

# Predator-prey interactions: a selective review of North American research results

Interacciones depredador-presa: una revisión selectiva de resultados de  
investigaciones norteamericanas

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## ABSTRACT

A very large body of literature covers the interactions of vertebrate predators and their prey in North America. Subjects range from analyses of predator diets, to evolutionary effects on the species involved, to contemporary effects on population density of both predator and prey. Approaches to the study of predation cover the spectrum of field, laboratory, and theoretical investigations. Abundant evidence shows that predation has been a strong selective force on the morphology and behavior of prey species. There is less evidence of closely coupled, i.e., coevolutionary effects. Population density and escape success of prey species seemingly exert more effect on the population density of vertebrate predators than vertebrate predators do on the population density of their prey. Immediate needs in the study of predator-prey interactions are reviews and syntheses of the diffuse literature. These would provide a basis for planning future study. Also, stronger bridges need to be built between empirical and theoretical approaches to predation.

Key words: Predation, vertebrate, evolution, population regulation, trophic-level interaction.

## RESUMEN

Una gran cantidad de literatura cubre las interacciones de los depredadores vertebrados con sus presas en Norteamérica. Los tópicos cubiertos varían desde el análisis de las dietas de depredadores y los efectos evolutivos sobre las especies involucradas, hasta los efectos contemporáneos sobre la densidad poblacional, tanto de depredadores como de presas. Los acercamientos al estudio de la depredación muestran un espectro, que incluye las investigaciones de terreno, las de laboratorio y las teóricas. Abundante evidencia muestra que la depredación ha sido una fuerte presión selectiva sobre la morfología y conducta de las especies presa. Existe menor evidencia sobre las interacciones más fuertemente acopladas, tales como los efectos coevolutivos. La densidad poblacional y el éxito de escape de las presas aparentemente ejercen más efectos sobre la densidad poblacional de los depredadores vertebrados que sobre la densidad de sus presas. Necesidades inmediatas en el estudio de las interacciones depredador-presa son revisiones y síntesis de la literatura dispersa. Ellas debieran proveer la base para la planificación de estudios futuros. También es necesario establecer conexiones más firmes entre los acercamientos empíricos y los teóricos a la depredación.

Palabras claves: Depredación, vertebrados, evolución, regulación poblacional, interacción trófica.

## INTRODUCTION

This is a review of the various approaches taken in North American studies of predator-prey interactions. Key results as well as gaps in what is known about predation in North America are discussed. Focus of the coverage is on the interaction of predator and prey. Peripheral areas such as predator-predator relationships are not included unless they affect between-trophic-level relationships. I present evidence of the effects of predation on two levels: (1) the evolution of both predator and prey, and (2) the present density and distribution of predator and prey.

Constraints of space and time did not allow a comprehensive review of the vast literature on this subject. I have tried to provide representative sources and, particularly, citations which provide access to a much larger body of literature. Taxonomic coverage is limited to tetrapod vertebrate predators in the classes Amphibia, Reptilia, Aves, and Mammalia, and prey taken by those groups. Coverage is biased toward predatory birds and to a lesser extent toward mammalian predators because of my personal interest and experience. Insectivorous birds, amphibians, and reptiles receive less attention. Several sources cited below, however, allow entry into the literature on those groups.

Predation is defined for this paper as the process in which animal species kill outright and eat individuals of other animal species. Predation has been viewed as opposing selective forces where the prey evolves to reduce the interaction and the predator to continue it (Pianka 1983), but see Abrams (1986) for a less simplistic approach. Long-term effects of these interactions do appear to have caused complex changes in morphology, behavior, and ecology in both predator and prey. Vermeji (1982), however, interprets predator-prey interactions to be more important as selective forces on the prey than on the predator. Other factors such as competition, community structure, abiotic factors, and, quite probably, stochastic events may interact with predation making it harder to understand.

Determining if predation is important as an ecosystem process is a primary consideration. Is predation persistent or intense enough to have a significant effect on the populations involved? Does it affect the communities of which the interacting species are a part? Evidence today suggests that predation does play a role in structuring some communities (Glasser 1979, Katz 1985, Sih *et al.* 1985). The most convincing support for this role of predation comes from rocky intertidal communities and is covered by Paine & Castilla elsewhere in these proceedings. Little similar evidence is yet available for terrestrial systems (Jaksić 1986). Sih *et al.* (1985) and Toft (1985) noted in recent reviews that competition has received much attention as a structuring force in communities and that predation deserves to be examined in the same light.

Laboratory, field, and theoretical approaches have all contributed to the understanding of what happens between predator and prey. Thousands of papers published on various facets give clues to predation's complex nature. No one, apparently, has attempted a complete review of this literature. See Errington (1976) for an early review and Curio (1976), Taylor (1984), and Feder and Lauder (1986) for more recent reviews on selected areas of predation.

Most of the studies included in this paper were done in North America, but some of the work was conducted in the Caribbean and Central America. Some key studies done in other geographic areas

which have had a major impact on the predator-prey research and theory in North America have also been included.

#### DOCUMENTING PREDATOR-PREY INTERACTIONS

##### *Predator diets and their implications*

A necessary first step in studying predator-prey relationship is to identify the interacting species, *i.e.*, what eats what. Literature dealing with the diets of predators constitutes the largest category of material on predation. Papers of this type range from those simply reporting diets of single predators (even single individuals) to sometimes complex analyses of prey preference, size, dietary diversity, and other trophic parameters. Detailed review of literature limited to food habits is beyond the scope of this paper. Several bibliographies, though, provide access to much of this information. Some of these cover insectivorous birds (Morse 1971, Hespheide 1975, Dickson *et al.* 1979), raptors (Olendorff & Olendorff 1968, Earhart & Johnson 1970, Clark *et al.* 1978, Sherrod 1978), mammalian carnivores (Rosenzweig 1966, Gittleman 1985) amphibians and reptiles (Arnold 1972, Toft 1985, Feder & Lauder 1986), and all vertebrate predators (Vezina 1985).

Predator diets establish two-species interactions. Longer chains of interactions are identified in tracing community food webs (Pimm 1980, 1982). Food webs have been explored in a number of ways. Paine (1966) reviewed the relationship of energy flow through food webs to community structure and diversity. Briand (1983) compiled a catalog of food chains which has stimulated much analysis; Cohen & Newman (1985), for example, found that proportions of basal species, intermediate species, and top predators in food chains are roughly invariant in the ratios of 0.19: 0.53: 0.29. Energy flow in food webs has also been examined. It was long considered that energy transferred upward between trophic levels was uniform at about 10% (see references in May 1986). However, Pimentel *et al.* (1975) and Humphreys (1979) showed that the 10% conversion efficiency is not uniform and may vary over two orders of magnitude; terrestrial ecosystems are often much less efficient than aquatic ones (Golley 1968).

Food habits data have been used to better understand trophic parameters of predator's niches. The calculation of prey species diversity/food niche breadth has been productive for understanding the degree to which predators are specialists or generalists in prey capture (Pianka 1975, Jaksić & Marti 1981, Brown & Parker 1982, Jaksić *et al.* 1982, Jaksić & Marti 1984, Marks & Marti 1984, Steenhof & Kochert 1985).

The relationship between body sizes of predators and their prey has been another productive area of research. These investigations reveal the overall prey-size range of a predator and possibly the optimum prey-size range. Examples of this information by predator types are: amphibians (Fraser 1976), reptiles (Schoener 1968, Pianka 1969, Reynolds & Scott 1982), mammals (Rosenzweig 1966, Gittleman 1985), and raptors (Storer 1966, Marti 1974, Jaksić & Marti 1981, Jaksić *et al.* 1982, Jaksić & Marti 1984, Marks & Marti 1984, Reynolds & Meslow 1984, Steenhof & Kochert 1985). Predator-prey size ratio studies can also assist in understanding the impact of predation on prey species and facilitate energetic studies of predator-prey interactions.

Schoener (1969) predicted that predator-prey body size ratio would be most critical in predatory birds and mammals where size restricts the ability to overtake, capture and kill prey. He also predicted that smaller predators should take a decreased diversity of prey sizes compared to larger predators. These predictions have been largely supported by empirical results in papers cited above. Wilson (1975) suggested that the efficiency of prey capture by predators is described by a curve which increases rapidly from the minimum prey size, reaches a plateau, and then descends slowly with increasing prey size. In general, small predators are limited to smaller size classes of prey but large predators can utilize both small and large prey. This relationship has been documented in hawks (Storer 1966), owls (Marti 1974, Marks & Marti 1984), insectivorous birds (Hespenheide 1975), mammalian carnivores (Rosenzweig 1966, Gittleman 1985), and a variety of terrestrial vertebrates (Vezina 1985).

Rosenzweig (1966) found that prey size clearly increased with body size in North American Carnivora. Gittleman's (1985) analysis of world-wide Carnivora dem-

onstrated that both prey size and prey-size diversity were positively correlated with predator body size. Predator body weight was not found to be correlated with other attributes such as latitude. Gittleman (1985) concluded that the relationship between predator and prey size is the result of larger predators having the equipment (size and weight) to subdue and kill a wider range of prey, and that larger predators have larger home ranges thus potentially encountering more prey types. The availability of prey of different sizes is also likely to be important in this relationship. Smaller predators may be able to specialize on normally numerous small prey species, but larger predators need to retain flexibility in prey size because larger prey species are less numerous. Social behavior of some predators, though, affects predator-prey size ratios; pack hunting increases the relative prey size that predators can subdue (Hespenheide 1975).

Prey size can also be important in determining capture success; Balgooyen (1976) found that American kestrels (*Falco sparverius*) were much more efficient in capturing insect prey than vertebrate prey (90% vs 40%). Body size in Norway rats (*Rattus norvegicus*) directly limited domestic cats (*Felis catus*) to capturing juvenile and subadult rats (Childs 1986).

#### *Predator foraging modes*

Foraging strategies are another important link between predators and their prey. How and where predators forage is important in determining which prey species may be encountered. Foraging strategies have been studied by field observations of predator behavior (*e.g.*, Crisler 1956, Root 1967, Schreiber *et al.* 1975, Pinkowski 1977, Freed 1980). Such studies have found that foraging behavior varies with habitat (Root 1967), weather (Peterson 1977), prey availability (Morton 1967), season (Ligon 1973) and from one population to another (Ligon 1968). Mangel & Clark (1986) recently attempted to build a unified model of animal foraging. See Stephens & Krebs (1987) for a major synthesis of foraging strategy.

Schoener (1971) theorized that opposite ends of the spectrum of foraging strategy should be represented by sit-and-wait predators and wide-foraging predators. Huey & Pianka (1981) examined the consequen-

ces of this in lizards. They concluded that, as predators, lizards which use the strategy of sit-and-waiting for prey have fewer chances to capture prey (but spend less energy) than wide-foraging lizards. However, sit-and-wait lizards have less risk of themselves becoming prey of another predator. Thus, both capturing prey and avoiding being eaten by other predators have probably shaped the foraging mode of lizards. Conversely, active prey species expose themselves to sit-and-wait predators as well as wide-foraging ones.

Habitat structure can be an important variable affecting predator foraging. Wakeley (1979), Baker & Brooks (1981), and Bechard (1982) reported that vegetative density is more important than prey density in determining where visually-hunting raptors forage. Janes (1985) produced a model of habitat preference which relates foraging behavior to habitat structure for raptors which hunt by sight. An untested assumption that might be derived from these studies is that prey species should seek habitats where their predators are at a disadvantage.

A body of theoretical literature attempts to measure cost versus benefits in foraging behavior. Predictions can then be made on how a predator should behave in situations where there are choices in what to eat, where to forage, how long to forage in one place, and how to move about in foraging. The assumption is that predators will make decisions which maximize their benefits (usually measured in energy gained) and minimize their costs in obtaining and processing energy from their food, *i.e.*, optimize their activity. Central-place foraging, where an animal forages from a base such as a nest, is an application of optimal foraging in which several of the previous choices interact with each other (Orians & Pearson 1979).

Optimal foraging theory began with the publications of MacArthur & Pianka (1966) and Emlen (1966). These were followed closely by a series of North American papers (Emlen 1968, Levins & MacArthur 1969, Rapport 1971, Schoener 1969, 1971). An explosion of papers on optimal foraging occurred in the 1970s and early 1980s. Several reviews of this literature have already been produced. The most recent contains 298 citations (Pyke 1984). Pyke (1984) noted that optimal foraging has been criticized as not testable and is

said to be doomed to failure because of the complexity of the natural world. However, he remains optimistic because studies that genuinely test optimal foraging theory have found a reasonably good level of agreement between predicted and observed foraging behavior.

Optimal foraging theory began with simple models based on assumptions that may not be valid. The literature (some of which is reviewed in this paper) shows that foraging patterns are affected by many factors other than choices based on maximizing energy budgets. Morse (1980) suggested that animals might not conform to the simple rules of optimal foraging because of interference from competitors, risk of predation, nutrient requirements dictating that prey items of low ranking be included in the diet, or that characteristics of resources may shift in space and time too rapidly to allow conformity to a simple model. Some of these problems may be resolved in long-term optimization models by Katz (1974) and Craig *et al.* (1979). Another approach was taken by Hughes (1979) who developed a more complex model to incorporate some of the constraints listed above.

The majority of papers dealing with optimal foraging are theoretical. Some explicit tests, however, do support predictions concerning optimal foraging behavior. A good example is the study of predation of northwestern crows (*Corvus caurinus*) on whelks (*Thais lamellosa*). Zach (1979) first examined the breakage of different sizes of whelk shells dropped from different heights. Then, with knowledge of the energy content of whelks of different sizes, he was able to predict what size of whelk a crow should choose, how high to fly with it before dropping it, and how many times to drop a particular whelk. Watching crows, he found that observed results and the empirically derived optima were in close agreement, *i.e.*, the crows performed optimally in this activity. They selected the largest whelks; the size that broke most easily and contained the greatest energy reward. The crows also carried the whelks only to the minimum height necessary to break them. A study of heron foraging, on the other hand, found foraging efficiency to be about 10% below that predicted (Kushlan 1978).

Pyke (1984) cautions that predictions of most optimality models apply only to

the time an animal actually spends in foraging. What occurs in other parts of an animal's time budget has been mostly ignored. Herbers (1981) points out that inactivity has received very little attention as a behavioral category. She says that even though quiescence can serve valuable ecological functions, not all inactivity has biological functions. Herbers' model predicts that for many combinations of activity levels and resource spectra, time spent looking for food is less than the time spent not looking. The ironic outcome is that inactivity can be the result of efficiency by a predator. Extremely efficient predators have more free time while less efficient predators have little free time and appear to be doing something of consequence most of the time.

#### *Predator search cues/prey vulnerability*

Investigation of the cues predators use to find prey has been another productive area of research in establishing links between predator and prey. These studies also provide insight into what makes prey vulnerable even though most of this research has focused on predators. Conspicuousness, oddity, size, and level of activity of prey have all been studied, mostly in laboratory investigations.

Dice (1947) conducted pioneer laboratory studies on the detection of prey which contrasted in color with their background. He found that mice which resembled the color of the substrate enjoyed a 20% survival advantage over mice which contrasted in color when both were subjected to predation by owls. Kaufman (1974a, 1974b) also observed that owls selected color strains of mice which contrasted with the soil color in seminatural enclosures. However, Trumpy *et al.* (1983) found no difference in selection by owls between two color strains of *Peromyscus maniculatus*. Differences in experimental methods and/or the degree of difference between the various color strains of mice used in these experiments may explain the conflicting results.

Helmut Mueller conducted a series of laboratory experiments in prey selection using raptors as predators (Mueller 1971, 1975). He believed that a specific search image was developed by the predator with oddity of the prey being more important than conspicuousness as a search cue.

Marti & Hogue (1979) found that screech owls (*Otus asio*), given simultaneous choices, selected smaller over larger mice of one species. Postler & Barrett (1982), though, reported that screech owls took more of the larger of two mouse species. Contradictions in results between Marti & Hogue (1979) and Postler & Barrett (1982) may be the result of differences in method (laboratory vs. semi-natural) and prey type (one species vs. two species).

Metzgar (1967) found that transient mice (*Peromyscus leucopus*) were preyed upon at a higher rate by screech owls than were resident individuals of the same species. Similar results were reported by Ambrose (1972) for barn owl (*Tyto alba*) predation on voles (*Microtus pennsylvanicus*). The higher level of activity by transient mice was identified as the probable reason for their vulnerability in both of these studies. Other investigators specifically examined the role of prey activity as a search cue for predators. Snyder (1975) discovered that a red-tailed hawk (*Buteo jamaicensis*) took more of active prey than inactive prey when offered simultaneous choices in a laboratory test. Size of the prey, however, was a factor; the hawk tended to take less active prey when given large rats. Evidence from field studies suggests that predators which specialize on large, active prey have a strong bias towards young, old, or ill individuals (Mech 1966, Cole 1972).

The above papers all focused on predators which hunt primarily or entirely by sight. Several other sensory modes are, of course, important in the capture of prey by many predators. Auditory cues are used by bats (Griffin 1953), owls (Payne 1962), and northern harriers (*Circus cyaneus*) (Rice 1982). The prey's scent is also an important cue used by many predators; Cushing (1985) showed that estrous mice were more susceptible to predation by weasels than were diestrous females. David & Jaeger (1981) found that *Plethodon* salamanders can locate immobile prey by scent, and Burghardt (1967) found that chemical perception of prey by newborn snakes is species-specific and clearly related to their natural feeding ecology.

#### RECIPROCAL PREDATOR-PREY EFFECTS

The question of whether coevolution, strictly defined as reciprocal genetic changes

that occur in two or more ecologically interacting species, occurs between predator and prey seems to be unanswered (Futuyma & Slatkin 1983). Bakker (1983) may have found evidence that it does occur in certain groups. His model system was large cursorial predators and their ungulate prey. The prey species in these cases should evolve toward the longest, swiftest limb form. Paws of their canid predators, however, must retain some ability to dig and cannot be fine-tuned for speed as in the ungulates.

#### *Field studies*

Remarkably few data are available on the population dynamics of both predator and prey. This is probably largely due to the extreme difficulty of collecting this information for vertebrate predators. One of the best understood large predator-prey systems in the world is the wolf (*Canis lupus*) – moose (*Alces alces*) interaction on Isle Royale in Lake Superior, USA. A series of investigators has studied this interaction for about 25 years (Mech 1966, 1970, Jordan *et al.* 1967, Peterson 1977, Allen 1979, Peterson *et al.* 1984). The one prey-one predator system on Isle Royale was thought to be predictable after the first 9 years of study. Later, it became clear that the system was not so simple nor as stable as first thought. Several additional strong interactions were identified which affect the stability: the unpredictability of weather coupled with browse availability and the wolf social system. Thus, we are left with the realization that the most intensively studied vertebrate predator-prey system in North America still is not fully understood.

#### *Theoretical studies*

The logistic curve, developed originally by Verhulst (1845) and again, independently, by Pearl (Pearl & Reed 1920) permitted the beginning of ecological modeling. Lotka (1925) modified the logistic for use in studying predator-prey interactions; he accounted for losses to the prey species relative to the population size of the predator and prey. At the simplest level, it is assumed that the prey is the only food of the predator and that the only source of prey death was predation. No inter-specific competition and no density de-

pendent feedback on either population were modeled. This system produces coupled oscillations of predator and prey populations.

As a model to represent real populations with density dependent limits, the logistic curve has been criticized because it does not consider age structure, time lags, and random environmental events – all factors which affect natural populations. The development and history of the logistic equation was thoroughly reviewed by Hutchinson (1978). May (1981) and Vandermeer (1981) reviewed the application of the logistic curve to predator-prey modeling and discussed further advances in predator-prey theory.

Lotka-Volterra predator-prey equations and a variety of more robust models have been explored by many investigators in attempts to elucidate predation (*e.g.*, Tanner 1975, Gatto & Rinaldi 1977, Taylor 1984). Numerous other approaches have also been attempted. For example, Rosenzweig & MacArthur (1963) devised a graphical model for predator-prey interactions. Chesson (1983, 1984) developed models for switching of prey preferences by predators. Learning behavior for predators faced with varied prey densities was modeled by bobisud & Voxman (1979). Recently, consideration of pseudorandom dynamics has entered ecological theory bringing the possibility that ecosystem behavior is chaotic (Gilpin 1979, Schaffer 1985).

#### EFFECTS OF PREDATORS ON THEIR PREY

##### *Effect on prey morphology and physiology*

The intense selective pressure by predators has apparently led to the evolution of an astonishing array of adaptations to reduce predation. It is not possible to test that these adaptations were actually the result of evolution under the selective pressure of predation (although, see Kettlewell 1961). However, most make no sense in any other context. The types of prey defenses are too numerous to review fully in this paper. I concentrate here on examples of studies which tested prey defenses experimentally. Edmunds (1974) and Vermeij (1982) provide good reviews of antipredatory adaptations.

A widely occurring form of defense is crypsis, *i.e.*, being visible but camouflaged to resemble the environment. This may be as simple as being the same color as the background; Dice (1947) in a laboratory situation showed that owls more readily found dead mice by sight which contrasted in color with their background than mice which were similar in color to the background. Heatwole (1968) tested crypsis in Caribbean lizards by using human observers to simulate visually-hunting predators. Certain body patterns were missed more often and thus considered to be most cryptic. Underwing moths (*Catocala* spp.) roosting on exposed tree trunks selected the best background and aligned themselves for the best crypsis (Sargent 1966). Pietrewicz & Kamil (1981), though, discovered that bird predators could learn to find hidden moths. However, variation in the wing pattern among the moths made it harder for birds to develop a search image. Thus, being a little different was a survival advantage for individual moths.

Some prey species avoid producing indirect evidence of their presence. Palatable caterpillar species were found to minimize visible leaf damage so as not to attract the attention of predators but unpalatable caterpillars made no attempt to conceal their damage (Heinrich & Collins 1983).

Various arctiid, geometrid and noctuid moths detect bats acoustically before the bats detect them (Roeder 1966). When bat-to-moth distance is great (judged by lower intensity of bat sonic pulses) the moth simply turns and flies straight away. When bats are detected at closer range, the moths either fly in wild gyrations or drop to the ground to escape.

At least one vertebrate group also has developed hearing adaptations to avoid their predators. Kangaroo rats (*Dipodomys*) have enormously expanded auditory bullae. The function of these was unknown until Webster (1961, 1962) showed that they make possible an extreme sensitivity to low-frequency sounds (1-3 khz). Webster discovered that wing noise of owls and noise of snake scales scraping on the substrate produce the low frequency sounds to which the rodents are sensitive. Kangaroo rats were able to hear the approach of these predators and avoid attack through a sudden vertical leap.

Aposematic coloration advertises that an animal is unpalatable or dangerous. Con-

siderable evidence shows that vertebrate predators can learn to associate unpalatability with color and avoid these species by sight. This mechanism has been studied extensively in the monarch butterfly (*Danaus plexippus*) by Lincoln Brower and his associates. Monarchs as larvae feed on milkweeds (*Asclepias* spp.) from which they ingest cardiac glycosides. These chemicals are retained throughout the monarch's life in quantities sufficient to cause vomiting in birds which eat them (Brower 1969, Brower *et al.* 1967, Platt *et al.* 1971). Cardiac glycosides can be lethal to birds and mammals if retained in the digestive tract. Naive bluejays (*Cyanocitta cristata*) learned to avoid monarchs in 1 or 2 trials. Some monarchs, though, feed upon milkweeds not containing cardiac glycosides and thus are palatable (Brower *et al.* 1968, Brower 1969). These individuals are protected from predation by looking exactly like unpalatable monarchs (automimicry). Some birds, however, can overcome the chemical defenses (Fink & Brower 1981).

Closely allied with aposematism as an antipredator defense is Batesian mimicry; a palatable species gains protection from predation by closely resembling an unpalatable or dangerous one. This mechanism is well documented in butterflies (Brower 1958). Although most known mimicry is visual, at least one case of acoustic mimicry has been documented (Rowe *et al.* 1986).

Repellents are another common means of defense. Vetter (1980) found that black widow spiders (*Latrodectus hesperus*) used silk strands with sticky blobs against predatory mice. Spiders with spinnerets experimentally blocked were three times more likely to be killed when attacked by mice. Several salamander species produce sticky secretions which have been shown to be effective repellents against their snake predators. *Ensatina eschscholtzi*, for example, tries to hit attacking snakes in the head with its tail. Sometimes it is able to glue the snake's mouth shut or otherwise glue the snake to itself (Arnold 1982).

Bombardier beetles (*Brachinus* spp.) squirt boiling hydroquinones at their predators (Aneshansley & Eisner 1969). Grasshopper mice (*Onychomys* spp.), though, successfully prey upon stink beetles (*Eleodes*) by aiming them away or pushing the beetle's abdomen into the soil to deflect

the noxious chemical (Eisner & Meinwald 1966).

Autotomy, the mechanical release of body structures in order to escape predation, has evolved in many forms of animals; Dial & Fitzpatrick (1983) reported that it is found in 13 of the 20 or so families of lizards. Dial & Fitzpatrick (1983, 1984) showed that autotomy in lizards does significantly increase survival when attacked by a predator. Further, they found that autotomized tails that thrashed a great deal were more effective in preventing predation of the lizard than were tails which thrashed only a little.

#### *Effects on prey behavior*

It is obvious that the risk of being preyed upon affects the behavior of prey species. Pulliam & Caraco (1984) provide a brief review of the tradeoffs whereby prey species balance the risk of predation with other necessary activities. Ydenberg & Dill (1986) developed a model to predict how lost feeding opportunities and risk of predation interact to produce an optimal flight distance from approaching predators. Caraco (1981) found that small ground-feeding birds spent more individual time looking up for predators as flock size decreased, and thus had less time to feed. Lima & Valone (1986) reported that a diurnal tree squirrel took smaller items than would be predicted by optimal foraging alone. The conclusion being that by gathering smaller food items the squirrels put themselves in less danger of predation. Bildstein & Althoff (1979) discovered that mice froze when silhouettes of flying raptors were pulled overhead.

Clarke (1983), in a laboratory study, discovered that mice altered their activity significantly in relation to light intensity — they stayed closer to cover and froze in response to sounds when light was brighter. Several investigators have noted that in the wild small mammals also appear to alter their activity patterns in response to the intensity of moonlight (Kaufman & Kaufman 1982, Price *et al.* 1984). Kotler (1984, 1985) manipulated food resources and light intensities in a field experiment. He concluded that some desert rodents altered their foraging patterns in response to light levels but others did not. The most abundant predator in the area was the long-eared owl (*Asio otus*). Larger rodents,

those less likely to be taken by these owls, were largely unaffected by differences in light levels. Smaller species, though, did change their activity pattern in response to increased illumination. Price (1984) concluded that the effects of predation risk on microhabitat affinities of desert rodent assemblages are less pronounced than the effect of competition coupled with patchily distributed food.

Clustering in large numbers may reduce the risk of predation for individuals. Numerous individual prey in one place reduces the chances of an individual being taken (Arnold & Wassersug 1978, Calvert *et al.* 1979).

Alarm calling is another mechanism through which social animals may reduce predation. Using a theoretical approach, Charnov & Krebs (1975) predicted that an individual giving an alarm call may, instead of making itself more vulnerable by calling attention to itself, actually lower its own vulnerability. Sherman (1977) found that predictions about alarm calls based on kin selection theory were upheld in the colonial Belding's ground squirrel (*Spermophilus beldingi*). Females, which are sedentary and likely to live near close relatives, gave more alarm calls than males. Males move around more and are less likely to be near and thus less able to warn close relatives of danger.

Schall & Pianka (1980) tested the hypothesis that prey having a diversity of escape behaviors should create more difficulty for predators to form search images. Their data on escape behavior diversity of a lizard, however, could also support an entirely different model: one in which lizards learn to be wary when attacked by predators.

#### *Effects on prey population density*

Field studies by Errington (1956, 1967) were very influential for many years in shaping the idea that predation had little impact on prey populations. Errington believed that prey population densities were limited primarily by factors intrinsic to the prey. Craighead & Craighead (1956) pioneered the study of the impact of an assemblage of predators upon prey species, an approach expanded by Jaksic *et al.* (1981). Craighead & Craighead (1956) concluded, in contrast to Errington, that predation can be a factor limiting a prey population's numbers.



A widely-cited paper by Hairston *et al.* (1960) further promoted a shift from the beliefs fostered by Errington. They concluded that populations of herbivores are limited by external factors including predation. Predators, though, were considered to be food-limited. Hairston *et al.* (1960) reached these conclusions through logic and did not support them with data. Murdoch (1966) and Ehrlich & Birch (1967) found problems with the logic in Hairston *et al.* (1960) and criticized the ideas proposed as being untestable.

Predation on voles (*Microtus* spp.) and its effect on vole population density have been studied by many investigators. Pearson (1966, 1971) concluded initially that predation is an essential part of the *Microtus* population cycle. He thought that predation could help bring the mice to low densities after something else, for example weather, initiated a decline in the population density. Later, in reviewing predation on *Microtus*, Pearson (1985) said that we know what eats *Microtus* but not what effect predation has on predator or prey populations. Krebs & Myers (1974) believed that predation could not possibly account for density changes at peak vole populations. Boonstra (1977) also decided that predation is not necessary to initiate or maintain a decline in *Microtus townsendii*, but Beacham (1979) thought that predation on voles by raptors was density dependent. Baker & Brooks (1982) were not certain what affect predators had on populations of the *Microtus* they studied. They believed, however, that density of vegetative cover was very important in affecting this predation.

The role of predation in cyclic populations of hares and grouse has long been of interest. Elton & Nicholson (1942) noticed that cyclic fluctuations of lynx (*Felis lynx*) and snowshoe hare (*Lepus americanus*) resembled classic Lotka-Volterra prey oscillations. However, recent evidence suggests that hare cycles are the result of hare-vegetation interactions and that lynx may follow passively (Keith 1983). Lloyd B. Keith and his associates studied the interactions of vegetation, prey (snowshoe hare and ruffed grouse, *Bonasa umbellus*), and their predators (lynx, great horned owl, *Bubo virginianus*, and red-tailed hawk) for 15 years (Meslow & Keith 1968, Keith *et al.* 1977, Rusch & Keith 1971, Rusch *et al.* 1972, Luttich *et al.* 1971 and summariz-

ed in Keith & Windberg 1978). Predation appeared to play its greatest role by intensifying and prolonging the prey population's cyclic decline but not in initiating the decline or in preventing depressed prey populations from recovering. Wagner (1981), though, concluded that coyote (*Canis latrans*) predation on jackrabbits (*Lepus californicus*) did result in Lotka-Volterra oscillations.

The impact of vertebrate predators on arthropod prey has also been evaluated. Several researchers, using predator exclosures, have concluded that predation can significantly reduce prey populations (Holmes *et al.* 1980, Gradwhol & Greenberg 1982, Pacala & Roughgarden 1984).

Predator removal projects may offer some insight into whether or not predators regulate prey numbers. However, most of them were done with the objective of increasing populations of game species and were not meant to answer any fundamental questions about predator-prey relationships. One of the most famous, but also most poorly documented of these projects, involved the Kaibab deer herd in northern Arizona (Rasmussen 1941, McCulloch 1986). A massive predator removal campaign coupled with a ban on deer hunting and removal of domestic livestock from the range seemed to cause a huge increase in the deer population. This event is commonly mentioned in biology textbooks as a classic case of population irruption in response to release from predation. However, it occurred in the early 1900s and only anecdotal observations are available to document what happened. Caughley (1970) criticized the conclusion that predator control alone was responsible for the increase in the Kaibab deer herd. He said that data on deer numbers were too unreliable and that the reduction in domestic livestock and the effects of fire may also have played a role in the irruption.

Many modern predator removal experiments have been attempted. Most of these were relatively short term and lacked controls. The effects of predator removal have been examined on waterfowl (Balser *et al.* 1968, Duebbert & Kantrud 1974, Duebbert & Lokemoen 1980), pheasant (*Phasianus colchicus*; Chesness *et al.* 1968), white-winged dove (*Zenaida asiatica*; Blanksinship 1966), ruffed grouse: Edminster 1939, Crissey & Darrow (1949), and deer (Beasom 1974, Kie *et al.* 1979). All of

these produced essentially the same conclusion: predator removal caused an increase in production of young but no long-term detectable increase in the adult populations. A more comprehensive project was carried out by Trautman *et al.* (1974). Eight 100 sq. mile study areas were delineated in South Dakota. One was left as a control, four were subjected to intense reduction of red foxes (*Vulpes vulpes*), and all small carnivores were reduced in the remaining three. No response was detected in densities of small mammal prey, jack-rabbits greatly increased in response to fox control, and pheasants showed a large increase when all carnivores were reduced.

Related in concept to predator removal experiments are studies from natural predator-free islands (Troyer 1960, Schnell 1968, Windberg & Keith 1976). Results from these show higher prey species densities in the natural absence of predators. A possible confounding factor in these studies is that dispersal from islands may be limited or nonexistent, producing a higher population density than on mainland areas.

All the above studies may suffer from the same problem: asking too simple a question (Taylor 1984). It appears that predator-prey population research must be long-term or designed in a way to separate out the effect of predation from other factors depressing prey populations. Bergerud (1971) made progress in research design by studying total mortality in 1- to 6-month-old caribou (*Rangifer tarandus*). He then removed lynx from one area and compared mortality in the removal area with a control area. Thus, he was able to attribute a certain portion of total mortality to predation. The long-term effect upon the population was still not known, however.

#### EFFECTS OF PREY ON THEIR PREDATORS

##### *Effect on predator population densities*

Most research concerning the impact of prey species on their predators has emphasized functional or numeric responses of the predators to changing prey densities. These responses were first identified by Solomon (1949); he described the functional response as a change where an in-

dividual predator eats proportionally more or less of a prey species as the prey changes in density. The term numeric response describes a change where a predator increases or decreases its own numbers in relation to changes in prey density. Holling (1959) investigated these responses in a series of influential laboratory and field studies of predation by small mammals on sawfly (*Neodiprion sertifer*) larvae. He determined that three species of small mammal predators showed different patterns of numeric and functional responses to changing densities of prey.

Many investigators have documented numeric and/or functional responses in predatory birds in response to changes in densities of their prey (Pitelka *et al.* 1955, Luttich *et al.* 1971, Rusch *et al.* 1972, Phelan & Robertson 1978, Adamcik *et al.* 1979, Baker & Brooks 1981, Steenhof & Kockert 1985). Pearson (1966), MacPherson (1969), Clark (1972), and Brand *et al.* (1976) did so with mammalian carnivores. The most elucidative study of this type was by Frances Hamerstrom (Hamerstrom 1979, Hamerstrom *et al.* 1985). She found a marked numeric response in northern harriers over a 25-year period. Vole density had a major effect on the number of harrier nesting attempts and their success. Vole density also affected the harrier mating system; harriers are most commonly monogamous but in periods of high vole density polygyny was recorded (Hamerstrom *et al.* 1985).

Murdoch (1969), by extending Holling's model to multispecies prey conditions, developed a model for switching of prey. Switching has occurred when the number of attacks by a predator on a prey species is disproportionately high when the prey is abundant relative to other prey and vice versa.

Using snake assemblages as a model, Arnold (1972) investigated the hypothesis that predator species density should increase with the number of available sympatric prey species. He concluded that much of the variance in numbers of sympatric snake species is related to prey species densities and not due to a common correlation with latitude. This analysis supports the view that where there are more species of prey, more species of predators can coexist. This may be because there are more ways to avoid competition.

*Effects on predator morphology and behavior*

It is generally accepted that adaptations involving prey capture abilities of predators are responses to selective pressures caused by efficiency of prey in escaping. Vermeij (1982) cautions, though, that the selective pressure on predators is much less than that on the prey. Few good analyses of the anatomical and physiological adaptations of predatory mechanisms exist. Griffin (1953) reported that bats could locate and capture prey using echolocation. The anatomical and physiological mechanisms of this tactic were further elucidated by Griffin *et al.* (1960) and Grinnell (1963a, 1963b).

The most intensively studied sensory adaptation for prey capture is that of auditory prey location in the barn owl. Begun by Payne (1962), this work was pursued by Masakazu Konishi and his students (Konishi 1973, Quine & Konishi 1974, Konishi & Kenuk 1975, Knudsen & Konishi 1979, Knudsen 1981, Knudsen *et al.* 1982, Knudsen & Knudsen 1985). These studies showed that barn owls can locate and capture prey using only auditory cues. The barn owl is the most accurate in sound localization of all animals tested. It uses memory to recognize sounds made by prey and discriminate them from background noise.

Rice (1982) found that the northern harrier has converged on the same prey-detection mechanism. Harriers are only slightly less accurate in locating sounds than barn owls but are considerably more accurate than two other diurnal raptors tested.

Goslow (1971) analyzed the approach and strike mechanisms of several raptor species using very high speed cinematography. He discovered differences in speed of approach and limb extension that may help explain the type and size of prey taken by different raptor species. These field studies were supported by anatomical and physiological studies of raptor limbs (Goslow 1972).

#### CONCLUSIONS AND SUMMARY

We know much about predation and its effects on organisms and populations, and a lesser amount about its effects on com-

munities. The knowledge, however, is uneven. For example, we know a great deal about the diets of many predators, but for the most part, we have very little information about what segments of prey populations are most vulnerable and why. Evidence at present strongly suggests that the greatest effect of terrestrial vertebrate predators on their prey has been to cause evolutionary changes in morphology, physiology and behavior. Conversely, prey seem to influence their predators mostly by affecting the predator's population density.

Several approaches are needed to progress in our understanding of predator-prey interactions. First is a gathering together of the available information into comprehensive reviews of literature. The diffuse nature of this literature is a real hindrance to understanding predator-prey relationships. These reviews may range from coverage of predation by a single species to predation by assemblages of predators regardless of their taxonomic position. Broad syntheses are also badly needed in order to integrate results from diverse but interacting aspects of predation. For example, the sensory systems of predators have a great deal of influence on what kinds of prey are most vulnerable to the predator. Reviews not only make a body of material accessible, they also pinpoint the gaps in knowledge.

A second area of need is investigations involving equal effort of study on both trophic levels. For terrestrial vertebrate predators and their prey this type of investigation is usually difficult and expensive. Nevertheless, there are no apparent alternatives to obtain the needed understanding.

Thirdly, more long-term studies should be undertaken. The few available examples illustrate that long-term studies reveal that random or unpredictable events may drastically change conclusions of shorter studies (Weatherhead 1986).

Fourthly, our understanding of predator-prey relationships needs to be integrated with other, possibly interacting species-species relationship, *e.g.*, competition and parasitism. See, for example, Moore's paper in these proceedings for examples of how some parasites modify their host's behavior to make the host more vulnerable to predation.

Finally, there is a need to strengthen bridges between empirical and theoretical studies. Theoreticians have advanced a plethora of hypotheses in need of testing in the natural world.

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