed in open (away from vegetation) only when forced to do so by aggression	Hinsley <i>et al.</i> (1995)
Willow tit (<i>P. montanus</i>)	Raptors	m	Feed in open only when forced to do so by aggression	Koivula <i>et al.</i> (1994)
Sparrows (2 emberizid spp.)	Raptors	m, M	Willingness to feed in open related to escape tactic	Lima (1990a)
Anna's hummingbird (<i>Calypte anna</i>)	Terrestrial birds	m	Avoid profitable feeding opportunities close to ground	Lima (1991)
Small granivores (7 spp., mostly emberizids)	Raptors	M	Large-scale habitat choice influenced by escape tactics	Lima and Valone (1991)

(continued)

TABLE IV (Continued)

Prey	Predator ^a	Scale ^b	Results	Source
Downy woodpecker (<i>Picoides pubescens</i>)	Raptors	m	Choice of feeding site reflects vigilance–escape trade-off	Lima (1992)
Brambling (<i>Fringilla montifringilla</i>)	Raptors	M	Prefer forest habitat over profitable but risky open habitat	Lindström (1990)
Duck (<i>Anas penelope</i>)	Raptors, humans	m	Reluctant to feed far from water (refuge)	Mayhew and Houston (1989)
Sparrows (3 emberizid spp.)	Raptors	m	Avoid open areas, even those with high food density (except one sp.)	Repasky and Schluter (1994)
Small granivores (several spp., old-world granivores)	Raptors	m	General avoidance of relatively profitable but open areas	Schluter (1988)
White-crowned sparrow (<i>Zonotrichia leucophrys</i>)	Raptors	m	Feed in open only when forced to do so by aggression	Slotow and Rothstein (1995)
Titmice (2 <i>Parus</i> spp.)	Raptors	m	Feed in open only when forced to do so by aggression	Suhonen (1993a,b; Suhonen <i>et al.</i> (1993))
Small birds (several spp., mostly passerines)	Raptors	M	Small (vulnerable) species avoid nesting in vicinity of (up to 1 km or more from) falcon nests	Suhonen <i>et al.</i> (1994)
Blue tit (<i>P. caeruleus</i>)	Raptors	m	Avoid profitable but open (risky) feeding sites	Todd and Cowie (1990)
Sparrows (2 emberizid spp.)	Raptors	m, M	Choice of feeding location influenced by escape tactics	Watts (1990)
Savannah sparrow (<i>Passerculus sandwichensis</i>)	Raptors	m	Reluctant to feed far from vegetated refuge	Watts (1991)
Mammals: Rodents				
Gerbils (2 <i>Gerbillus</i> spp.)	Owls	m	Avoid open (nonvegetated) areas when risk is increased under field conditions	Abramsky <i>et al.</i> (1996)
Kangaroo rat (<i>Dipodomys merriami</i>)	Owls (?)	m	Avoid profitable but risky open microhabitats	Bowers (1990)

White-footed mouse (<i>Peromyscus leucopus</i>)	Mammals, raptors	m, M	Avoid feeding opportunities in open habitats	Bowers and Dooley (1993)
Squirrels (<i>Sciurus</i> and <i>Tamias</i> , 2 spp.)	Raptors	m	Avoid profitable but risky open microhabitats	Bowers <i>et al.</i> (1993)
Kangaroo rats (2 <i>Dipodomys</i> spp.)	Snakes	m	Avoid feeding opportunities in vegetation that might be occupied by active snakes	Bouskila (1995)
Desert rodents (2 heteromyid, 1 sciurid)	Raptors (mainly)	m	Avoid open areas, but kangaroo rats are more likely to be in open habitat than other species	Brown (1989)
Crested porcupine (<i>Hystrix</i> <i>indica</i>)	Large mammals	m, M	Avoid profitable feeding opportunities in open habitats	Brown and Alkon (1990)
Fox squirrel (<i>S. niger</i>)	Raptors/mammals	m	Avoid profitable but risky open microhabitats	Brown <i>et al.</i> (1992a); Brown and Morgan (1995)
Gerbil (<i>G. allenbyi</i>)	Owls (?)	m (M?)	Perceive increased risk in rocky habitats, which are usually avoided	Brown <i>et al.</i> (1992b)
Guinea pig (<i>Cavia aperea</i>)	Raptors/mammals	m	Appear to perceive higher risk when away from vegetation	Cassini (1991); Cassini and Galante (1992)
Prairie dog (<i>Cynomys</i> <i>ludovicianus</i>)	Raptors	m	Avoid feeding far from refuge (burrow) unless feeding in groups	Devenport (1989)
House mouse (<i>Mus</i> <i>domesticus</i>)	Mammals	m, M	Seek out vegetated habitats under increased risk	Dickman (1992)
Gerbil (<i>G. tytonis</i>)	Raptors/mammals	m	Avoid profitable but risky open microhabitats	Hughes and Ward (1993); Hughes <i>et al.</i> (1994)
Field vole (<i>Microtus</i> <i>agrestis</i>)	Raptors/weasels	m	Avoid open areas in presence of kestrel, may avoid cover when in presence of weasels	Korpimäki <i>et al.</i> (1996)
Gerbils (2 <i>Gerbillus</i> spp.)	Owls	m	Avoid profitable but risky open microhabitats (can distinguish risk posed by different owl species)	Kotler (1992); Kotler <i>et al.</i> (1991, 1994a); Kotler and Blaustein (1995)
Gerbils (2 <i>Gerbillus</i> spp.)	Snakes	m	Avoid feeding opportunities in vegetation that might be occupied by active snakes	Kotler <i>et al.</i> (1992, 1993a,b)
Degu (<i>Octodon degus</i>)	Raptors	m	Appear to perceive higher risk when away from vegetation	Lagos <i>et al.</i> (1995a,b)
Desert rodents (4 heteromyids, 1 cricetid)	Owls	m	Avoid open areas, but kangaroo rats are more likely to be in open habitat than other species	Longland and Price (1991)

(continued)

TABLE IV (Continued)

Prey	Predator ^a	Scale ^b	Results	Source
Townsend's vole (<i>M. townsendii</i>)	Mammal C	m	Avoid feeding opportunities in open habitats	Merkens <i>et al.</i> (1991)
Desert rodents (2 heteromyids, 1 cricetid)	Snake	m	No consistent effect of snakes on use of space (on very constrained spatial scale)	Pierce <i>et al.</i> (1992)
Small rodents (5 spp., mostly cricetids)	Raptors	m	Avoid open areas (which may not be very profitable)	Simonetti (1989)
Ground squirrels (<i>Spermophilus</i> and <i>Tamias</i> , 2 spp.)	Raptors, mammals	m	Avoid profitable but risky open microhabitats; faster species feeds farther from cover	Smith (1995)
Porcupine (<i>Erethizon dorsatum</i>)	Mammals	m, M	Avoid feeding in open but more profitable habitats	Sweitzer and Berger (1992)
Mammals: Nonrodent				
Bighorn sheep (<i>Ovis canadensis</i>)	Large mammals	m, M	Pregnant sheep leave relative safety of steep terrain for better foraging	Berger (1991)
Hedgehog (<i>Erinaceus europaeus</i>)	Badger	M	May choose habitats in which predators are absent	Doncaster (1993, 1994)
Pika (<i>Ochotona collaris</i>)	Raptors, mammals	m	Avoid profitable but risky microhabitats away from refuge	Holmes (1991)
Ibex (<i>Capra ibex</i>)	Large mammals	m (M?)	Preference for cliffs over flat terrain may be due to increased perceived predation risk in latter habitat	Kotler <i>et al.</i> (1994b)
Jackrabbit (<i>Lepus californicus</i>)	Raptors/mammals	m	Perceive higher risk when away from vegetation	Longland (1991)
Buffalo (<i>Synacerus cafer</i>)	Lions	m, M	No clear indication that lions influence use of space, despite spatial variation in predation risk	Prins and Iason (1989)

^a C, chemical scent of predator only; otherwise predators were present in environment.

^b m, microscale; M, macroscale.

Dill (1990). In Table IV, the "microscale" category refers to an animal's use of its immediate surroundings, very often in the vicinity of a refuge from attack. The "macroscale" category is more difficult to specify, but refers to a scale at which changes in the use of space require a significant investment in movement. The absolute spatial scale of macro- and micro-habitat use is, of course, species-specific.

1. Invertebrates

Studies on invertebrates (Table IV) show a tendency for individuals to avoid risky micro- or macrohabitats, even if such habitats offer good feeding opportunities. Rochette *et al.* (1995) describe an unusual case in which whelks avoid predatory starfish on a macroscale, but feed close to prey-consuming starfish on a microscale; starfish occupied by prey consumption are not dangerous, and produce "scraps" on which whelks can feed. Similarly, hermit crabs with ill-fitting shells may be attracted to areas of recent predation on gastropods in an attempt to obtain a better fitting shell; individuals with proper-fitting shells often flee from such area (Rittschoff *et al.*, 1992).

Note that I have already reviewed the use of space by certain invertebrates in other contexts. For instance, diel vertical migration in zooplankton (see Section III,B) involves a macroscale change in the use of the water column. Nocturnal drift in stream-dwelling arthropods (Section III,B) also involves a macroscale change in location within a stream. Sih and Wooster (1994) and Wooster and Sih (1995) provide excellent reviews of drift behavior in stream animals and its consequences for local prey population regulation; subsequent work by Crowl and Covich (1994), Forrester (1994a,b), Rader and McArthur (1995), and Kratz (1996) will also interest anyone working in this general area.

Taking a different perspective, inadequate antipredator behavior may be a major determinant of the large-scale distribution of certain invertebrates. For instance, *Daphnia oregonensis* is largely absent from lakes occupied by a predator toward which its antipredator behavior is ineffective (Ramcharan and Sprules, 1991). Larval damselflies typical of fish-free ponds exhibit antipredator responses that are inadequate against the fish in permanent ponds, and vice versa (Blois-Heulin *et al.*, 1990; McPeek, 1990; McPeek *et al.*, 1996). Henrikson (1988) suggests similarly that inappropriate escape responses toward fish limit a libellulid dragonfly larva to fish-free lakes. Note, however, that these odonate larvae do not directly make decisions regarding their distribution among ponds or lakes; such decisions are made by ovipositing adults.

2. Fish

Many recent studies demonstrate that predators are a major determinant of the use of space by fish. At the microscale, fish tend to remain in or

near safe habitats (e.g., shallow water, vegetation, safe substrates), while at the macroscale they avoid predator-rich or refuge-poor habitats (Table IV; see also Sih, 1987; Lima and Dill, 1990; Milinski, 1993). Eklöv, Persson, and colleagues provide an unusually complete look at the use of space by small fish, which covers the spectrum from mechanistic studies of prey behavior (Eklöv and Persson, 1996) to field studies examining whole-lake phenomena (Persson *et al.*, 1996). Most fish-related studies in Table IV deal with lake systems, but the distribution of fish within and among stream pools is also influenced by predators (Brown and Moyle, 1991; Harvey, 1991; Fraser and Gilliam, 1992; see also Power *et al.*, 1985; Schlosser, 1987; but see Grossman *et al.*, 1995). Along these lines, Fraser *et al.* (1995) link small-scale decisions regarding the use of space to whole-drainage patterns in the distribution of killifish.

3. Amphibians and Reptiles

Work on the use of space by these animals has been limited (Table IV), and there is a clear need for work on reptiles. The few existing studies suggest that predator-induced effects in larval amphibians are similar to those seen in fish (see also Lima and Dill, 1990). Some studies also show that larval amphibians stay as far from predators as possible in small laboratory containers (e.g., Hews, 1988; Skelly and Werner, 1990), suggesting that their microhabitat use might be predation-risk dependent. Morey (1990) and Heinen (1993, 1994b) also found that frogs and toads, respectively, choose substrates against which they are most cryptic; this has obvious implications for the use of space under the risk of predation. On a large scale, some studies link inadequate antipredator behavior to the distribution of larval amphibians within streams (Sih, 1992b; Feminella and Hawkins, 1994) or among temporary versus permanent ponds (Kats *et al.*, 1988; Werner and McPeek, 1994). As in similar cases with invertebrates, however, the choice of temporary versus permanent ponds is made not by these larvae but by adults (Resetarits and Wilbur, 1989).

4. Birds

An emerging avian theme is that the use of space relative to vegetative cover is determined to a large extent by escape tactics (Lima, 1993). Birds with vegetation-dependent escape tactics are reluctant to feed far from vegetative cover (Table IV). Observations of raptor predation on birds confirm the adaptive nature of this reluctance to feed in the open (Watts, 1990; Suhonen, 1993a,b; Hinsley *et al.*, 1995). Although less well studied, birds with vegetation-independent tactics may avoid vegetative cover altogether (Lima, 1993).

Most avian studies take a microscale perspective (Table IV), but patterns at this scale may also translate to larger spatial scales (Lima and Valone, 1991; Watts, 1991). Bland and Temple (1990) describe a situation in which a bird's gravity-assisted, downhill escape tactic may explain its geographic restriction to mountainous terrain. Birds may enter macrohabitats not well suited to their escape tactics, or relatively risky macrohabitats, only (1) if forced to do so by aggression (e.g., Cresswell, 1994b), or (2) if such habitats offer exceptional foraging opportunities (e.g., Lindström, 1990). On a different note, the location of falcon nests may also influence the large-scale distribution of breeding passerines (Suhonen *et al.*, 1994).

5. Mammals

Recent work shows convincingly that small mammals (mostly rodents) avoid feeding far from protective cover (e.g., vegetation), even at the cost of forgoing high-quality feeding opportunities (Table IV). Thermophysiological stress in the open cannot account for the avoidance of open areas (Bozinovic and Simonetti, 1992; Sweitzer and Berger, 1992; Kotler *et al.*, 1993d; Bowers *et al.*, 1993; Lagos *et al.*, 1995a), but such effects deserve more attention. The strong attraction of woody vegetative cover for desert rodents can be reduced or reversed when such vegetation harbors predatory snakes (Table IV). In this regard, Kotler *et al.* (1992) and Korpimäki *et al.* (1996) note the possibility of "predator facilitation" in which the avoidance of vegetative cover makes prey more available to open-hunting predators (or vice versa; see also Daly *et al.*, 1992). Schooley *et al.* (1996) note furthermore that vegetation may present obstacles to escape and predator detection for some diurnal rodents, hence their preference for open areas.

Work on large mammals is sparse and mixed (Table IV). Predation risk may be a factor in the use of space by bighorn sheep (Berger, 1991) and ibex (Kotler *et al.*, 1994b), but perhaps not by African buffalo (Prins and Iason, 1989).

Work on the use of space by mammals usually focuses on small spatial scales (Table IV). Doncaster's (1993, 1994) work on hedgehogs provides a notable exception. It nevertheless seems likely that the ubiquitous microscale avoidance of open areas by small mammals (Table IV) will translate to larger spatial scales. In other words, habitats with little vegetative cover will probably be avoided by animals reluctant to forage away from such cover (see also Price *et al.*, 1994).

B. POPULATION-LEVEL CONSEQUENCES

Antipredatory decision making could in principle influence many aspects of prey population dynamics and regulation (e.g., Desy *et al.*, 1990; Chesson

and Rosenzweig, 1991; Schluter and Repasky, 1991; Sinclair and Arcese, 1995). This possibility is readily apparent given the long-term negative effects of predator-induced stress (Table III). However, translating behavioral decisions to their population-level consequences has proven difficult. Actually, the extent to which this is true depends on the scale of analysis. The influence of predators on *local* population dynamics can often be understood in terms of decisions affecting the large-scale distribution of animals (see previous section). Nevertheless, studies covering whole populations are unusual.

The "whole population barrier" has been broken by some experimental studies focusing on small lakes in which entire populations of predators and prey can be manipulated and monitored (although often with limited replication). He and Kitchell (1990) provide a particularly good case in point. They showed that the "crash" in the prey population following the introduction of pike into a lake was caused by a large-scale movement of prey fish out of the lake and into the outflow stream (see also He and Wright, 1992). Tonn *et al.* (1992) also performed a whole-lake manipulation of predators. In this case, predatory perch induced an almost exclusive use of the shallow (safe) littoral zone by young crucian carp. This led to a competitive bottleneck that ultimately limited recruitment to adult life stages relative to a control population (see also Diehl and Eklöv, 1995). Individuals surviving this bottleneck grew much larger than control fish after shifting to the competition-free pelagic zone. This scenario parallels that in Werner *et al.*'s (1983) landmark study in a bass–sunfish system. Recent work in similar systems suggests that such bottlenecks can alter the competitive relationship among prey species (Brabrand and Faafeng, 1993; see also next section). Furthermore, an understanding of these predator-induced bottlenecks can provide insight into the nature of stock-recruitment relationships of importance to fisheries management (Walters and Juanes, 1993).

Models of predator-prey population dynamics abound (Crawley, 1992), but very few incorporate adaptive antipredator behavior. Abrams (1993b) argues that most predator-prey models actually suffer from assumptions not easily supported by adaptive antipredator behavior. Ruxton (1995) found that adaptive antipredator behavior acts to stabilize otherwise oscillatory predator-prey population dynamics, complementing results from earlier modeling (Ives and Dobson, 1987). Crowley and Hopper (1994) present an extraordinary modeling attempt linking a stochastic-dynamic game between predator and prey to stock-recruitment curves and resulting population dynamics.

Predator-prey population cycling might also be influenced by antipredator decision making by prey. Hik (1995) presents evidence that energetic

stress following a predator-induced microhabitat shift by snowshoe hare (*Lepus americanus*) causes a lowering of hare reproductive output, which then hastens the decline and lengthens the recovery phase in the cyclic population dynamics of hare and their mammalian predators. Similarly, Ylönen (1994) and Oksanen and Lundberg (1995) suggest that predator-induced breeding suppression (see Section VI,G) hastens the crash phase in the cyclic population dynamics of boreal voles and their mustelid predators. Ylönen (1994) outlines the specific idea that breeding suppression represents an attempt by female voles to ride out (in a high-survival, nonreproductive state) the high-predation part of a population cycle, after which they and their offspring would have a better probability of survival. Lambin *et al.* (1995) leveled some harsh criticism against this idea regarding breeding suppression and vole population dynamics, claiming that many of its key assumptions are unsupported (especially the assumption of enhanced survivorship in nonreproductive females). Ylönen's idea still has considerable merit, but there is clearly a need for critical experimentation and quantitative modeling regarding the role of breeding suppression in predator-prey population dynamics.

C. SPECIES INTERACTIONS

Recent studies illustrate how antipredator decision making might influence species interactions. These studies emphasize the role of indirect interactions between predators and other species mediated by the predators' effect on the behavior of a third (transmitter) species (Abrams, 1995). Such indirect interactions have been termed higher order interactions (Werner, 1992) or trait-transmitted indirect effects (Abrams, 1995), but for clarity I will use the term behaviorally transmitted indirect effects.

Behaviorally transmitted indirect effects may act in a variety of ways to alter the outcome of interspecific competition (Werner, 1992). For example, similar refuging behavior under a high risk of predation may lead to one (transmitter) species excluding another from the refuges. This has the effect of leaving the lesser competitor exposed to greater *predation*, which may ultimately tip the competitive balance in favor of the transmitter species. Such a scenario may apply in fish-crayfish systems (Hill and Lodge, 1994; Söderbäck, 1994) and a fish-salamander-isopod system (in which fish consume both salamanders and isopods; Huang and Sih, 1990). Werner (1991) argues that greater larval bullfrog activity (movement) in the presence of predators gives them a competitive advantage over larval green frogs; these two species are evenly matched competitors in the absence of predators. This effect of differential activity ultimately interacts with direct predatory effects in determining the distribution of these two species among perma-

ment versus temporary ponds (Werner, 1994; Werner and McPeek, 1994). Similar movement-related effects may influence competition between larval mosquitos (Juliano *et al.*, 1993; Grill and Juliano, 1996). On the other hand, Tayasu *et al.* (1996) argue on empirical and theoretical grounds that similar levels of predator-induced inactivity in two shrimp species may allow for coexistence that would not otherwise be possible. Here, lowered activity in the superior competitor favors coexistence via a reduction in the overall level of interference competition.

Behaviorally transmitted indirect effects may also be evident when predators influence a particular species' use of space (Werner, 1992). Leibold (1991) describes a case in which competitive exclusion between two zooplankton species may be prevented by a predator-induced habitat shift in the superior competitor (the transmitter species). Cases have also been reported in which the similar use of space in the presence of predators intensifies interspecific competition among fish (Persson, 1991, 1993; Brabrand and Faafeng, 1993) and desert rodents (Hughes *et al.*, 1994). Finally, recent work on gerbils provides a cautionary tale regarding the use of space and its ultimate effects on species interactions. Despite the fact that two competing gerbil species may use space differently in the presence of predators (Kotler *et al.*, 1991), the temporal partitioning of activity appears to form the basis for their coexistence (Kotler *et al.*, 1993c; Ziv *et al.*, 1993; Brown *et al.*, 1994).

Behaviorally transmitted indirect effects have also been implicated in cases of strong "top-down" ecosystem regulation; such regulation dictates that a change in the abundance of top predators causes indirect ecological effects, which are transmitted all the way down to the lowest trophic levels of a food web (Power, 1992). For instance, Turner and Mittelbach (1990) found that the strong indirect effect of piscivorous bass on zooplankton communities is transmitted by predator-induced changes in the use of space by planktivorous sunfish. Diehl and Eklöv (1995) and Persson *et al.* (1996) describe a very similar situation in a piscivore → perch → invertebrate trophic system (arrows indicate predator → prey relationships). In a sunfish → salamander → isopod system simulated by Huang and Sih (1991), a positive effect of fish on isopods is transmitted primarily via a strong refuging response by salamanders to the presence of fish. Turner (1997) provides an extreme case of behaviorally transmitted top-down effects in a simulated predator → snail → algae system in which the mere chemical scent of predation drives the system. Finally, Hill and Lodge (1995) describe a case in which the (nonlethal) presence of predators mediates top-down effects in a fish → crayfish → macroinvertebrate → plant system via both behavioral changes and increased mortality in crayfish (the latter being caused by increased fighting for refuges).

The importance of behaviorally transmitted indirect effects in ecological systems has also been explored theoretically in recent years. Abrams (1992, 1995) and Abrams and Matsuda (1993) make a convincing case that (1) community-level models ignoring such indirect effects may be misleading, and (2) a variety of indirect effects may be expected if both predator and prey can change their behavior adaptively (see also Kotler and Holt, 1989). Abrams (1995) notes also that such adaptive behavioral traits may make it difficult to even distinguish and classify direct versus indirect effects. Indirect effects also figure prominently in models suggesting that ecological communities will be more speciose if prey exhibit predator-specific rather than generalist antipredator behavior (Matsuda *et al.*, 1993, 1994, 1996; see also Brown and Vincent, 1992, for a different perspective on this issue).

IX. ADDITIONAL CONSIDERATIONS

In this section I group four disparate topics about which relatively little is known. These topics nonetheless address several important issues in the study of decision making under the risk of predation.

A. PHYSIOLOGICAL STRESS RESPONSE AND DECISION MAKING

A threatening situation often induces the classic "fight or flight" physiological (neuroendocrine) stress response, which involves (among other things) the immediate production of hormones like cortisol, epinephrine, and norepinephrine (Weiner, 1992); recent work suggests that this response is even greater than previously thought (Le Maho *et al.*, 1992). One of the short-term physiological effects of the basic stress response is to make more energy available for immediate action like escape (Weiner, 1992). Many stimuli will produce this stress response, such as aggressive conspecifics, unfamiliar terrain, novel objects, and so on (Boissy, 1995). Of course, predators may also induce such a response, but relatively little work addresses the effects of predators per se (but see Levine *et al.*, 1993; Boissy, 1995). However, work on stress caused by being approached or handled by humans (Le Maho *et al.*, 1992; Boissy, 1995) has an obvious relationship to physiological stress caused by predators.

The physiological stress response is well known, but its relationship to antipredator decision making represents unexplored territory. Indeed, the relationship between the basic stress response and subsequent behavior is not always clear (Boissy, 1995). Experimental work in which the stress response is chemically blocked does suggest, however, that elevated levels of stress hormones affect (in part) various antipredator behaviors (Berco-

vitch *et al.*, 1995). Boissy (1995) argues further that individual differences in "fearfulness" among animals are related causally to such differences in the stress response.

It thus seems likely that the physiological stress response is mechanistically linked in some way to antipredator decision making. It is, in fact, conceivable that the stress response is to a significant extent a target of selection in the evolution of antipredator behavior in general, especially as it relates to short-term changes in responsiveness to predators. It is also conceivable that an unusually extreme stress response may actually impair decision making in some way; Mesa *et al.* (1994) suggest such a possibility with regard to non-predator-induced physiological stress, but the same might well hold for stress caused by chronic exposure to unusually high predation risk (see also following discussion). It is also tempting to speculate further that certain aspects of antipredator decision making are designed to avoid the long-term effects of a chronic physiological stress, such as stress-induced diseases and suppression of the immune system (Ader *et al.*, 1991); such a realization may have important implications for the design of experiments on antipredator behavior (see following discussion). As mentioned earlier, the reproductive effects of such physiological stress may also impinge on our interpretation of predator-induced breeding suppression (see Section VI,G).

All of the forgoing discussion on physiological stress pertains to vertebrates. In fact, most research has been conducted on only a small number of mammals, birds, and fish of economic or medical importance (Schreck, 1990; Mesa *et al.*, 1994; Boissy, 1995). The results obtained thus far probably apply to most vertebrates, but their relevance (if any) to physiological stress and the antipredator behavior of invertebrates seems largely unexplored.

B. ASSESSING THE RISK OF PREDATION

An assessment of the risk of predation must in some way form the basis for antipredator decision making (Blumstein and Bouskila, 1996), but little is known about the way in which such assessments are made. A great deal is known about the sorts of predatory stimuli that animals interpret with alarm (see Curio, 1993, for an excellent discussion), but the way in which animals integrate information on predator abundance, the likelihood of escape, and so on, into some sort of assessment of predation risk is unknown. Following Lima and Dill (1990), it seems likely that animals use "rules of thumb" in assessing the prevailing risk of predation. It also seems likely that any such assessment will be fraught with uncertainty. In this regard, Bouskila and Blumstein (1992) argue that animals might adaptively overestimate the risk of predation to avoid the relatively high costs of underesti-

mating risk. Abrams (1994) cautions, however, that underestimating the risk of predation can be favored under certain circumstances.

Work on the chemical detection of predators might shed light on this issue of assessing risk. Scores of studies show that a variety of animals can detect a threat of predation via chemicals emitted by predators (for recent reviews, see Weldon, 1990; Smith, 1992; Larsson and Dodson, 1993; Dodson *et al.*, 1994; Kats and Dill, 1998). As argued by Kats and Dill (1998), the concentration of such chemicals might provide an accurate estimate of predation risk. This might explain why the strength of antipredator behavior in zooplankton (Ramcharan *et al.*, 1992; Loose and Dawidowicz, 1994) and tadpoles (Horat and Semlitsch, 1994) increases with the concentration of fish-emitted chemicals. However, very few studies examine behavioral responses to varying chemical concentrations, nor have such concentrations been related to mortality, predator abundance, and so on. Future work in this area might well demonstrate that predator-emitted chemicals provide many types of animals with an accurate estimate of the risk of predation (Kats and Dill, 1998).

C. PREY ACTION AND PREDATOR REACTION

The study of antipredatory decision making is hindered by a lack of information on the way in which predators respond (in ecological time) to the antipredatory actions of their prey. In fact, a tacit assumption in the vast majority of studies reviewed herein is that factors like attack rate are fixed entities to which prey determine their optimal response. There are nonetheless many scenarios in which prey behavior might influence predator behavior (and thus the components of risk controlled by predators, e.g., Lima, 1990b).

The smattering of studies addressing this issue of "action and reaction" cover a wide range of phenomena. Johansson and Englund (1995) consider explicitly the behavioral interaction between a refuging prey and a persistent predator. Piscivorous perch change from an active to a sit-and-wait foraging mode when their prey shift from an open to a refuge-rich habitat (Eklöv and Diehl, 1994). Of conceptual importance in the study of vigilance are observations that predators avoid attacking relatively vigilant prey (FitzGibbon, 1989; Krause and Godin, 1995). On a different note, piscivorous pike may defecate away from their feeding areas so as to avoid being detected chemically by prey (Brown *et al.*, 1995). Recent attempts to model multi-trophic-level games of habitat selection (Schwinning and Rosenzweig, 1990; Hugie and Dill, 1994; Sih, 1998) provide notable instances in which the crux of the matter is the real-time interaction between prey response and predator reaction.

D. SCALING TO THE REAL WORLD

To what extent do small-scale laboratory microcosms simulate the situation faced by animals avoiding predators in their natural environment? Lima and Dill (1990) raised this question with regard to the common experimental situation in which predator and prey are maintained in very close proximity. Under such situations, the prey's response to predators may be so strong as to be potentially misleading. Richardson and Brown (1992) report just such a situation in which a strong response by snails to nearby crabs in the laboratory could not be replicated under field conditions. Similarly, the relatively brief reduction in gerbil activity following an encounter with an owl under semifield conditions (Abramsky *et al.*, 1996) did not reflect the marked reduction in gerbil activity following an exposure to captive owls at close quarters (Kotler, 1992). Perhaps the application of most laboratory studies to the real world would not be so problematic, but I nevertheless urge caution in the use of experimental protocols in which prey and predator are in close proximity. Such caution may also be warranted in light of the possibility that decision making may be impaired by an abnormally intense physiological stress response under these circumstances (see Mesa *et al.*, 1994).

The general issue of "scaling to the real world" concerns not just the spatial proximity of predator and prey, but also the temporal scale of the interaction. Many studies demonstrate that animals respond markedly to a brief but acute exposure to predators, perhaps with a complete cessation of feeding. In effect, these animals are able to "ride out" a short period of high risk. However, such strong responses may not be indicative of those to a chronic exposure to high risk; animals must eventually eat.

X. CONCLUSIONS AND SUMMARY

Recent years have witnessed increasing interest in the study of antipredatory decision making and its consequences. This recent work is much too vast to summarize in detail, but some notable recent advances include clear demonstrations that antipredatory decision making (1) may influence many aspects of reproductive behavior, (2) has demonstrable long-term consequences for individual fitness, and (3) may influence the nature of ecological systems themselves. There have also been many advances in the theory of antipredator behavior, which should provide a sound conceptual basis for further progress. Overall, combined with earlier work (Sih, 1987; Lima and Dill, 1990), these recent advances lead to the inescapable conclusion that the risk of predation may influence any aspect of animal decision making.

Just about all of the areas covered in this review deserve more attention. This is particularly true of areas that have emerged most recently. In this

regard, of great value would be further work on the effects that predator and prey have on the other's behavioral decisions. The range of reproductive behaviors influenced by the risk of predation also requires much more investigation. Work on the long-term costs of antipredator decision making needs more empirical documentation and greater taxonomic diversity. Work on the ecological implications of antipredatory decision making has only "scratched the surface," especially with regard to population-level effects and species interactions. Theoretical investigations should also play a prominent role in future work. While I am not sanguine about the possibilities that such theoretical models can be tested quantitatively, theory is nevertheless essential to the continued conceptual development of the field. Finally, I suspect that research exploring the link between antipredator decision making and the physiological stress response will prove rewarding.

What are the next "big steps" in the study of decision making under the risk of predation? Two areas seem to have particularly good prospects. The first concerns the aforementioned application of antipredator decision making to the understanding of ecological systems. Such work will be particularly interesting given that the early development of behavioral ecology was spurred (in part) by the prospect that behavioral studies might provide key insights into the workings of ecological systems; this prospect may well be realized in the study of predator-prey interactions. The second area concerns the development of a view of antipredator decision making that encompasses phenomena expressed over both ecological and evolutionary time. Work in this area promises to integrate the study of antipredator decision making with recent advances in the larger field of evolutionary biology. I have not been able to cover this emerging area to any great extent, but Sih (1992b) and McPeek *et al.* (1996) provide thoughtful discussions and examples of how such an integration might proceed.

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