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Predation Risk and Behavioral Life History

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It is generally good to be afraid because predation risk is omnipresent. If we extend our definition of *predator* to disease organisms, parasites, and herbivores (for plants), then the vast majority of organisms end their lives by falling victim to predation. Indeed, most organisms will be killed before they manage to produce even one surviving descendant offspring. The odds for a female ant leaving her nest to begin a new colony, or for an acorn navigating toward becoming an oak, are probably in excess of 10,000 to 1 against success. Even in humans, it is estimated that in an ancestral type of hunter-gatherer society the average reproductively mature woman gave birth to 8.09 children in her lifetime (Hill & Hurtado 1996). Assuming a stable population (i.e., each woman needs to produce 2 replacement adults for herself and her mate), it is obvious that the majority of children never survived to become either the "average" reproducing woman or man.

All is not lost, however. Predation may be almost inevitable, but predators can be successfully avoided, misdirected, or repelled for some time if prey act in an appropriate manner. Appropriate behavior will vary across species. For some, it will be hiding in safe refuges. For others, it will be increased vigilance and increased proclivity to flee when perceiving danger. In some cases, social behavior will create effective group defense mechanisms. Finally, for many organisms, the proper response may be a morphological one, such as making shells or other hard outer coverings, growing spines or thorns, or producing or sequestering poisonous substances.

Nevertheless, such defense mechanisms are clearly not without costs and demand trade-offs of energy or time allocated to defense or other activities. A hiding or fleeing animal is not a foraging animal. Group living can also create competitors for scarce resources or mates. Energy channeled into armaments or defensive structures is energy unavailable for attracting mates, reproducing, or parental care. Any organism that makes a poor allocation among these functions suffers on the lathe of natural selection. Indeed, given the ubiquity of predation across all life stages, one can argue that natural selection acts more strongly on antipredator behavior than anything else in the organism's repertoire. This is what makes studying predation and responses to predation risk so fascinating. To make an analogy to life history theory, those traits that are expressed earlier in life are likely under stronger selection than traits expressed late in life (Roff 1992). Thus, for all the fundamental selective importance of reproductive behavior (see chapters 20–26), many animals never have an opportunity to choose mates or produce offspring. Yet almost every animal is likely to be under some predation risk.

The effects of predation risk are evident in both flexible and fixed traits of organisms. Flexible traits (plasticity; see chapter 6) are evident in decisions about where and how long to forage, willingness to tolerate the presence of others, and the amount invested in mate choice and parental care (Lima & Dill 1990). Fixed characteristics can be general personality types (e.g., bold or shy; Sih et al. 2004b; chapter 30, this volume), developmental ontogeny of behavior, physiology, and other morphological features. The underlying assumption is that both types are shaped by natural selection. Flexible traits imply that the ability to evaluate risk and modify actions is adaptive (Nonacs & Dill 1993) and plasticity is favored (chapter 6). Fixed traits imply that predation risk is pervasive and constant in expression across multiple generations and plasticity adds little to no benefit.

Through the evolutionary perspective, we can then ask, "When does a given predation risk select for any type of antipredator defense?" The simple answer is that responding to predation risk is selectively advantageous when it produces higher fitness than ignoring predation risk. This seems like an obvious truism, but there may be many instances when ignoring predation risk is the better option. Even if being aware of or defending against predators increases survival, the functional form of that increase could have critical evolutionary implications.

Consider an organism with a fixed pool of energy, resources, or time that it can devote to either reproduction or antipredator function. If it invests a proportion (x) in antipredator defense, it will have $1 - x$ remaining for reproduction. Before we go any further, it is valuable to realize how flexible the variable x can be. The investment can be a fixed cost for morphological features such as spines, horns, shells, or toxins. It can be a behavioral energetic cost such as for fleeing from a real or perceived predator or giving loud alarm calls. Finally, the cost can be lost opportunities such as a reduced foraging rate due to vigilance behavior or foraging in safer but less rewarding food patches to avoid predators. In all cases, antipredator defenses or behavior take away energy that could be conceivably used for increasing reproductive output.

From a behavioral ecology standpoint, a most interesting question is, how can we find what the optimal level of investment, x, should be? To do so, we need to quantify the trade-off between gain in survival and loss in reproduction. Let's begin with a simple assumption: investment in antipredator function has an *S*-shaped payoff in survival. Initial investments do not increase survival greatly. However, as investment amount increases, survival starts to rapidly rise. Finally, at higher levels of investment, the gain in survival decreases and asymptotes to a maximum. Obviously the relationship between survival and investment need not be *S*-shaped, but it is a reasonable starting point. Furthermore, to describe such a relationship, we can use the general logistic curve, which has a long history in ecology and behavior (Richards 1959). Thus, we can map survival for our trade-off as follows:

$$\mathrm{P(survival)} = 0.01 + [0.98 / (1 + e^{-b(x - m)})]^{n} \quad (13.1)$$

where b and m are constants. The former determines how rapidly the curve rises, and the latter determines the level of investment that produces the most rapid gain in survival. Primarily by varying m, we can produce functional relationships in which low, intermediate, or high levels of investment in antipredator defense are required to significantly increase expected survival for each predator encounter (figure 13.1). Expected overall survival will depend on the number of predator encounters (n). Notice that we have added the constants 0.01 and 0.98 to the equation. We do this in order to have survival across all predator encounters range between 0.01 and 0.99. Thus, no matter how little or great the investment in defense or how many predators are encountered, neither death nor survival are ever completely certain. Using equation 13.1, we can estimate fitness as a multiplicative relationship between overall expected survival and the proportion of resources left to allocate to offspring production, such that:

$$\mathrm{Fitness} = (1 - x)\mathrm{P(survival)} \quad (13.2)$$

Using equation 13.2, we can calculate the expected fitness for any level of x across the survival functions in figure 13.1 when the animal expects to encounter 1, 10, or 100 predators (figure 13.2). Figure 13.2 suggests two predictions. First, that fitness is highest when effective antipredator defense has low costs. This, in and of itself, is rather obvious and therefore unsurprising. There are some evolutionary implications. Consider that a behavioral antipredator defense mechanism may have lower maintenance costs (i.e., behavior can be turned on and off as needed, whereas a morphological response is not so flexible). Thus, one would predict that antipredator behaviors would likely be more common in nature than would antipredation physical morphologies. The latter would likely appear only when predation risk is

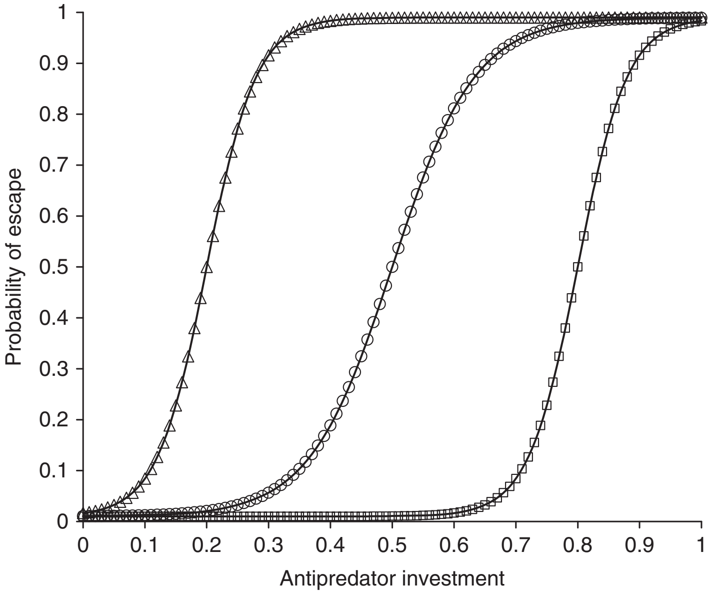

FIGURE 13.1 Probability of escaping a predator's attack per unit of investment into antipredator defenses (x). Strategies reflect where minimal investment (triangular points, $b = -25$; $m = 0.2$ in the logistic equation), moderate investment (circles, $b = -15$; $m = 0.5$), or high investment (squares, $b = -25$; $m = 0.8$) in defense assures a high probability of successful escape. For all lines, $n = 1$.

constantly significant (i.e., when antipredator defense should never be turned "off") and behavioral options produce limited success. Therefore, the world should have far more animal species that are alert, wary, and observant of their environment rather than loaded with sharp spines, poisons, and hard shells.

The second prediction is that as more predators are likely to be encountered, the optimal level of defense generally increases (and not surprisingly, expected fitness declines because more is invested in defense and survival is lower). However, looking at figure 13.2, one can see that this is not always true. For example, when the survival function requires a high level of investment to be effective, high predator encounter rates ($n = 100$) produce a radical shift in strategies: the optimal policy invests nothing in antipredator defense. Because expected survival is so low, the best evolutionary response may be to invest entirely in early reproduction and little, if any, in defense against predation.

We can better visualize the shifts in investment strategy by plotting the predicted optimal level of investment (for the three survival functions from figure 13.1) against the expected number of predator encounters (figure 13.3). This figure illustrates the central prediction from our simple model: that investment in antipredator defense is highest when individuals expect to encounter an intermediate number of predators. When predators are rare, defense investment can be lower because it is less needed. There is a point, however, when predation risk becomes so pervasive that no defense strategy is likely to be effective. Then it becomes better to simply ignore predation risk and put all resources into (rapid) reproduction.

Therefore, figure 13.3 can be considered to represent what we would call the *intermediate predation risk hypothesis* (IPRH): antipredator behaviors and morphologies are most likely to evolve and be maintained under intermediate levels of predation risk. A corollary prediction of the IPRH is that the intermediate zone is generally wider for behavioral traits than morphological traits. This follows from behavioral traits having less of a fecundity cost at low levels of investment because they may still yield high-efficacy payoffs. The results from our simple model are also very similar to a more detailed approach employed by Lima and Bednekoff (1999). They also predict that antipredator investment can be increased to be effective against any single predation attempt. If a large number of such attempts

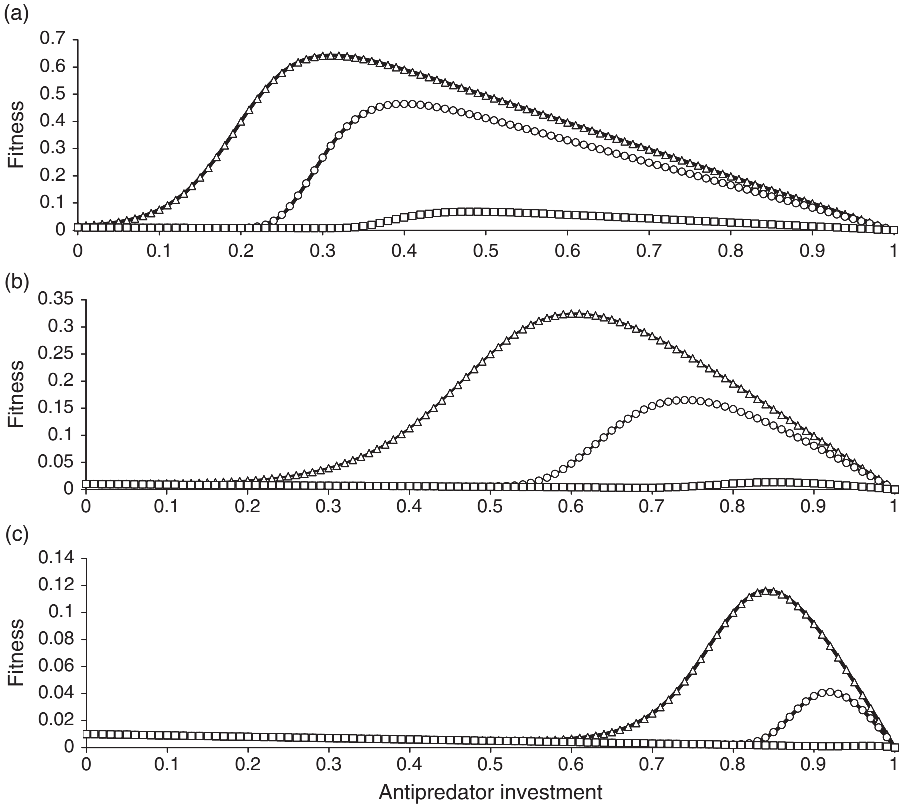

FIGURE 13.2 Fitness payoff (fecundity × survival) for various levels of investment into anti-predator defense. Panels reflect strategies that require (a) low, (b) medium, or (c) high investment to be effective (see figure 13.1). The symbols indicate where individuals expect 1 (triangles), 10 (circles) or 100 (squares) encounters with potential predators (*n*). The optimal investment level is found at the highest point of each curve.

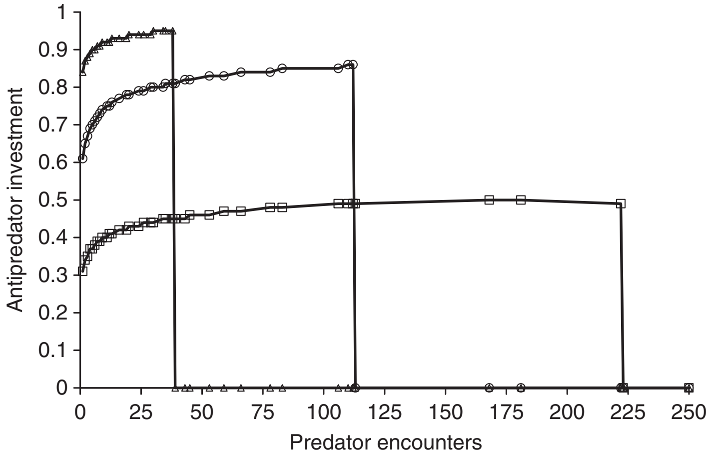

FIGURE 13.3 The optimal level of investment into antipredator defenses as the number of expected encounters with predators increases. Lines with square, circular, or triangular points reflect strategies that require low, medium, or high investment to be effective (see figure 13.1). All strategies predict an initial increase in antipredator defense as more encounters are expected. However, for all levels of defense effectiveness, there is a point at which no investment in defense becomes the optimal strategy.

are expected, however, then long-term survival will not increase enough to offset the cost of the added defense.

The concept of a trade-off between antipredator defense and other biological goals forms the basis for our review of the behavioral ecology of predation risk. First, we consider evolutionary responses to predation risks that can change on a daily or moment-to-moment basis, or remain constant across many generations. Second, we consider how both the immediate behavior and the evolutionary history of species might affect the conservation and preservation of biodiversity in a changing world.

EVOLUTIONARY BEHAVIORAL ECOLOGY OF PREDATION RISK

Vigilance

Prey cannot detect predators without some level of vigilance, but vigilance can take away from other activities. If predation risk is not constant over time, antipredator vigilance should vary dynamically and ultimately can be related to the relative time individuals are in high- and low-risk situations (Lima & Bednekoff 1999). Envision a ground squirrel or a skunk living beneath the path of a raptor migratory route. During the migration season, prey may encounter many thousands more raptors than during the rest of the year. Should animals vary vigilance and foraging during each season? Or consider the variation in risk that darkness and moon cycles create. How should animals allocate time to vigilance and foraging during risky moonlit nights?

Lima and Bednekoff's (1999) *risk allocation hypothesis* predicts that animals will be the most vigilant when high-risk situations are rare. Consider two environments, a high-risk one (H) and a low-risk one (L). The optimal times allocated to feeding in the high- and low-risk environments (f_H) and (f_L) are as follows:

$$f_H^* = \frac{R}{(\alpha_H / \alpha_L)(1-p)+p} \qquad (13.3)$$

$$f_L^* = \frac{R}{(1-p)+(\alpha_L / \alpha_H)p} \qquad (13.4)$$

where R = the average rate of foraging required to meet an energetic demand, α = the attack rates in the different environments, p = the proportion of time spent in the dangerous situation, and thus $(1-p)$ = the amount of time spent in the relatively safe situation. In these equations, optimal time foraging is expressed as a function of need (R) divided by a ratio of attack rates combined with the time spent in the different patches. By doing so, our units work out to time foraging.

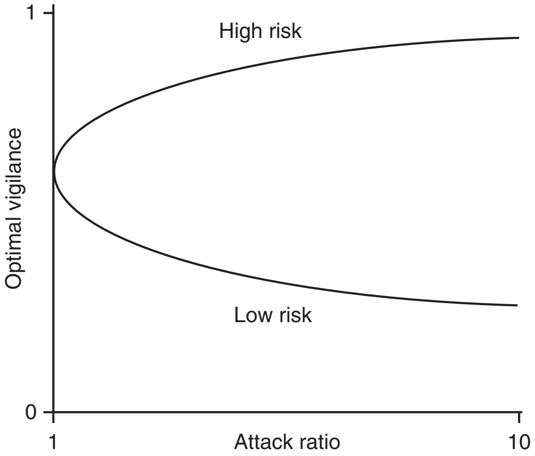

FIGURE 13.4 The optimal vigilance model. As risk in the high-risk situation relative to the low-risk situation (i.e., the attack ratio) increases, animals should become more vigilant in the high-risk situation and less vigilant in the low-risk situation. Redrawn from Lima and Bednekoff (1999).

The key to understanding risk allocation is seen by setting $\alpha_H = \alpha_L$, in which case, $f_H = f_L = R$. This shows that the average foraging rate required to meet energetic demand is not influenced by the actual level of risk, but rather the relative difference in risk between the low- and high-risk times (or environments). Thus, the *attack ratio*, (α_H / α_L), determines variation in vigilance and antipredator behavior. As the attack ratio increases, animals should feed more in the low-risk situations and the optimal level of vigilance should decrease in the low-risk situation (figure 13.4).

The situation is more complex when the relative time spent in different risk situations begins to vary. Figure 13.5 illustrates the predicted optimal levels of vigilance when the proportion of time spent in the high-risk situation is 0.3, 0.5, and 0.7. For any given attack ratio, vigilance in the low-risk situation (solid lines) is affected more by the proportion of time in the high-risk situation than is vigilance in the high-risk situation. Thus, when risks are substantial and rare, it pays to invest a lot in vigilance.

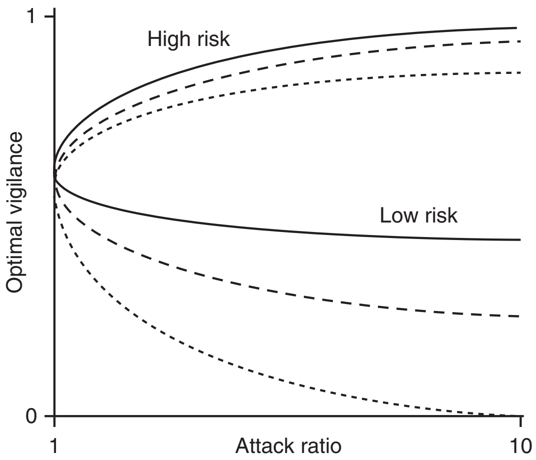

FIGURE 13.5 Optimal vigilance as a function of time spent at high risk (p). Optimal vigilance is plotted for individuals that spend 30% (solid lines), 50% (dashed lines), or 70% (dotted lines) of their time in the high-risk environment. As the proportion of time spent in the high-risk state decreases, the risk allocation hypothesis predicts more vigilance for individuals who live in low-risk situations than for those in high-risk situations. Redrawn from Lima and Bednekoff (1999).

The consequence of this is to bias foraging toward lower-risk locations or at lower-risk times. Therefore, predation risk, particularly temporally variable risk, impacts other activities and otherwise should structure time budgets. Although the risk allocation hypothesis applies generally to any antipredator behavior, behavioral correlations (i.e., syndromes, discussed below) may prevent adaptive allocation of antipredator behavior as predicted by the hypothesis (Slos & Stoks 2006).

Strong empirical support for the risk allocation hypothesis is lacking. Some of the best support comes from Sih and McCarthy (2002), who exposed snails to chemical cues associated with their predatory crayfish in different temporal scenarios. Snails living in high-risk situations were exposed to a pulse of low risk, whereas other snails typically living in low-risk situations were exposed to a pulse of high risk. Snail behavior varied based on the temporal pattern of risk. Snails typically living under high risk were relatively inactive but when risk was suddenly decreased, they foraged a lot more. Snails from low-risk situations were moderately active. Unexpectedly, these snails did not respond as predicted by the risk allocation hypothesis to pulses of high risk. In another experiment, Van Buskirk et al. (2002) kept frog tadpoles in artificial ponds with either many or few caged dragonfly larvae. Although tadpoles responded aversively to the predators, they did not vary their feeding behavior as predicted by the risk allocation hypothesis. Finally, Sundell et al. (2004) did not find strong support for the risk allocation hypothesis when they manipulated predation risk to voles by exposing them to weasels in large outdoor enclosures. Again, variation in feeding behavior was not influenced by pulses of risk, leading these authors to suggest limitations in the ability of the voles to properly assess risk. These studies clearly indicate that more work is required to understand how animals assess risk and then to manipulate risk to adequately test the risk allocation hypothesis. Failure to find support for the risk allocation hypothesis could also stem from limited phenotypic plasticity. Future comparative studies could explore the situations under which species should respond to temporally variable risk.

However, before we reject empirical tests of the hypothesis, a recent study by Creel et al. (2008) provides perhaps the best support for the risk allocation hypothesis under natural conditions. They focused on elk (*Cervus elaphus*) that had to survive snowy winters as well as the risk of predation by wolves (*Canis lupus*). In Yellowstone National Park, elk lived in areas with and without wolves and thus experienced different amounts of background predation risk. In areas with wolves, elk encountered wolves periodically. Therefore, there were pulses of predation risk. They evaluated a set of alternative statistical models that contrasted the risk allocation hypothesis against a null model (vigilance was not influenced by predation risk) and two alternative models (a risky times model and a risky places model). The risk allocation model explained the data the best: elk modified their vigilance based on both background levels of predation risk and the temporal change in predation risk.

Flight

Once detected, prey may or may not elect to flee. The decision to flee upon detecting a predator depends on both the costs and benefits of flight and thus is another antipredator behavioral trade-off (Ydenberg & Dill 1986). Eventually, all individuals will flee an approaching threat (Blumstein 2006a), and this deceptively simple observation has generated a

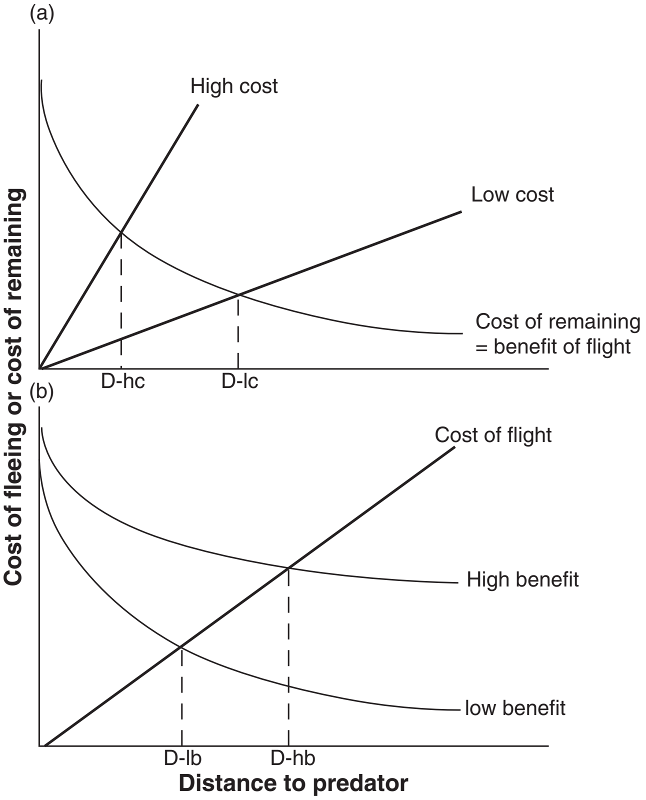

FIGURE **13.6** A summary of Ydenberg and Dill's (1986) model of flight initiation distance (FID). The intersection of cost and benefit of flight curves predicts the optimal FID. In (a), FID is found for fixed benefits of flight and variable costs of remaining. *D-hc* and *D-lc* are the optimal distances to flee when there are high or low costs of remaining, respectively. In this case, animals with high costs (e.g., those less able to move, or who will lose valuable resources by fleeing) will tolerate closer approaches. In (b), FID is found for fixed costs of flight and variable benefits from fleeing that could reflect the different risks from different predators. *D-hb* and *D-lb* are the optimal distances to flee when there are high or low benefits of flight, respectively. Thus, for a fast-moving, high-risk predator, for any distance, there would be a higher benefit of flight compared to a slower-moving, lower risk predator. Therefore, animals should flee at greater distances from higher-risk predators.

rich literature that identifies a variety of factors that influence flight (Stankowich & Blumstein 2005).

Following Ydenberg and Dill (1986), we present a simple economic model of flight (figure 13.6). This model assumes that animals should minimize overall fitness costs. The costs of fleeing or remaining, *c* and *b,* are both affected by distance to predator. The cost of remaining equals the benefit of flight. Therefore, as this cost goes up, so does the benefit of flight. In other words, the benefits of fleeing are increased fitness relative to not fleeing, whereas the costs of fleeing equals energy, opportunity, and any increased conspicuousness to predators.

Realistically, the cost of remaining (i.e., the risk of capture) is highest when the predator is very close and lower the farther away the predator is. Therefore, the cost of flight is 0 if the predator is on top of the prey, and cost increases with increasing distance. The cost of flight might be lost foraging opportunities. Like many such graphical optimality models, the crossover point is where flight distance is optimized (figure 13.6). Thus, prey should let predators get closer as the cost of flight decreases. Similarly, the relative benefit will also influence the optimal distance to flee the predator. For any given cost of flight, flight initiation distance (FID) will vary based on the cost of remaining. If some predators are more effective than others at a given distance, then this should also influence FID.

What might influence the relative cost of remaining versus leaving? Let us first focus on what might cause flight distance to increase with risk. Some species are sensitive to the speed with which a predator approaches. For species that use refugia, distance to protective cover should influence FID. Interestingly, some studies have found an effect of distance to refuge, whereas others have not (Stankowich & Blumstein 2005). The positive results are consistent with the hypothesis that prey reduce risk of predation by modifying their FID. However, not all animals seem to do this, and a more complex consideration of the costs and benefits of flight may be needed. For instance, as animals are farther from refuge, the cost to escaping increases because they have to expend more energy both moving between the cover and the presumably good foraging area.

The Ydenberg and Dill (1986) model also assumes that prey are cost minimizers. Thus, they move when the benefits of fleeing exceed the costs. However, animals that maximize the difference between the benefits and costs of fleeing will do better. The point is that both costs and benefits increase as the distance to burrow increases. If costs differ across species, this might account for some of the variation in the response of distance to safety and FID. A positive relationship between FID and distance to safety would be consistent with benefits of flight exceeding the costs.

What about costs of leaving? For an animal to leave a good patch could be costly. If you lived in a desert, it may take a lot to get you to leave an oasis! It turns out that birds on productive wetlands in generally desert-like Southern California typically are very tolerant of human approaches (Blumstein unpublished data). An individual's relative competitive ability can also influence the cost of leaving. Subordinate animals might not be able to forage at equally high rates before a disturbance as dominants and may be more likely to tolerate closer approaches. All animals are neither created equal nor remain equal throughout their lives.

Blumstein (2003) modified Ydenberg and Dill's model in a manner consistent with the intermediate predation risk hypothesis. Specifically, if the risk is too great, all animals should immediately flee. And if the risk is too low, animals should never flee. It is only in a zone of intermediate risk that the dynamics of flight become relevant and animals make trade-offs. Cooper and Frederick (2007b) further argued that the Ydenberg and Dill model was not an optimal solution because prey were assumed to break even (i.e., costs would equal benefits), rather than maximize their fitness (i.e., the location where benefits most greatly exceeded costs). They developed two optimality models for maximizing fitness. One had prey losing all residual reproductive value upon death, and the other retained it after death. Overall, they concluded that optimality models are better than break-even models in explaining the existing data on flight.

Although quite variable, flight initiation distance can be viewed as a species-specific trait (Blumstein et al. 2003). For instance, in a comparative study of 150 species of birds, body size explains a substantial portion of the variation in FID. Other variation was explained by diet (species eating living prey flee at greater distances) and sociality (cooperative breeders flee at greater distances). These results suggest some carry-over effects from foraging and sociality on FID, such that species eating living prey have better motion detection and social species are vigilant for reasons other than predator detection (Blumstein 2006a). Additional studies have explored whether birds with larger eyes are more likely to detect a threat, but in a phylogenetically corrected analysis, no significant relationship was found (Blumstein et al. 2004a). Some variation in FID was also explained by the age at first breeding (species that need to live longer to first reproduction flee at greater distances). Thus, FID is a trait influenced by many aspects of life history.

A number of recent studies also focus on dynamic "hiding games" between prey and predators (Cooper & Frederick 2007a). For species that use refuges (e.g., burrows) to reduce predation risk, the benefits of hiding eventually are outweighed by the risk of starvation and prey must eventually emerge. Like FID, the dynamics of hiding should be sensitive to the risk of predation and the benefits and costs of hiding. Anything reducing cost for remaining in a refuge (e.g., lowering metabolic rate while in a burrow) would presumably enable prey to reduce the risks of both starvation and predation.

Alarm Calling

Alarm calls are signals emitted when prey detect a predator and are remarkably plastic. Not all individuals produce alarm calls and calling appears sensitive to the trade-off between increased detectability to the predator and escape benefits (Blumstein 2007). What is particularly attractive to studying alarm calls is that we can study their trade-offs at either an ultimate or proximate level.

At the ultimate level, how does giving an alarm call increase fitness? Fitness can be increased through two nonmutually exclusive pathways. First, calling may increase the caller's likelihood of survival. For example, calls can signal predator detection and therefore discourage active pursuit. Or calling can create pandemonium among other potential prey that then allows the caller to escape. The second fitness-enhancing pathway is through warning kin, either one's own offspring or other nondescendent kin. Because alarming calling is often assumed to be altruistic (i.e., callers increase exposure to predators while warning others), many studies have focused on the conspecific warning function of alarm calls. Although the importance of signaling to predators is often downplayed, in rodents alarm calling seems to have initially evolved as detection signaling toward predators (Shelley & Blumstein 2005). Thus, in rodents, the conspecific warning functions may be exaptations (chapter 2).

Independent of its ultimate function, the proposition that alarm calls increase predation risk is often assumed but rarely tested. This involves a proximate question of call detectability. Because researchers often use alarm calls to locate callers, they assume that if it helps them, it should also help the predators (Blumstein 2007). Tests of raptors' ability to localize alarm calls, however, demonstrate that some calls may be difficult to localize (e.g., Klump et al. 1986; Wood et al. 2000). In contrast, hungry snakes are attracted to the foot thumps of banner-tailed kangaroo rats (Randall & Matocq 1997). Other evidence for a cost of calling comes from Sherman's (1985) study of Columbian ground squirrels (*Spermophilus columbianus*), which scurry for cover before or while calling when pursued by a rapidly moving aerial predator, but call in place when responding to a terrestrial predator.

Interestingly, the structure of calls shows that some are cryptic, whereas others are easy to localize. For instance, mobbing calls (not, strictly speaking, an alarm call) of many birds are rapidly paced with a wide frequency band. Their bandwidth makes them easy to localize. High frequencies predictably attenuate to allow distance estimation, and broadband sounds have more "sound" present to stand out against background noise—increasing their detectability. Thus, these calls function, in part, to recruit others to mob the predator. By contrast, many birds emit "seet" calls when they encounter an aerial predator (Marler 1955). These high-frequency, narrow bandwidth calls are difficult to localize because of their frequency and because they also fade in and out. Therefore, by examining the acoustic structure of alarm signals, we can infer something about the risk associated with producing them.

A second line of proximate investigation involves the energetic and opportunity costs of calling. At one level, calls are usually brief and there is no convincing evidence that they have an energetic cost (Blumstein 2007). Opportunity costs, however, may be quite real and must be evaluated from the signaler and recipient's perspective. If the signaler has already increased its vigilance, calling has a limited opportunity cost. From the recipient's perspective, this is an information problem. We can examine two aspects of information: (1) is a predator truly present, and (2) does the call identify a specific type of predation risk?

Suppose there is a situation in which Nervous Nelly calls at the drop of a leaf and Cool Hand Lucy calls only when certain of a predator (Blumstein 2008). We should expect receivers to use this difference in caller reliability (Blumstein et al. 2004b). In some species of primates and sciurid rodents, calls from unreliable individuals are discounted and individuals reduce their vigilance after hearing repeated calls from unreliable individuals (following the fable of "the boy who cried wolf"). In contrast, yellow-bellied marmots (*Marmota flaviventris*) respond to unreliable calls by increasing vigilance (Blumstein et al. 2004b). It might be that unreliable marmots provide limited, but possibly true, information about predation. Thus, those hearing them might need to independently validate the information.

More controversial in terms of communication is whether alarm callers specifically identify the predator. Calls that function like basic words and communicate information about external objects or events are *functionally referential* alarm calls (Evans 1997). Marler et al. (1992) defined functional reference so as to avoid implications about higher-level cognitive abilities. Evidence of functional reference requires that the calls be produced only to a specific set of stimuli and that playbacks in the absence of a predator elicit the appropriate response. This may not immediately seem that interesting, but referential ability is a key feature of human language (Hockett 1960) and once thought to be a uniquely human attribute. Subsequent research has shown some degree of referential abilities in a number of primate, rodent, and bird species.

Macedonia and Evans (1993) provided perhaps the best explanation for the evolution of functionally referential alarm calls. Species that have unique and mutually incompatible escape strategies seem especially likely to have referential alarm calls. For instance, vervet monkeys (*Cercopithicus aethiops*) must deal with snakes, which elicit investigation and avoidance; raptors, which elicit taking cover in the safety of a dense tree crown; and leopards, which elicit taking cover on peripheral tree branches (Cheney & Seyfarth 1990). Such mutually incompatible escape strategies create an opportunity to communicate specifically about them. Thus, vervet monkeys have functionally referential calls. Playback of snake-elicited calls in the absence of snakes causes monkeys to stand on their toes and look around. Playback of raptor-elicited calls causes monkeys to run to trees and hide near the trunk. And playback of leopard-elicited calls produces hiding on peripheral branches of trees. Once such referential abilities evolve, more complex cognitive processes may follow. Therefore, selection to avoid predation may be an integral pathway to complex cognitive abilities. How such abilities might be costly is unknown, although some interesting possibilities are being tested (chapter 10).

Multiple Goals and Common Currencies

The effect of predators on prey populations has been part of theoretical ecology for a long time (e.g., Volterra 1926; Lotka 1932). The incorporation of behavior into predictive models, however, took several decades longer until the rise of optimal foraging theory (OFT; Schoener 1971; Charnov 1976; Pyke et al. 1977). This body of work was the first attempt to predict behavior in an economic context based generally on the maximization of the net rate of energy intake. OFT was relatively quickly expanded by the seminal work of Sih (1980, 1982) showing that animals could balance between two simultaneous goals: the collection of food and the avoidance of predators. A multitude of studies followed that demonstrated trade-offs between avoiding predators and gathering food, habitat selection, prey choice, sociality, and group functioning (see reviews by Lima & Dill 1990; Brown & Kotler 2004).

Although it is demonstrably obvious that animals often trade off food, mating opportunities, and group status to reduce predation risk, it is more difficult to show that such trade-offs maximize fitness. This is known as the common currency problem (McNamara & Houston 1986; Gilliam & Fraser 1987; Nonacs & Dill 1990). The currency for predation is being alive or dead. A currency for foraging is energy collected over time. So how much energy should an animal give up to reduce predation risk by a given amount? One answer is to empirically ask animals themselves how much energy they are willing to sacrifice for increased safety. These are known as *behavioral titrations*, in which two factors such as food availability and predation risk are allowed to covary (Abrahams & Dill 1989). When animals are trading off across the factors, it allows experimenters to measure the value of one factor in the currency of the other factor.

Abrahams and Dill (1989) did a behavioral titration for the value of predation risk in terms of food for guppies (*Poecilia reticulata*). The fish were placed in an aquarium with two separated feeders. Initially, without a predator present, the fish arranged across the two feeders as predicted by the ideal free distribution, such that all fish fed at about equal rates (figure 13.7). A predation risk was associated with one feeder and this caused a shift in preference, measured as shift in fish distribution, toward the safer feeder. This shift created a difference in feeding rates across the two feeders that could be used to estimate the energetic value guppies assigned to predation risk. This also allowed Abrahams and Dill to estimate in a second experiment how much fish would have to receive in food to return to the risky side in numbers equivalent to the initial ideal free distribution (figure 13.7). Interestingly, only females equated food with risks. For males, even when one feeder was 17 times more rewarding, they would not go to the risky feeder. This sex difference in response to predation risk is probably due to reproductive success in female guppies being closely tied to their feeding rate. Access to females, rather than feeding rate, matters more to males.

Researchers can also use patch *giving-up density* (GUD; the amount of food left behind in a patch at the point the forager leaves the patch) to estimate the food costs of predation risk (Brown & Kotler 2004). Thus, in the presence of owls, two species of gerbils, *Gerbillus a. allenbyi* and *G. pyramidum*, have far higher GUDs in seed trays that are placed in open rather than protected microhabitats (Kotler & Blaustein 1995). Furthermore, species-level differences are evident as *G. a. allenbyi* requires twice

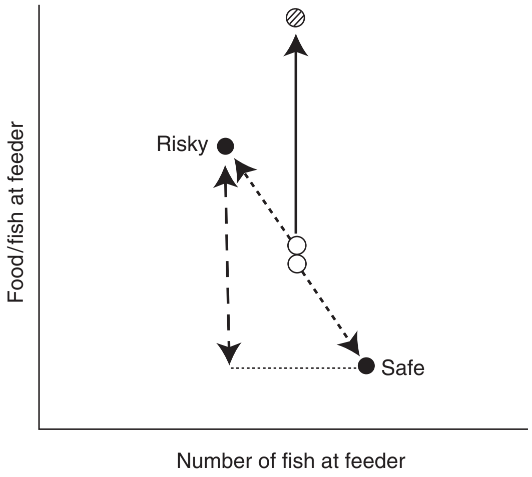

FIGURE 13.7 Measuring the energy equivalent of risk. In the experiments of Abrahams and Dill (1989), guppies were allowed to distribute themselves across two feeders. The fish arranged into an ideal free distribution such that all the fish at both feeders fed at similar rates (the two open circles). In one experiment, a predator was added to the one patch (which became the risky patch). Thereupon more guppies started using the safe feeder, and thus intake rates were no longer equivalent across the two feeders (dotted arrows pointing to black points). The difference between intake rates (the dashed arrow) is a measure of the energetic equivalent of predation risk for guppies. This measure was then used in a second experiment as the amount of food/fish (solid black arrow and hatched point) that had to be added to the riskier patch in order to have the same number of fish at the risky patch as were present in the original ideal free distribution.

as much food in risky patches as *G. pyramidum* to harvest the same number of seeds (i.e., it abandons patches with much more food left in them). Another solution with modular organisms, such as ant colonies, is to measure whether behavioral choices maximize growth and reproduction. Therefore, Nonacs and Dill (1990, 1991) presented *Lasius pallitarsis* colonies with a dichotomous choice in foraging patches that varied inversely in food quality and mortality risk. The colonies preferentially foraged in the patches that maximized colony growth rate as measured by the net of the increase in biomass due to food collected minus the loss in biomass due to predation. Whether or not foraging ants brave mortality risk is therefore a function of the expected gain in colony biomass across patches.

In conjunction with strictly empirical measures, theoretical models have been developed to predict multifaceted behavior. Particularly relevant are those that predict dynamic behavior. These models take into account that organisms have changing states, and optimal behavior should be influenced by those changes (e.g., hungry animals should take more risks for food than satiated animals). Numerical solutions, using the techniques of stochastic dynamic programming (McNamara & Houston 1986; Mangel & Clark 1988; Clark & Mangel 2000; chapter 8, this volume), have come to dominate the trade-off literature. This is true for predicting specific behaviors such as female wasp parasitoids exploiting patches of host eggs (Wajnberg et al. 2006) and broad patterns of behavior across numerous species. For example, optimal foraging models that do not simultaneously consider predation risk will consistently underestimate the time animals stay in patches (Nonacs 2001a).

Dynamic trade-off models have also been particularly useful in understanding mass regulation by animals. For example, for many species of birds, individuals seem to be on a permanent diet: they are skinnier than local food availability would predict. This becomes obvious when the environment becomes worse or more variable. Under such worsening conditions, birds get fatter (chapter 12). Mass regulation appears to be influenced by a trade-off between the risk of predation (a heavier bird is slower) and the risk of starvation. In a good, predictable environment, a bird can afford to be skinny because a meal is always readily available. Thus, starvation risk is low and birds can regulate their mass to maximize maneuverability. In poorer or unpredictable environments, birds need to carry a fat buffer because the next meal is uncertain (chapter 12). Therefore, birds will pay to reduce starvation risk by increasing predation risk (Houston et al. 1997).

Nonacs (2001a) showed, however, that predation risk could produce the same phenomenon in another way. Rather than assuming that weight correlates with predation vulnerability, Nonacs asked whether spatial location mattered. For example, if a predator employs a sit-and-wait ambush strategy, the time prey spent in a patch without being attacked increases the likelihood that this patch is predator-free. Therefore, animals may remain far longer in patches than predicted by net-energy maximizing criteria alone. A byproduct of staying where it is safe rather than always moving to find more rewarding patches is that animals stay skinny. Independent of whether location or weight itself affects predation risk, the tendency to stay skinny in the presence of plentiful food may be a quite common life history strategy in nature (although our own species appears to be a very notable exception to this rule!).

Behavioral Syndromes

Animals may behave in predictable ways that indicate behaviors are not always independent of one another (Sih et al. 2004b; chapter 30, this volume). Behavioral syndromes are seen when there is a correlation across situations or contexts. For instance, if individuals that are bold around predators are also bold when courting, a boldness syndrome has been identified. Such syndromes may inhibit the ability of traits to track environmental variation if they create a trade-off. Assume, for example, that females prefer to mate with bold males, but bold males are more likely to be killed by predators. Thus, the expression of boldness in a population will be highly dependent upon the predation risk. If this syndrome did not exist, then the traits might vary independently according to variation in the costs and benefits of their expression. Antipredator behavioral syndromes have been identified in a number of species, and in the future we will have a better understanding of their importance. Describing and understanding them can illustrate how trade-offs may explain seemingly maladaptive behavior (Sih et al. 2004b).

Social Behavior and Group Living

Groups can form for selfish reasons, in which individuals cluster in an attempt to reduce their own exposure to predators (Hamilton 1971a). Group living, however, also has tremendous potential to create effective antipredatory mechanisms (chapter 17). Regardless of whether animals aggregate to increase foraging efficiency or to reduce the probability of predation, once aggregated, novel antipredator defenses can emerge. Consider the group defenses of muskox (*Ovibos moschatus*) that form a defensive line against wolves or the group defenses of schooling fish, such as anchovies (family Engraulidae), that form a constantly moving three-dimensional mass.

Group living also allows the creation of a group phenotype that is unattainable by solitary individuals. The mutualistic benefit gained through the interactions of genetically nonidentical individuals is called social heterosis (Nonacs & Kapheim 2007, 2008). If genetic diversity within groups increases the variety of vigilance tactics or other antipredator techniques, this can reduce all group members' per capita predation risk relative to living solitarily or living in a genetically homogenous group. A possible example of the advantages of behavioral diversity could be a situation in which individuals adopt defined roles such as "sentry" (Wang et al. 2009). Indeed, a recent example with babblers (*Turdoides bicolor*) showed that sentry behavior was especially effective at reducing predation-related costs and increasing foraging intake (Hollén et al. 2008).

Sex and Alternative Reproductive Tactics

Lima and Dill (1990) argued that the degree to which predation risk might shape variation in reproductive tactics across species' life histories was greatly underappreciated. We believe this still to be the case and that predation risk may play a significant role in exaggerating behavioral and morphological differences across the sexes, alternative strategies within a sex, and species-level differences. First, consider a spider species that catches prey in a fixed web. For mating, males have to search for females. Relative to the number of expected predator encounters (x-axis in figure 13.3), males would inescapably experience considerably more risk. Hence, males and females could differ dramatically when females exhibit high investment into antipredator defense and males invest next to nothing. These differing optima could result in exaggerating sexual dimorphism such that males, when compared to females, are (1) physically unimposing and (2) behaviorally insensitive to risk to the point that they readily approach highly cannibalistic females (Andrade 2003).

Second, in many species, males (and less commonly females) exhibit alternative reproductive tactics that can differ both behaviorally and morphologically (Shuster & Wade 1991; Gross 1996; Sinervo 2001; Oliveira et al. 2008; chapter 25, this volume). A key element across these tactics is that they impose significantly different survival costs. For example, a male salmon that follows the small jack strategy will forgo an extra year of foraging in the ocean. Such males expect to survive at a higher average rate to breeding maturity, if for no other reason than that they encounter fewer predators (Gross 1996). Again, such differences in cumulative predation risk would suggest that small jack and large, nonjack males would reside at different points on the curves in figure 13.3. A (currently untested) prediction would then follow that jacks should be more likely to show antipredatory behavior and awareness of predation risk than their larger male brethren.

Species Differences

Some animals appear bolder in the face of predation risk than others. For example, you might notice that you (or your dog) can get closer to the average chipmunk than to either a jay or a deer. This certainly cannot be because the chipmunk is more able defend itself or escape your dog's jaws. However, the intermediate predation risk hypothesis may yield part of the answer from where one would plot these species on figures 13.1–13.3. Jays have a much more effective escape mechanism than chipmunks (flying versus running). Hence, in figures 13.1 and 13.2 jays may lie on the triangles, whereas chipmunks lie on the squares. Thus even though both may have many potential predators, over a large range of predation risk one would expect the jay to invest more into vigilance and predator avoidance (i.e., compare the squares and triangles in figure 13.3). In contrast, because a deer is a large animal, its size would reduce its number of potential predators relative to the chipmunk (hence the n for deer in equation 1 would be smaller than for chipmunks). Therefore, even if both hypothetically lie on the same line for "running" animals in figure 13.3, one might find the deer on the hump of the curve and the chipmunk at the bottom.

It turns out that size is a reasonably good predictor of an animal's potential life span (Roff 1992). To the degree to which predation causes this relationship, the IPRH predicts that animals of an intermediate size would invest the most in antipredatory behavior. Very small or large animals may experience so many or few predators, respectively, that high levels of vigilance would either be of little effect or not worth the cost. Blumstein (2006a) demonstrated this empirically with species-specific flight behavior in birds. Large birds generally flee a human at a greater distance. However, the largest birds (emus, *Dromaius novaehollandiae*) actually approached humans. Unarmed humans are of little risk to an emu. The smallest birds (e.g., hummingbirds) also tolerated close approaches. The relationship between body size and vulnerability may explain a substantial amount of variation in risk. Alternatively, body size may be associated with the ability of animals to detect an approaching threat (e.g., Blumstein et al. 2004c).

In all of the above examples, predation risk could create evolutionary feedbacks that increase the effects of inter- and intrasexual selection and species competition. Thus, it would be interesting to examine situations in which species have experienced prolonged evolutionary periods with reduced predation risk, such as isolated island faunas. Here all individuals may find themselves at or near zero in figure 13.3, with low investment in antipredator defenses having the highest fitness. Therefore, it would be predicted that (1) sexual dimorphism would be reduced (e.g., Blondel et al. 2002), (2) alternative reproductive strategies within a sex would be rarer, and (3) species-level characters, such as size, would not predict the remaining levels of antipredator awareness or flightiness.

PREDATION RISK AND CONSERVATION BIOLOGY

Predicting Successful Invasive Species

In 1890, Eugene Schiffelin felt that Americans suffered in not being able to experience firsthand all the birds mentioned in Shakespeare's writings. Therefore, he released bevies of larks and other nonnative birds into the New York area. Thanks to Mr. Schiffelin's efforts, we now have over 200 million starlings in North America, but despite his efforts, no nightingales. This disparity of success highlights a major question in conservation biology. Why do some introduced species survive and become pests, whereas others do not (see chapter 29)?

Following from the intermediate predation risk hypothesis, successful invasive species may be those that have evolved life histories that invest relatively less in antipredator defenses because they are on the right-hand side of the curves in figure 13.3. Effective invasiveness could occur for two reasons. First, such species are released from their natural predators. This is an obvious advantage for any introduced species. Second, if the introduced species is evolutionarily in an intermediate zone of predation risk, it still may considerably invest in antipredatory defense against absent predators. This cost would not be borne by species in which low levels of antipredatory defense have been evolutionarily favored. This saved investment could tip the competitive balance against natives. Simply not investing in antipredatory defenses, however, cannot by itself determine a successful invasive (otherwise continents would overrun by pests from distant oceanic islands rather than vice versa!). Instead, successful invasives may come from the right-hand side of figure 13.3 curves. That is, these species have adapted to strong predation pressures by evolving life histories that may maximize reproduction at the expense of long-term survival. Thus, even if such species are susceptible to novel predators in an introduced range, it may not offset their intrinsic fecundity. Therefore, in predicting which species are likely to become future economically damaging invasives, it may be helpful to gauge their boldness and their response to predation risk.

The Loss of Antipredatory Behavior

If you are lucky enough to spend time on small oceanic islands, you may find that ground-dwelling species are very tolerant of your presence. The intermediate predation risk hypothesis may provide one clue in that there is little predation here and therefore there will be little fear. But another clue may come from the observation that although most species have more than one predator, some species live in virtually predator free environments.

In general, if we assume that predators have selected for a variety of antipredator behaviors, optimality theory would predict antipredator behavior to disappear when the predators are no longer present. The loss of predators occurs naturally via colonization and extinction, and unnaturally when prey species are moved to predator-free locations. Guppies for which predation pressure was eliminated illustrate this nicely; they rapidly become sexier (or at least more colorful), and we infer that this is because the expression of this sexually selected trait is no longer traded off against predation risk (Endler 1995). We note that this seems at odds with our above suggestion that loss of predators should disfavor sexual dimorphism. The discrepancy may be that the observed changes in guppies are an evolutionarily short-term response over relatively few generations. If predators and parasites were absent for many generations, the good genes function within mate choice for male coloration would become less relevant. Whether a larger, drabber, longer-lived, more female-like male would eventually evolve in this context is an interesting, open question.

When antipredator behavior is lost, species may become particularly vulnerable to new predators and such species may be particularly vulnerable to exploitation and accidental extinction. However, in some cases, we see remarkable persistence of antipredator behavior. Antisnake adaptations persist in ground squirrels, wallabies retain group size effects and predator discrimination abilities, and pronghorn antelope (*Antilocapra americana*) retain their remarkable athletic abilities long after the extinction of important predators (Blumstein 2006b). Thus, understanding the specific conditions under which antipredator behavior is lost has important conservation implications.

It is important to realize that prey species seldom have only one species of predator (Lima 1992; Sih et al. 1998). The multipredator hypothesis capitalizes on this truism and therefore expects the evolution of linked, pleiotropic, or potentially fixed antipredator traits when the costs of expressing them in the absence of a predator are not extreme (Blumstein 2006b). Specifically, the multipredator hypothesis predicts that for species with multiple predators, the loss of a single predator may have no effect on its antipredator behavior for that predator. Why? Imagine a young ungulate that relies on both camouflage and immobility to hide from predators. Individuals not possessing both of these traits would be at a selective disadvantage. Now let us elaborate on this theme. Imagine a population of prey that had to avoid both foxes and eagles. Some could be super fox avoiders, whereas others could be super eagle avoiders. However, in an environment with both types of predators, we would expect that only those individuals that were good at avoiding both predators would persist. Thus, we expect the presence of multiple predators to select for suites (or syndromes) of antipredator behavior. Some of these suites are likely to result from linkage or pleiotropy. If so, we would expect a limited evolutionary response if suddenly one predator went extinct. In support of the multipredator hypothesis, tammar wallabies (*Macropus eugenii*) were found to retain group size effects and some degree of predator discrimination in populations in which there were some predators but not in a population in which there were no predators (Blumstein & Daniel 2002; Blumstein et al. 2004a).

The multipredator hypothesis has two important implications for future research. First, all predators that a species encounters may have effects. An individual can have the best antipredator response to a terrestrial predator, but if it never looks up in the sky it will be particularly vulnerable to aerial predators. We might expect selection to create suites of antipredator behavior because being the best responder to coyotes (*Canis latrans*) doesn't count for much in an area with eagles. Second, are antipredator traits retained following the relaxation of selection pressures located on the same chromosomes? Have these traits and genes been fixed? Our growing ability to identify and map significant genes will ultimately answer this question and provide valuable integration between phenotypic responses and genotypic architecture.

FUTURE DIRECTIONS

We believe that major advances in our understanding of how prey respond to predation risk will occur in three areas. First, both the multipredator hypothesis and the intermediate predation risk hypothesis have yet to be tested in a variety of systems. If these predictive models work, then we have made a significant advance in understanding the evolution and maintenance of antipredator behavior. Species like sticklebacks (family Gasterosteidae), in which predator loss is replicated many times, and for which there is great genomic knowledge, make an ideal system to test the multipredator hypothesis. Second, as suggested by Lima and Dill (1990), predation risk interacts with other processes that affect life history evolution. The exact nature of these interactions remains a fertile ground for new research. Third, predation risk has largely been ignored in both theory and practice of conservation biology. Many conservation actions fail, and predation is often implicated in their failure. Thus, the field of conservation behavior (Blumstein & Fernández-Juricic 2004) will profitably benefit from the cross-pollination of antipredator behavioral theory. For instance, knowledge about the ontogeny and evolution of antipredator behavior can inform captive rearing programs when animals destined to be reintroduced in natural environments that contain predators.

SUGGESTIONS FOR FURTHER READING

Tim Caro's (2005) recent book is the authoritative go-to volume on antipredator behavior in birds and mammals. Curio (1976) provides a classical ethological review of antipredator behavior. Lima (1998) and Preisser et al. (2005) provide a more ecological perspective on the consequences of antipredator behavior. General foraging theory, including examples of how understanding predation risk is essential to understand foraging decisions, is covered in Stephens and Krebs' (1986) book. More recently, in the Stephens et al. (2007) book, chapters by Ydenberg et al., Bednekoff, and Brown and Kotler discuss numerous examples of how foraging gain and predation risk trade-offs can affect both immediate behavior and community structure.

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