

Nonlethal Effects in the Ecology of Predator–Prey Interactions

What are the ecological effects of anti-predator decision-making?

Steven L. Lima

Predator–prey interactions have long captured the attention of ecologists, and with good reason. Predation leads inevitably to the removal of prey individuals from ecological systems, which can have major impacts on prey population dynamics and on entire ecosystems. Interest in predator–prey interactions can be traced to the foundations of modern ecology, from early work on predator–prey population dynamics by historical figures such as Lotka, Volterra, and Gause (Taylor 1984) to classic work on the role of predation in regulating species diversity (e.g., Paine 1966). Ecologists continue to be greatly interested in predation and its effects on populations, communities, and ecosystems (Crawley 1992, Carpenter and Kitchell 1993).

A perusal of any recent textbook on ecology will not only confirm the importance of predation in modern ecology, but also illustrate the pre-eminence of the “lethal” perspective on predation—that is, predation is seen as important only insofar as it results in the death of prey and their removal from the system. However, the obvious and sometimes dramatic lethal aspects of predation can obscure the nonlethal effects of the mere presence of predators in an ecological system. In the presence of predators, prey may alter their behavior so that they are more difficult

A complete understanding of predator–prey interactions requires an appreciation of the behaviorally induced nonlethal effects of predators

to capture, detect, or encounter. Because of the adaptive flexibility in prey behavior in response to a changing risk of predation (that is, anti-predator decision-making), predators may have large impacts on ecological systems independent of actual predation. In this article, I highlight recent work on such behaviorally mediated, nonlethal predator–prey interactions. Although lethality will always remain a critical aspect of predator–prey interactions, a complete understanding of such interactions also requires an appreciation of the nonlethal effects of predators.

Behavioral ecology of predator–prey interactions

During the past 15 years, several hundred papers have been published on the behavioral ecology of predator–prey interactions (Lima 1998). This work demonstrates predation risk–driven flexibility in many as-

pects of prey behavior, such as sociality, mating, foraging, and predator detection. Here, I provide a brief sketch of the subset of this work most directly relevant to population and community ecology.

Tradeoffs. Work on anti-predator behavioral flexibility revolves around two simple ecological truisms: First, virtually all animals are both predators (in some sense) as well as potential prey for other predators, and second, the same behavioral options that make an animal an efficient predator (or forager) often increase its risk of becoming a meal for some other predator. These truisms imply that natural selection should act to produce animals that can somehow arrive at an appropriate tradeoff between the benefits of energy intake and the costs (in terms of Darwinian fitness) of an early death due to predation. Such a process of adaptive “decision-making” has been demonstrated in both invertebrates and vertebrates (Sih 1987, Lima and Dill 1990).

One of the best ways to demonstrate experimentally that animals balance safety against feeding is to deprive them of food. Hungry animals face a heightened risk of starvation and must, therefore, feed at a relatively high energy intake rate to meet their energetic needs. If an animal’s riskier behavioral options are also those that result in a higher rate of energy intake, then relatively food-deprived animals would be expected to accept a greater risk of predation while feeding. For ex-

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ample, hungry aquatic insects spend relatively little time in the safety of refuges (Kohler and McPeck 1989); hungry fish may occupy energetically profitable but risky habitats (Pettersson and Brönmark 1993), such as the periphery of a school (Krause 1993); and hungry ground squirrels spend relatively little time alert for predator attack (Bachman 1993). The many recent studies demonstrating hunger-dependent risk-taking suggest that anti-predator tradeoffs are common in many animal taxa and in many different contexts (Lima 1997).

Some tradeoffs between predation risk and energy intake are seen in changes in an animal's use of space (e.g., choice of habitat); such tradeoffs are particularly relevant to the ecology of predator-prey interactions. Foraging animals make tradeoffs in the use of space when the most energetically profitable places are also the most dangerous. An animal's use of space under such circumstances reflects both the benefits of feeding and the risks of predation (Lima 1998). For example, the small desert rodent *Gerbillus allenbyi* (a gerbil) removes many more seeds from artificial seed patches placed below protective bushes than from those placed only 1 m away from such bushes (Figure 1; Kotler et al. 1991). Because these gerbils experience a progressively lower energy intake rate as they remove more seeds from a patch, the results show that gerbils prefer to feed in the safety of bushes at a low intake rate than to risk death for a higher rate of return in the open "microhabitat." Other small mammals, as well as birds and fishes, show similar tradeoffs in the use of space (Lima and Dill 1990). The physical structure of a habitat (e.g., the presence or absence of bushes) appears to be a key determinant of risk and, hence, of the use of space in many vertebrates.

Also of great relevance to the ecology of predator-prey interactions are tradeoffs related to levels of activity in prey animals; activity levels determine energy intake, predator exposure, and predator detection (Werner and Anholt 1993). Animals almost always increase refuging (i.e., periods of inactivity spent in a refuge

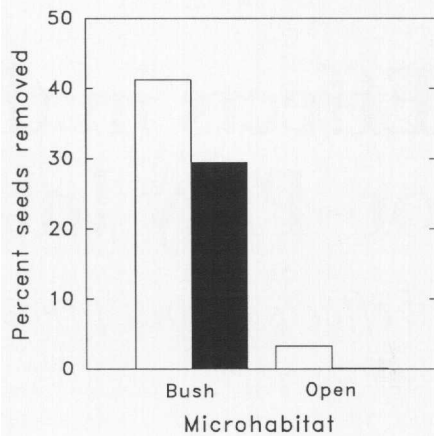


Figure 1. Microhabitat use by gerbils (*Gerbillus allenbyi*), as indicated by their removal of seeds from artificial food patches placed under bushes or in the open (1 m from the nearest bush). Data are given for seed removal under ambient risk (white bars) and elevated risk (the presence of nearby owls; black bars) under dark (moonless) conditions. Data were averaged over more than 100 patches presented to gerbils over three experimental periods. Both the effects of patch placement and level of risk were significant at $P < 0.05$. Data are from Kotler et al. (1991).

such as a burrow or rock crevice) or decrease movement (i.e., speed, frequency, or length of moves) outside refuges when the risk of predation is high (Sih 1987, Lima and Dill 1990). More than 60 recent studies indicate that such activity responses are ubiquitous across diverse invertebrate and vertebrate taxa (Lima 1998).

Consequences for individual prey. Most studies on anti-predator decision-making accept the idea that any such decisions have both benefits and costs in terms of an animal's fitness. How much do behavioral ecologists really know about actual benefits and costs in the context of anti-predator behavior?

Benefits of anti-predator decision-making. The clear fitness benefit of anti-predator decision-making is a reduction in the immediate (and possibly long-term) risk of predation. Although it is intuitively clear that an increase in anti-predator behavior in the presence of predators will lower an animal's risk of predation, demonstrating such benefits is not always easy. Several studies have, nevertheless, done so. A particularly good example is the finding that

hungry guppies (*Poecilia reticulata*) feed with greater intensity than well-fed guppies and are, therefore, less alert for predators and more likely to be killed than their alert counterparts (Godin and Smith 1988). It is also well documented that a decrease in activity lowers an animal's risk of predation (via the probability of being detected or encountered by a predator; Lima 1998). A particularly convincing example of this effect comes from the finding that dragonfly larvae are more likely to capture active rather than partially anesthetized tadpoles (Skelly 1994).

Most demonstrations of effective anti-predator decision-making come from the aquatic realm, within which it is easiest to manipulate and monitor predators under realistic conditions. Nevertheless, some experimental evidence from mammalian systems and some exceptional observational studies on birds provide evidence that reduced risk-taking does, in fact, lead to lower mortality (Lima 1998). Despite these findings, it is important to note that even strong anti-predator responses can sometimes fail to prevent significant mortality (Sih 1992).

Costs of anti-predator decision-making. The immediate cost of increased anti-predator behavior is lowered energy intake, which presumably translates into a reduction in reproductive output or in long-term survival. However, relatively few studies have demonstrated such costs of anti-predator decision-making.

The most convincing demonstrations of the long-term costs of anti-predator behavior come from studies of aquatic insects with nonfeeding adult life stages, such as mayflies (Ephemeroptera). These insects are ideal for identifying such costs because adult fitness is a function of the energy reserves they inherit from the larval stage. Thus, it has been possible to show that a marked reduction in feeding activity by mayfly larvae in the presence of predators (e.g., Kohler and McPeck 1989) leads to slower growth and development, which ultimately translates into smaller adults and fewer eggs (Figure 2; Peckarsky et al. 1993, Scrimgeour and Culp 1994). Similar effects are apparent in chironomids, another group of aquatic insects with a

nonfeeding adult stage (Ball and Baker 1996).

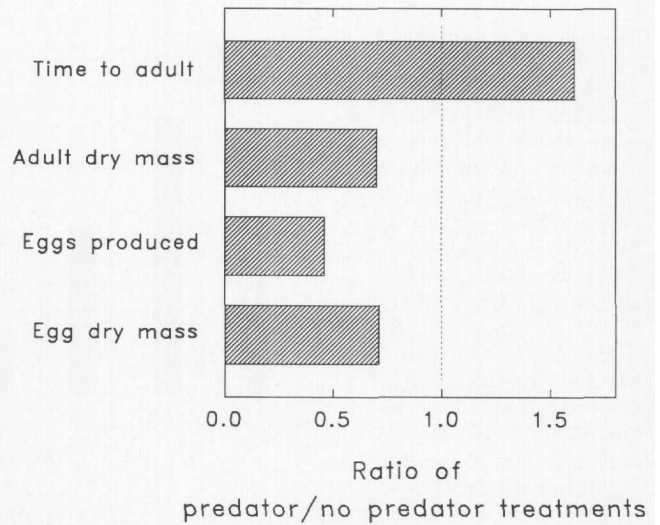
Demonstrating the full extent of the reproductive costs of anti-predator decision-making in vertebrates has proven difficult. However, several studies suggest that slower growth rates in fish and larval amphibians can result from predator-induced decreases in feeding activity (e.g., Skelly and Werner 1990) or from shifts to poorer (but safer) habitats (e.g., Werner et al. 1983, Persson and Eklöv 1995). The precise consequences of slowed growth for adult fitness are not always apparent, but there are good reasons to suspect that slowed growth entails a substantial fitness cost. The situation is considerably less clear for birds and mammals, whose growth is often largely complete before they strike out on their own. For such animals, the long-term cost of anti-predator behavior may be decreased body condition (Hik 1995, Sinclair and Arcese 1995), leading to lower fecundity in females and to lowered competitive ability in males.

Optimal tradeoffs. An optimal tradeoff ought to exist between the immediate benefits and long-term costs of avoiding predators. Just how close animals come to achieving this optimal solution is, however, an open question. It is difficult not only to quantify these costs and benefits, but also to determine the optimal tradeoff itself. A study on worker ants foraging under a threat imposed by larger ants (Nonacs and Dill 1990) perhaps comes closest to this end. In this study, the risks taken by workers were shown to reflect the potential increase in colony growth as a result of extra foraging.

Population-level consequences of decision-making

Anti-predatory decision-making could, in principle, influence many aspects of prey population regulation and dynamics (Sinclair and Arcese 1995). The possibility of such nonlethal predatory influences on prey populations is readily apparent, given the negative reproductive consequences of anti-predator behavior (e.g., Figure 2). Translating behavioral decisions to their population-level consequences has proven

Figure 2. Biological consequences of reduced activity in the mayfly *Baetis tricaudatus*. For each biological measure (i.e., time to adult, dry mass of adults, number of eggs produced, and dry mass of eggs), the ratio of its average value in the presence of predators (small artificial fish) relative to that in the absence of predators is given; a ratio smaller or greater than 1.0 (dashed vertical line) indicates, respectively, a smaller or larger value in the presence of predators. The effect of predator presence was significant ($P < 0.05$) for all biological measures considered. Data apply only to females and were averaged over two food treatments. Data are from Scrimgeour and Culp (1994).



to be a challenge, but recent work suggests several ways in which the nonlethal effects of predators influence prey populations.

Local population effects. The nonlethal effects of predators on local prey populations can sometimes be understood in terms of decisions affecting an animal's use of space. Such decisions determine, in part, the density and dispersion of prey over relatively large areas. I discuss the nonlethal effects of predators on entire prey populations in a following section.

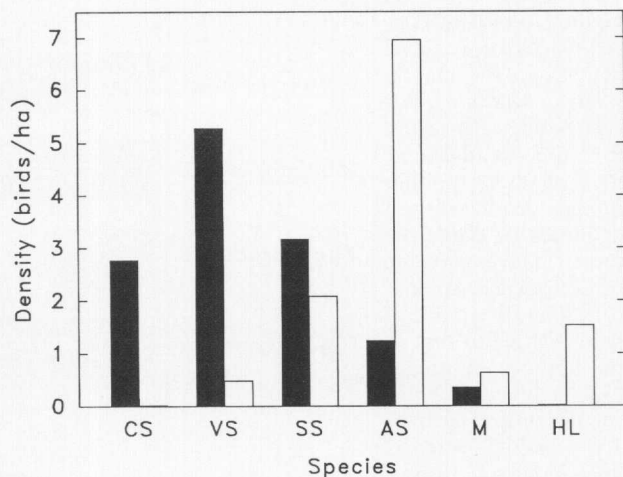
Stream systems. Recent studies on small stream-dwelling animals provide good examples of the local, nonlethal effects of predators. Small streams are often a series of relatively deep pools connected by shallow riffles. Large predators (e.g., large fish) are typically confined to pools, whereas smaller prey can move between pools. Pools may vary considerably in the abundance of predators; accordingly, prey density is relatively low in pools with many predators and relatively high in pools and riffles with few predators (Harvey 1991). For example, Crowl and Covich (1994) found that in a stream system in which shrimp are both predator and prey, distributional changes in prey (i.e., the smaller shrimp species) may occur on a short time scale as these smaller shrimp emigrate from risky pools. Such predator-induced emigration from pools is widespread

in stream-dwelling animals (Wooster and Sih 1995).

These effects in streams of predators on prey may shed light on longstanding inconsistencies in studies of the impact of predators on stream prey populations. Whereas some studies show a strong impact of predators, many do not. "Standard" models of predator-prey dynamics in streams suggest that prey immigration into pools can often overwhelm the local predators' collective ability to reduce prey populations (Wooster and Sih 1995). However, allowing for predator-induced emigration from pools can negate the expectation of standard models, which do not take anti-predator decision-making into account (Sih and Wooster 1994). In particular, predator-induced emigration from pools could mediate a strong impact of predators on local prey density. Such strong but nonlethal predatory effects have been demonstrated in an empirical study on the impact of predators on stream insects (Forrester 1994).

A consideration of differential prey emigration behavior in response to different types of predators may also help to clarify the impact of predators on local prey populations in streams. Wooster and Sih (1995) argue that emigration in response to relatively agile vertebrates is more risky than emigration in response to relatively immobile invertebrate

Figure 3. Effects of manipulating predation risk on the local population density of some desert grassland birds in Arizona. Species abbreviations are: CS = chipping sparrow (*Spizella passerina*), VS = vesper sparrow (*Pooecetes gramineus*), SS = savannah sparrow (*Passerculus sandwichensis*), AS = *Ammodramus* sparrow, M = meadowlark (*Sturnella* spp.), and HL = horned lark (*Eremophila alpestris*). Species are arranged from left to right in order of decreasing reliance on woody cover for escape from predators (mainly raptors). Black bars show population densities after 11 small bushes were added per hectare of open desert grassland; white bars show population densities in the absence of such woody cover. Data were averaged over three sites for each cover treatment. Differences in population densities were significant ($P < 0.05$) for all species except savannah sparrows and meadowlarks. Data from Lima and Valone (1991).



predators. Accordingly, they suggest that invertebrate predators induce prey emigration more consistently than do their vertebrate counterparts. This finding implies that some types of prey may actually accumulate in pools with vertebrate predators, leading to the erroneous conclusion that predators in general have relatively little impact on local prey populations. It may be more useful to distinguish between mobile, pelagic predators and less mobile, benthic predators rather than between vertebrate and invertebrate predators (Barbara Peckarsky, personal communication, Cornell University, Ithaca, NY), but the idea that different types of predators can have qualitatively different nonlethal effects seems valid.

Terrestrial systems. The large spatial scale of animal movement in terrestrial systems makes it difficult to study nonlethal predatory effects (or lethal effects, for that matter) on local prey populations, especially in vertebrates. Nevertheless, the absence of animals from certain terrestrial habitats may reflect the effects of predators on large-scale patterns in the use of space by prey. For instance, hedgehogs (*Erinaceus europaeus*) appear to avoid habitats with large numbers of predatory badgers (*Meles meles*; Doncaster 1994). Similarly, mountain sheep

(*Ovis canadensis*) may avoid flat (and energetically profitable) valley terrain in which predators may have the advantage in an attack (Berger 1991). In a unique experimental system, Suhonen et al. (1994) used nest boxes to manipulate the distribution of European kestrels (*Falco tinnunculus*), which prey on small birds. The presence of a kestrel nest reduced nesting attempts by small birds in an area of several square kilometers around the kestrel nest. This effect was most evident in migratory birds, whose relatively late arrival on their breeding grounds allowed them to choose nest sites away from already established kestrel nests.

Microhabitat use and local population effects. Most studies on the use of space under the risk of predation examine behavioral effects on a scale of square meters (Lima 1998). This spatial scale may not seem appropriate for making inferences about nonlethal population-level effects (local or otherwise), but the results can, in fact, be instructive.

The physical "structure" of a habitat may provide an important link between microhabitat selection and local population density. For instance, microhabitat use by many small birds is influenced by the proximity of woody vegetative cover (e.g., bushes and small trees). Most birds avoid venturing away from such pro-

tective cover, but species with cover-independent escape tactics may actually avoid cover (Lima 1993). A simple manipulation of woody cover over large areas may therefore markedly alter the risk of predation perceived by a given bird species and, ultimately, its density in that local area. Such effects should be escape-tactic dependent, with woody vegetation-dependent birds avoiding areas free of woody vegetation and vegetation-independent birds avoiding areas rich in woody vegetation. These effects were indeed observed in a desert grassland experimental system in which sparse woody cover was manipulated independently of any effect on food resources (Figure 3; Lima and Valone 1991). These sorts of behaviorally mediated, nonlethal predatory effects may be widespread in the avian world (Lima 1993).

Similar considerations probably apply to many small mammals, whose behavior is also influenced strongly by the proximity of protective vegetation (Figure 1; Kotler et al. 1991), as well as to some lake-dwelling fishes. The recent work of Persson and colleagues (1996), for example, shows that prey decisions about microhabitat use ultimately influence the prey population at both local and larger (whole-lake) scales.

How far can one go in making population-level inferences about the nonlethal effects of predators based on small-scale studies on the use of space? This question is still open, but I believe that these studies often yield considerable insight into local population-level phenomena. They also provide a good starting point for larger-scale investigations. In fact, one attempt to relate small- and large-scale population-level patterns indicates that the influence of piscivorous fish on the distribution of killifish (*Rivulus hartii*) within an entire watershed can be understood with respect to the influence of such predators on the small-scale use of streams by killifish (Fraser et al. 1995). However, in some situations the relationship between small- and large-scale patterns may not be straightforward. For instance, Rochette et al. (1995) noted that whelks (*Buccinum undatum*) are attracted to prey-consuming (and safely

preoccupied) starfish in an attempt to secure a few scraps of food. One might thus conclude that these whelks should prefer areas with abundant starfish. In fact, however, whelks generally avoid areas with abundant starfish, which prey on the whelks themselves. Although the extrapolation of small-scale effects to larger scales would clearly yield erroneous conclusions in this system, such situations appear to be the exception rather than the rule.

How do nonlethal effects on local populations translate ultimately to the population as a whole? The answer to this important question is largely unknown. At one extreme, these local effects may be strictly local, with predators acting merely to redistribute animals among habitat patches rather than to alter the overall size of the population. At the other extreme, nonlethally driven local changes in population density may initiate a series of events that propagate across the entire population (Persson et al. 1996). Determining where most ecological systems fall in this continuum awaits future research.

Whole populations. Small lakes have proven to be excellent systems in which to study the link between anti-predator decision-making and population-level phenomena. These systems allow ecologists to manipulate and monitor entire populations of both predator and prey. The value of lake studies was made clear in an early study by Werner et al. (1983), who divided a small experimental lake into two halves and introduced identical populations of bluegill sunfish (*Lepomis macrochirus*) into each. To one side, they introduced a few largemouth bass (*Micropterus salmoides*) as predators. Bluegill in the predator-free half occupied deep open water or shallow vegetated habitats, depending on which provided the greater return on foraging effort. In the half containing predators, only large bluegill chose habitats in this manner. Smaller, vulnerable bluegill avoided the dangerous open-water habitat, preferring instead the safer shallows. Over the course of a summer, the small bluegill, now crowded into the shallows, experienced a competitive bottleneck

in which they were limited by a dwindling food supply. These small bluegill thus grew at a slow rate. The larger bluegill in the predator half, by contrast, experienced an enhanced growth rate; these fish fed in the profitable open-water habitat, which was made even more profitable by the absence of competition from small bluegill.

A similar whole-lake manipulation of predators has demonstrated longer-term nonlethal impacts on prey populations. Tonn et al. (1992) found that the introduction of predatory fish (Eurasian perch, *Perca fluviatilis*) induced an almost exclusive use of the shallows by young crucian carp (*Carassius carassius*). These young fish experienced a competitive bottleneck that ultimately limited recruitment to adult life stages (see also Diehl and Eklöv 1995). Those individuals that survived this bottleneck grew much larger than control fish after they shifted to the food-rich pelagic zone (in which they were now safe from predators due to their size). Such population bottlenecks can ultimately alter competitive relationships among prey species (see next section; Brabrand and Faafeng 1993).

The existence of predator-induced changes in habitat choice by juvenile fish provides a mechanistic basis for understanding how predation and competition influence "stock-recruitment" curves. These curves, which are used in fisheries management, describe the expected recruitment of fish into the population based on the current breeding stock. Walters and Juanes (1993) suggest that the assumption common to most models—that an increase in the predator population will reduce competition for food within the population of prey fish—is erroneous. In fact, when a refuge habitat is available in which young fish can escape predation, predators might be expected to induce competition for food among young fish. It can, thus, be misleading to view predation or food alone as limiting the recruitment of fish into the adult population—both factors may combine to limit recruitment.

The effects of nonlethal predator-prey interactions on whole populations of terrestrial animals (vertebrates in particular) are largely

unknown. As mentioned above, the large spatial scale of movement by both predator and prey often limit one's ability to manipulate entire populations of predator and prey. Nevertheless, the "terrestrial gap" has been bridged to an extent by Sinclair and Arcese (1995) in their study of wildebeest (*Connochaetes taurinus*) populations in eastern Africa. Making the assumption that a wildebeest's vulnerability to predators is a function of its willingness (as dictated by its body condition) to take risks to obtain food, Sinclair and Arcese (1995) concluded that patterns in the body condition of living wildebeests and wildebeests that had been killed by predators or died of natural causes indicate that predators and food combine to limit wildebeest populations.

Predator-prey population cycling. Recent studies on nonlethal effects in predator-prey population cycling are also helping to bridge the terrestrial gap. Such cycles have long captured the imagination of ecologists as far back as the classic theoretical works of Lotka and Volterra in the 1920s (Taylor 1984). The most famous cycle is that involving lynx (*Lynx canadensis*) and hare (*Lepus americanus*), in which both predator and prey cycle with a periodicity of approximately ten years. A causal link between predation and the cycle itself has long been suggested, and a recent large-scale predator exclusion experiment suggests that predators play a major role in maintaining the cycle (Krebs et al. 1995). Much of the effect of predators is undoubtedly lethal, but predator-induced microhabitat shifts by hare (into safe but less profitable microhabitats) may hasten the decline and lengthen the recovery phase of the hare cycle (Hik 1995). The main effect of this habitat shift may be to lower the overall body condition of female hare and thus their reproductive output. Hare in predator enclosures showed no such change in body condition (Figure 4).

Predator-induced breeding suppression in prey may also hasten the "crash phase" in the cyclic population dynamics of voles and their weasel predators in Fennoscandia (Ylönen 1994). This recently identi-

fied phenomenon of breeding suppression can lead to a severe curtailment of reproductive activity when the risk of predation is high. According to Ylönen (1994), breeding suppression may represent an attempt by female voles to “ride out” (in a high-survival, nonreproductive state) the high-predation portion of a population cycle, after which they and their offspring would have a better probability of survival. Such a response to predators might indeed shape the overall population cycle, but quantitative modeling of the effects of breeding suppression on predator-prey dynamics would make a stronger case; the same can be said about the hypothesized nonlethal effects of predators on the hare cycle (see above).

Decision-making and population models. Mathematical models of predator-prey population dynamics abound (Taylor 1984, Crawley 1992), but few consider adaptive anti-predatory decision-making by prey. This omission is a major impediment to understanding the population-level effects of nonlethal predator-prey interactions. As Abrams (1993) argues, most predator-prey models suffer from making key assumptions that are not easily supported by adaptive anti-predator decision-making by prey.

A few modelers have begun to explore the issue of nonlethality in predator-prey dynamics. For example, Ives and Dobson (1987) found that adaptive anti-predator behavior can stabilize otherwise oscillatory predator-prey dynamics. Ruxton (1995) adds weight to this result in a similar model incorporating more realism in prey behavior. Crowley and Hopper (1994) have made a particularly impressive attempt to link an evolutionary “game” model, in which cannibalistic dragonfly larvae and their smaller, conspecific prey base their behavioral decisions on the actions of the other, to stock-recruitment curves and their ultimate consequences for prey population dynamics. Their analysis suggests that cannibalistic dragonfly

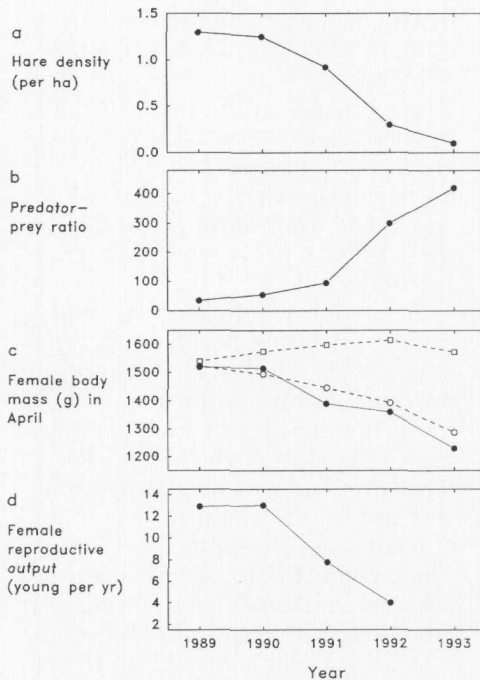


Figure 4. Biology of the decline phase of the hare population cycle (1989–1993) in the Yukon Territory. (a) Average hare density and (b) predator-prey ratio (an index of mammalian predator abundance relative to prey abundance) in unmanipulated populations. (c) Average female body mass in mid-April, when measurements were taken. Open squares and circles represent predator-free and control (predators present) experimental populations, respectively; experimental data were averaged over two food treatments. The effect of predator exclusion on female body mass was significant at $P < 0.05$. For comparison, solid circles represent averaged data from an unmanipulated population. (d) Average total reproductive output of female hares from an unmanipulated population. No reproductive data were given for 1993. Modified from Hik (1995).

larvae should generally exhibit non- or damped-oscillatory population dynamics that settle into stable equilibrium populations.

Nonlethality and the larger ecosystem

Recent studies provide concrete examples of the ways in which nonlethal predator-prey interactions might influence the nature of ecosystems indirectly—that is, nonlethal effects of predators on a given species are transmitted via the predator’s effect on a third (transmitter) species (or group thereof; Abrams 1995). These indirect effects have typically been assumed to be mediated by lethal effects, but in several instances, the

indirect effects of predators have been found to be transmitted nonlethally. Such nonlethal indirect effects have been called higher-order interactions (Werner 1992) or trait-transmitted indirect effects (Abrams 1995), but for clarity I use the term behaviorally transmitted indirect effects. Behaviorally transmitted effects may drive much of the impact that predators have on ecosystems (Kotler and Holt 1989, Abrams 1995).

Competitive outcomes. Behaviorally transmitted indirect effects of predators may alter the outcome of competition between prey species for a limited resource. For instance, two zooplankton species in the genus *Daphnia*, *D. pulicaria* and *D. galeata*, undergo a process of competitive exclusion in which *D. pulicaria*, which is inherently the superior competitor for food resources in the lake system studied, could, over time, conceivably exclude *D. galeata* from the lake (Leibold 1991). However, the large size of *D. pulicaria* makes it vulnerable to size-selective predators, such as sunfish. Consequently, in the presence of sunfish, *D. pulicaria* spends much of its time in the safer but food-poor, cold, deeper waters of the lake, where it not only grows more slowly than at the surface but is removed from direct competition with *D.*

galeata (Leibold 1991). This differential habitat selection under the risk of predation prevents competitive exclusion between the two species. In this case, *D. pulicaria* is the transmitter species, and *D. galeata* the recipient, of a positive indirect effect of predatory fish. Negative behaviorally transmitted indirect effects may also be apparent in systems in which similar spatial responses to the presence of predators intensify competition for resources (e.g., Persson et al. 1996).

Differential activity in the presence of predators may determine the qualitative outcome of competition between larval bullfrogs (*Rana catesbeiana*) and green frogs (*Rana clamitans*). In the absence of preda-

tors, these two species are more or less evenly matched competitors (Werner 1991). However, the simple presence of predatory larval dragonflies tips the balance in favor of bullfrogs. The key to this indirect effect is the fact that bullfrog larvae do not decrease their overall feeding activity in the presence of predators to the same degree as green frog larvae (the dragonfly predators were not allowed to actually capture prey). However, bullfrog larvae have since been found to be more vulnerable to the dragonfly predators than green frog larvae, probably as a result of their relatively greater activity (Werner and McPeck 1994). This finding suggests that green frogs might ultimately prevail over bullfrogs, but only in ponds free of relatively large fish, which strongly limit the abundance of dragonfly larvae. Fish also prefer green frog larvae over bullfrog larvae, which they find unpalatable; consequently, bullfrog larvae outcompete green frog larvae in ponds with fish. Thus, an understanding of these behaviorally transmitted predatory effects can help to explain why bullfrogs and green frogs are found largely in lakes with and without fish, respectively.

Similarity in activity may also mediate the nonlethal indirect effects of predators on competition among prey species. When faced with a high risk of predation, some prey may show similar refuging behavior. If refuges are in short supply, one species may outcompete the other for their use, leaving the lesser competitor exposed to greater predation. Such an indirect predator effect appears to occur in both a fish-salamander-isopod system (Huang and Sih 1990) and a fish-crayfish system (with two competing species of crayfish; Hill and Lodge 1994).

Top-down effects in ecosystems. One of the most fascinating recent developments in ecology is the demonstration of strong "top-down" effects in ecosystem regulation (Power 1992, Carpenter and Kitchell 1993). Strong top-down regulation dictates that a change in the abundance of top predators causes indirect ecological effects to "cascade" all the way down to the lowest trophic levels of a food chain. Despite some

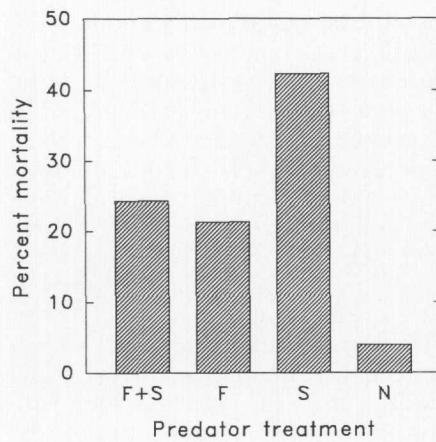


Figure 5. Mortality of isopods (*Lirceus fontinalis*) as a function of predator treatment (fish and/or salamander), as indicated by percentage of prey dead 6 hours after predator addition. Data were averaged over four replicates, and all major differences were significant at $P < 0.05$. F = fish (*Lepomis cyanellus*), S = salamander (*Ambystoma barbouri*), F + S = both predators present, N = neither predator present. Modified from Huang and Sih (1991).

contentious discussion about the generality of such top-down effects in ecological systems (Power 1992), these effects of predators are clearly among the strongest indirect effects ever demonstrated in ecology.

Most examples of top-down regulation come from aquatic systems. In an early example, the addition of bass to pools in an Oklahoma stream caused a marked increase in the standing biomass of algae (Power et al. 1985). The key transmitter species in this case was an herbivorous minnow (*Campostoma anomalum*), which avoids stream pools when bass, which prey on the minnows, are present. When bass were added to pools, these minnows decreased in abundance, allowing the algal population to grow. Following this logic, one would predict that the removal of top predators from a four-level food chain (e.g., big fish-small fish-herbivore-plant) would cause a marked increase in plant biomass; such an effect was, in fact, demonstrated experimentally by Power (1990) in a California stream system. Other cases of strong top-down regulation are known from lake systems (Carpenter and Kitchell 1993).

Top-down effects are typically assumed to be lethally transmitted,

but these indirect effects could also be behaviorally transmitted. Indeed, Power et al. (1985) suggested that much of the top-down effect they observed may have been transmitted behaviorally, as a result of minnows avoiding pools with the predators; such avoidance responses are known to occur in similar stream systems (e.g., Harvey 1991).

Turner and Mittelbach (1990) have since provided evidence of a strong (and perhaps entirely) behaviorally transmitted top-down effect in the bass-bluegill-zooplankton system examined by Werner et al. (1983; see above). In this study, the addition of bass to the pond system caused bluegill to seek shallow habitats, which in turn caused marked changes in the abundance and composition of the zooplankton community in open water (but had no significant effect on the phytoplankton). Diehl and Eklöv (1995) described a similar effect in a big fish-small fish-invertebrate lake system in which the addition of big fish had a marked effect on lake invertebrates. Behaviorally transmitted top-down effects were also apparent in an experimentally simulated fish-salamander-isopod stream system (Huang and Sih 1991). In this case, the positive effect of fish on isopods (i.e., lower isopod mortality in the presence of fish; Figure 5) was mediated primarily by a strong refuging response by salamanders in the presence of fish. An extreme case of behaviorally transmitted top-down effects was observed in a simulated predator-snail-algae system in which the predator itself did not need to be present (Turner 1997); the mere scent of the predator caused a decrease in snail grazing, which led ultimately to higher algal biomass. There are presently few demonstrations of behaviorally mediated top-down effects in ecological systems, but future work may show them to be common.

Some unresolved issues

A variety of conceptually important questions about the nature of nonlethal effects of predators in ecological systems remain unresolved. Are the spatial and temporal scales of existing studies adequate to assess the true ecological impact of nonlethal

effects? To what extent is it possible to assess the relative importance of lethal and nonlethal effects of predators in a given ecological system? Ultimately, the answers to these questions will determine the degree to which ecologists should be concerned with anti-predator behavior when assessing the importance of predators in ecological systems.

Problems of scale. As I have already mentioned, the vast majority of studies on nonlethal predator-prey interactions focus on spatial scales (e.g., a few square meters) and temporal scales (e.g., days or weeks) that may be too small to make extrapolations to larger ecological systems. To be fair, many studies of anti-predator decision-making are not designed to answer questions about the "big ecological picture," but even those that are so designed are almost always carried out on a small scale. Consequently, few studies actually demonstrate long-term consequences of nonlethal predator-prey interactions for population growth, size, or structure (but see Werner et al. 1983, Persson et al. 1996).

The relative importance of lethal and nonlethal effects. Predators clearly have nonlethal effects in ecological systems, but few studies have compared the relative importance of lethal and nonlethal effects. I thus cannot generalize about whether lethal predatory effects ultimately overwhelm even strong nonlethal effects in the long term. However, demographic analyses suggest that nonlethal effects can be relatively strong in both fish (Werner et al. 1983) and insects (Stamp and Bowers 1991), at least in the short term. A study on mayflies (McPeck and Peckarsky in press) suggests that strong demographic effects of predators can be almost entirely nonlethal in nature. Nevertheless, a four-year study of a lake fish population following the introduction of a predator suggests that in the long term, lethal effects can predominate over strong nonlethal effects (He and Wright 1992).

Another important issue is whether lethal and nonlethal effects produce qualitatively different ecological outcomes. On the surface, it might seem that lethal and nonlethal effects

would be qualitatively similar. For instance, strong top-down effects of predatory fish on stream algae populations (Power et al. 1985) might be the same regardless of whether predators eradicate herbivorous minnows from pools or simply cause minnows to emigrate from the pools. However, the long-term dynamics of the system are likely to be qualitatively different under each scenario. Whereas strong lethal effects might effectively eliminate herbivore populations from the system, strong nonlethal effects might ensure the herbivore's continued existence. Similarly, a habitat shift in the presence of fish may prevent the otherwise inevitable predator-driven extinction of a competitively superior zooplankton, while simultaneously allowing for the continued coexistence of a less competitive zooplankton congener (Leibold 1991).

Even less is known about the way in which lethal and nonlethal effects interact over time. One likely interaction between lethal and nonlethal effects may be driven by predator-induced habitat shifts, which can ultimately expose prey to an alternative predatory regime. A ten-year whole-lake study (Brabrand and Faafeng 1993) suggests that such interactions between lethal and nonlethal effects may greatly affect an ecosystem. Following the introduction of predatory pikeperch (*Stizostedion lucioperca*) to a lake, small roach (*Rutilus rutilus*) shifted from open water to shallow, near-shore (littoral) habitats. This habitat shift brought the roach into contact with (the less dangerous) predatory perch (*P. fluviatilis*), whose abundance increased markedly in the following years. The abundance of perch caused a reduction in the survival of juvenile roach, which may have catalyzed a further increase in predatory perch because juvenile perch and juvenile roach compete directly for food. The predator introduction thus left most of the lake's fish in the littoral zone and caused a shift in the dominant species from roach to perch. Overall, the long-term change in predation experienced by roach following pikeperch introduction would almost certainly have been different in the absence of the above behavioral habitat shift in juvenile roach.

Concluding remarks

Predators kill prey, a simple fact that has long dominated ecologists' view of predator-prey interactions. However, prey put much effort into avoiding predators, and ample evidence suggests that the ensuing nonlethal interactions between predators and prey may have important consequences for ecological systems. Nevertheless, much more work remains to gain a better understanding of the ecological effects of nonlethal predator-prey interactions. A particular challenge will be to relate nonlethal predatory effects to whole populations, especially outside of aquatic systems. Incorporating these nonlethal effects into models of population dynamics would be another important development. Ecologists also need good ways to quantify the relative ecological importance of lethal and nonlethal effects and their interaction over time. Furthermore, studies of nonlethal predator-prey interactions should assess the long-term ecological consequences of these nonlethal interactions. Determining these long-term consequences will be a tall order in many systems, but such assessments will ultimately determine the extent to which the average ecologist should be concerned with the "behavioral details."

If the ecological effects of anti-predator decision-making are even remotely as pervasive as the behavior itself, then a nonlethal perspective on predator-prey interactions may reveal a great deal about the nature of ecological systems. Such an outcome would be particularly fitting, 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.

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