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Prey and predator interactions

In Chapter 4 we learned how plants and herbivores can influence each other's abundance, distribution and evolution. Here we consider another important inter trophic level relationship that can have widespread ecological and evolutionary effects on biological communities, the interaction between prey and their predators. In an ecological sense, predators can dramatically affect the abundance and distribution of their prey populations, and reciprocal effects of prey on their predators are also inevitable, as prey are obviously an important food source for predators. Likewise, the diverse feeding habits of predators form linkages that are responsible for the flow of energy through food webs. Predation can also be a powerful evolutionary force with natural selection favoring more effective predators and less vulnerable prey. Thus, it is imperative that we understand the process of predation and its complex effects on species interactions, and population and community dynamics. In the sections that follow, we explore critical elements of prey-predator interactions, namely how prey and predators interact to affect each other's long-term population dynamics, what factors stabilize prey-predator interactions and promote their persistence, how multispecies interactions influence the role of predation in complex food webs, the contribution of behavior to a predator's total impact on prey populations, and how predators and prey have reciprocally influenced each other's evolution.

7.1 What is a predator?

In a very general sense, predation can be viewed as the consumption of one living organism (the prey) by another organism (the predator). Usually the whole prey item is killed and eaten. If the prey organism in question is a plant, then this general definition of predation includes herbivory. However, whole plants are usually only killed and eaten by a single predator when the plant is in the seed or seedling stage. Hence the terms seed predator and seedling predator are in common usage. In the context of this chapter, however, we restrict our definition of predation to acts of carnivory in which animals consume other animals. We define predators as animals that kill and consume all or parts of their prey, and require many prey items to reach maturity. This definition distinguishes predators from parasitoids, such as some small wasps and flies, which require and eat only one prey item during their life span. Parasitoids are free living as adults, and lay their eggs in or on a host. Larvae hatch from the eggs and live parasitically in or on the host, eventually killing it. For conceptual simplicity we discuss predators and parasitoids as representing distinct biological groups; however, the line distinguishing predators from parasitoids is often blurred, with biological reality perhaps better represented as a continuum rather than discrete categories.

Although a single parasitoid will directly consume a single prey item, an adult female parasitoid that oviposits on many hosts will ultimately be responsible for the death of many individuals. In this way, predators and parasitoids can have comparable ecological impacts, and prey-predator and host-parasitoid interactions share many important similarities. As a result, parasitoids have contributed much to the development of the theory surrounding predation (Raffel *et al.* 2008). Therefore, while the focus of this chapter is on predators and their prey, the relationship between parasitoids and their hosts will also be considered where relevant. A more detailed treatment of the ecological and evolutionary

biology of parasitoids, and the parasitic lifestyle more generally, is provided in Chapter 8.

7.2 The generalized feeding habit of predators

While it is convenient to think of predators as occupying a discrete trophic level that is functionally distinct from that of their prey, in reality predators are often generalized in their feeding habits and may consume not only prey, but also other predators and/or plant resources (see Chapter 13). In this circumstance, generalist predators are more accurately described as omnivores, consumers that feed from multiple trophic levels. For instance, big-eyed bugs are often labeled as generalist predators, but are actually omnivorous consumers whose diverse range of prey species includes aphid and lepidopteran eggs and larvae, as well as the pods, seeds and leaves of many plant species. To further complicate matters, big-eyed bugs also fall victim to predation by omnivorous fire ants that compete with big-eyed bugs for herbivorous insect prey. This special case of omnivory, when predators consume other predators with which they compete for a common prey resource, is called **intraguild predation**. **Cannibalism** is distinguished from intraguild predation as occurring when predators consume members of their own species. Wolf spiders (*Lycosa* and *Pardosa*), for example, are notoriously cannibalistic, consuming smaller individuals in the population and even their own offspring. As we will see in Chapter 13, generalist predators that engage in omnivorous feeding strategies, including plant feeding and intraguild predation, enhance the complexity of food webs and complicate our understanding of the role of predators in community dynamics.

Although many predators are generalists and feed on a diversity of prey species, there are some very specialized feeders. Ground beetles in the genus *Scaphinotus* feed selectively on mollusks and have a long head and mandibles adapted for reaching deep

into snail shells. In contrast to predators, parasitoids commonly exhibit a high degree of specialization, often feeding on only a single life stage of a particular group of insects. This level of specialization is likely the result of the intimate association between parasitoids and their hosts (see Chapter 8). Whether predators are generalists or specialists can have consequences for food web dynamics, as we will see later.

7.3 Predator effects on prey abundance

Excluding predators from or adding predators to natural prey populations provides evidence that predators indeed can reduce populations of their prey, very significantly so in some cases. For example, herbivorous planthoppers (*Prokelisia marginata*) and their wolf spider predators (*Pardosa littoralis*) co-occur on the inter-tidal marshes of North America. When spiders are removed from habitat patches, planthopper populations erupt to very high levels. If spiders are removed, but are then added back into habitat patches at natural densities, planthopper populations remain suppressed (Döbel and Denno 1994).

The biological control of crop pests following the release of natural enemies provides further evidence that predators suppress prey populations. With the accidental introduction of cottony cushion scale (*Icerya purchasi*) from Australia, the California citrus industry became seriously threatened by this severe insect pest. In the late 1800s, a predaceous ladybird beetle (*Rodolia cardinalis*) was collected in Australia and subsequently released into California citrus groves. Shortly after the release of this efficient predator, it completely controlled the scale insect and saved the citrus industry from financial ruin (Caltagirone and Doult 1989). The introduction of some insect growth regulators in the late 1990s that were highly toxic to *Rodolia* caused a re-emergence of cottony cushion scale, showing again that this predator remains the primary regulator of scale

populations (Grafton-Cardwell *et al.* 2006). Since this classic case, the encouragement or release of arthropod predators has frequently resulted in reduced pest populations (Symondson *et al.* 2002). There are cases, however, in which predator removal does not result in increased prey density. Often, such cases involve compensatory mortality, whereby the mortality inflicted by predation is replaced by mortality from another limiting factor like food shortage, or compensatory population growth of prey as a result of reduced intraspecific competition.

It is clear that predators can inflict high mortality on prey populations and that in the absence of predation, prey population eruption is possible (see Chapter 11). But what is the exact nature of this predation, and how do prey and predators interact to affect each other's long-term population dynamics? As we will see later in this chapter, predators can have both consumptive and non-consumptive (i.e., behaviorally mediated) effects on populations of prey. We focus first on the consumptive impacts of predators and how these effects are influenced by a predator's response to changes in prey density, as well as interactions among conspecific and heterospecific predators.

7.4 Predator responses to changes in prey density

The first step in understanding the prey and predator relationship is to understand the response of predators to changes in prey density. This can either be the response of an individual predator in its ability to catch and handle prey (functional response) or an increase in predator population size (numerical response) as prey densities grow (Solomon 1949).

7.4.1 Functional response

The functional response of a predator describes how an individual's rate of prey consumption changes in response to prey density. In a practical sense,

functional responses can be used to estimate rates of prey depletion, identify predator preferences for particular prey types, characterize linkages across trophic levels and may ultimately contribute to the prediction of community dynamics.

Using a component analysis approach, Holling was able to identify several predator-related factors that contribute to the functional response (Holling 1959a, b, 1961). In his now classic experiment, a blind-folded human “predator” foraged for 4 cm diameter sandpaper disks or “prey” that were tacked to a 9-ft² table. The number of disks captured in one minute by tapping the table until finding a disk and removing the disk from the table was recorded across a range of disk densities. These data were used to develop a general model of the predator functional response known as the Holling disk equation. The general disk equation is

$$N_A = \frac{aT_T N_o}{1 + aT_H N_o} \quad (7.1)$$

where N_A is the number of discs removed, N_o is the density of discs offered, T_T is the total time available for searching, T_H is the handling time and a is the searching efficiency or attack rate of the predator. This equation describes what is known as a Type II functional response curve in which the consumption rate of the predator increases at a decelerating rate until it levels off to an upper plateau (Figure 7.1). This saturating response is the result of a trade-off in the time available for a predator to search for prey (T_T) and the handling time (T_H), the time required to subdue, consume and digest each prey item. At low prey densities, predators spend most of their time searching for prey items. At high prey densities most of a predator’s time is spent handling captured prey and relatively little time is spent searching for additional prey. Eventually, predators become satiated and the response saturates since predators that are not hungry will not continue to consume additional prey items (Holling 1966). Thus, Holling’s work highlights four essential components of the Type II functional response: rate of successful search,

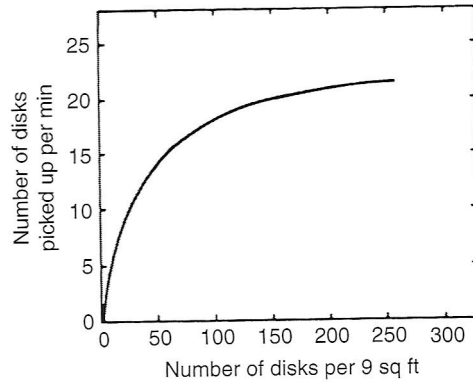


Figure 7.1 Graphical representation of Holling’s disk equation showing the rate of discovery by a human “predator” in relation to the density of sandpaper disc prey. From Holling (1959b).

time predator and prey are exposed to each other, handling time and hunger.

The basic Type II functional response curve originally described by Holling accurately represented the few published responses of natural enemies to prey density that existed at the time, all of which involved parasitoids or invertebrate predators, including eulophid and braconid wasps, corixid bugs and dytiscid beetles (Holling 1961). Further study revealed that alternative relationships between predator consumption rate and prey density were possible under different ecological scenarios. For example, vertebrate predators such as small mammals and birds produced a sigmoidal or S-shaped functional response. Only small variations on the disk equation were necessary to accurately reproduce these alternative functional response curves. Holling (1959a) described three major types of functional response (Figure 7.2):

Type I functional response – For predators exhibiting a Type I functional response, the consumption rate of a single individual is limited only by prey density. Thus, over a wide range of densities, per capita consumption and prey density are linearly related, up to a

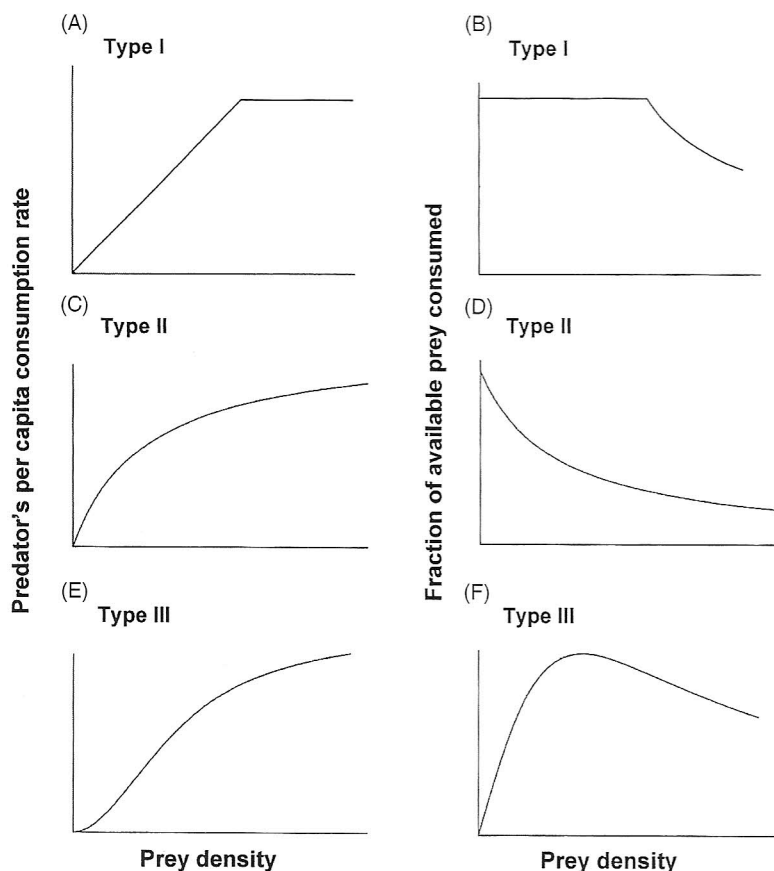


Figure 7.2 Three major types of functional responses. Per capita consumption rates are shown for predators exhibiting Type I, Type II and Type III functional responses (A, C and E, respectively), as is the proportion of prey taken of the total number offered for each type of functional response (B, D and F).

threshold density (Figure 7.2A). In this case, the proportion of prey captured of the total number offered remains constant and independent of prey density (Figure 7.2B). The Type I functional response is a specialized case that may be exclusive to “filter feeders,” including web-building spiders, which are able to snare many food items simultaneously (Jeschke *et al.* 2004).

Type II functional response – Most invertebrate predators (e.g., hunting spiders, praying mantids, ladybird beetles) and most parasitoids exhibit the Type II functional response described by the general disk equation above (Luck 1984, Fernández-Arhex and Corley 2003; Figure 7.2C). Notably, for predators with a Type II response, the fraction of prey captured of the available

total decreases with increasing prey density (Figure 7.2D). As prey density increases, such predators are less able to reduce prey population growth, thus providing prey with an ever-growing opportunity to escape from predation.

Type III functional response – Many vertebrate (e.g., birds and mammals) and some invertebrate predators and parasitoids show a sigmoidal or Type III functional response (Figure 7.2E). For such predators, consumption rate responds slowly to increases in prey density when prey are scarce. At somewhat higher prey densities, consumption rate rises rapidly, and at very high prey densities consumption rate saturates and is limited by handling time and satiation as in a Type II response. The rapid rise in consumption

rate at intermediate prey densities can be the result of multiple mechanisms. Predators may learn to discover and capture prey with increased efficiency (Holling 1959a, Tinbergen 1960), or they may simply increase their searching rate as they encounter more prey (Murdoch and Oaten 1975, Hassell *et al.* 1977). Prey switching can also lead to a Type III functional response (Oaten and Murdoch 1975). Generalist predators often switch to alternative prey when the density of their preferred prey species falls below a certain threshold abundance. Therefore, prey switching can transform a Type II response into a Type III because the consumption rate of focal prey is relaxed at low prey densities. With a Type III response, the fraction of prey consumed of the total offered is initially low, increases with prey density up to a point, and then eventually decreases (Figure 7.2F). The density-dependent predation that occurs at lower prey densities contributes to prey–population regulation and may promote stability in the prey–predator interaction, which we will see later.

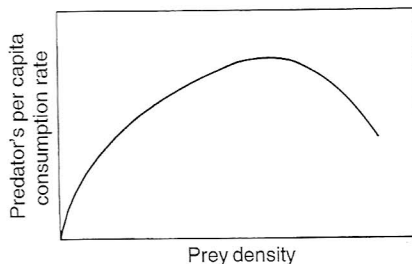


Figure 7.3 Hump-shaped functional response of a predator to a defended or distasteful prey. From Holling (1965).

N. pratti banksianae. These sawflies display a collective defense behavior, whereby sawfly larvae rear back and produce a resinous regurgitate when threatened by a predator, and this defense becomes more effective as colony size increases. Tostowaryk found that the predator's attack rate on sawfly larvae initially increased with an increase in sawfly density. However, prey eventually reached a density at which their collective defensive response became effective, and the attack rate of the predator declined. When the defensive response of the sawfly larvae was removed by treating the larvae in hot water, the humped functional response was no longer evident and a classic Type II response resulted (Figure 7.4).

7.4.1.1 Functional response to a defended prey

Holling (1965) also recognized that not all prey are uniformly susceptible to predation and that some prey species evolve defensive mechanisms against predators. When prey exhibit defensive behaviors, Holling predicted that the functional response would be humped with the number of prey taken, initially increasing with prey density, but eventually dropping off as the predator learns to avoid the defended prey or as the prey defense becomes more effective at higher prey densities (Figure 7.3). The first experimental demonstration of a humped functional response came from the work of Tostowaryk (1972) who assessed the effect of prey defense on the functional response of a predatory pentatomid, *Podisus modestus*, to varying densities of the colonial sawflies *Neodiprion swainei* and

7.4.1.2 Predator-dependent functional response

So far we have considered only the traditional prey-dependent functional response that describes the number of prey eaten by a predator as a function of prey density (e.g., Figure 7.5A). However, the density of predators co-occurring in a particular habitat may also play a significant role in determining the consumption rates of individual predators due to factors such as adaptive antipredator behavior by prey (e.g., refuge use or lowered activity levels of prey in response to the presence of predators) (Abrams 1993) and mutual interference among predators (Schenk *et al.* 2005). A functional response

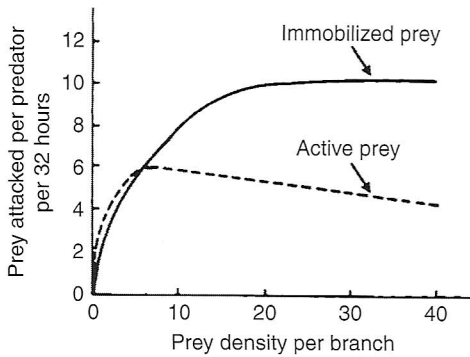


Figure 7.4 Functional response of third instar nymphs of the pentatomid bug, *Podisus modestus*, to normally active second instar larvae of the sawfly *Neodiprion pratti banksianae* that showed a defensive behavior in response to predator attack, and larvae of the same age and species that were immobilized by treatment in hot water and thus incapable of defense. Note that initially the active larvae are more heavily preyed upon as they are more visible to the predator, but as the prey density increases the colonial defensive behavior lowers the predation rate to less than 50% of that on the defenseless larvae. After Tostowaryk (1972).

that is influenced by changes in predator abundance is classified as predator-dependent (Holling 1961; e.g., Figure 7.5B). Ratio-dependent functional responses in which the response depends on the ratio of prey population size to predator population size are a specific case of predator-dependency (Arditi and Ginzburg 1989, Abrams and Ginzburg 2000). In nature, it is unlikely that functional responses will be purely prey- or purely predator-dependent, with interference among predators becoming inevitable at sufficiently high predator densities (a breakdown of prey dependency) and interference among predators improbable at sufficiently low predator densities (a breakdown of predator dependency) (Abrams and Ginzburg 2000).

Field studies measuring functional responses where the densities of both predators and prey are manipulated are rare, but necessary, if we are to understand the impact of predators on prey populations in a broader food-web context.

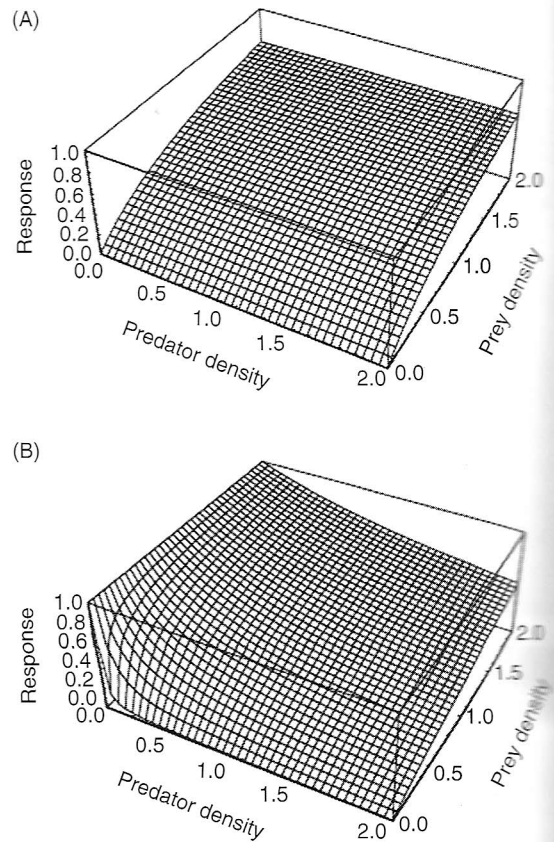


Figure 7.5 Functional responses as a function of both prey and predator densities. The traditional prey-dependent response (A) is unaffected by predator density. The ratio-dependent response (B) increases as predator density decreases. The ratio-dependent functional response is a special case of predator dependency in which the response depends on the ratio of prey population size to predator population size. Reprinted from *Trends in Ecology and Evolution*, Vol. 15, Abrams, P. A. and L. R. Ginzburg. The nature of predation: prey dependent, ratio dependent or neither? pp. 337–341, Copyright (2000), with permission from Elsevier.

A noteworthy case involves the predatory paper wasp, *Polistes dominulus*. Paper wasps are abundant generalist predators in South and Central Europe where they frequently attack larvae of the shield beetle, *Cassida rubiginosa*. Larvae of this beetle carry a fecal shield over their abdomen that provides mechanical protection against predation

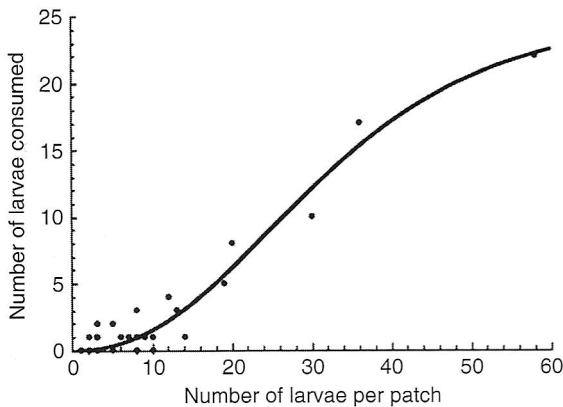


Figure 7.6 Type III functional response of the predatory paper wasp, *Polistes dominulus*, to manipulated densities of tortoise beetle larvae, *Cassida rubiginosa*, in the field. The beetles use fecal shields against natural enemies. From Schenk and Bacher (2002), by permission of Blackwell Publishing Limited.

(Eisner *et al.* 1967, Olmstead and Denno 1993). Initial studies to quantify the functional response of the paper wasp to shield beetle larvae were conducted in natural plots where only prey density was manipulated (Schenk and Bacher 2002). Video surveillance of predation events allowed an estimation of the functional response of the naturally occurring wasp population to the manipulated shield beetle larvae. In this open-field environment that potentially included alternative prey items for the generalist wasps, the functional response was characterized as a Type III (Figure 7.6). If no further study had been done, it might have been concluded that the functional response of the paper wasp is clearly prey dependent with the likely mechanism being that the generalist wasp is switching to alternative prey at low shield beetle densities. However, a follow-up study designed to test for predator dependency of the functional response by manipulating both prey and predator abundance in an open-field setting found that the functional response of this system actually lies somewhere between strict prey dependence and strict ratio dependence (Figure 7.7). Predator dependence in this case is the result of a decrease in the predation rate of

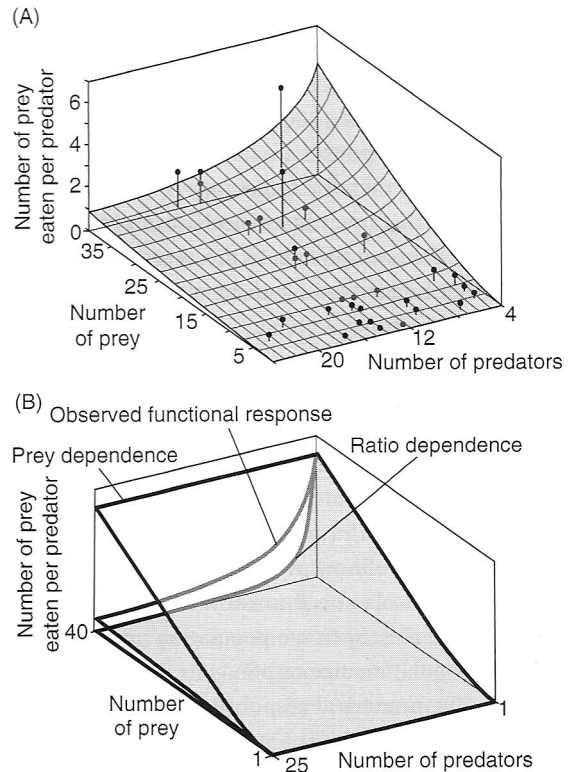


Figure 7.7 (A) The per capita consumption of tortoise beetle larvae, *Cassida rubiginosa*, by paper wasps, *Polistes dominulus*, as a function of both prey and predator densities. (B) The observed functional response of the wasp is dependent on both prey and predator densities, falling somewhere between strict prey- and strict ratio-dependence. From Schenk *et al.* (2005); by permission of Blackwell Publishing Limited.

paper wasps on shield beetle larvae with an increase in the number of wasps in the environment due to interference among predators (Schenk *et al.* 2005). To further complicate matters, it was found that the presence of a preferred alternative prey enhances the predator-dependent functional response, not by modifying the intensity of interference among predators, but by decreasing the effective number of predators foraging on the target prey (Tschanz *et al.* 2007). As an interesting caveat, there was no evidence of prey switching by the wasps despite the original

finding of a Type III functional response. This system corroborates the prediction that precise prey or predator dependence is likely to be rare in nature (Abrams and Ginzburg 2000) and highlights the fact that functional responses are likely to be influenced by species other than the target prey. Experiments such as these that investigate mechanisms of predation in natural food webs are necessary to advance our understanding of the outcomes of prey–predator interactions.

7.4.2 Numerical response

So far, we have considered only the consumption rate of an individual predator under conditions of increasing prey and/or predator density. To gain a complete picture of how predators might control prey populations, we also need to know how many predators are present in the population and how predator population size responds to increasing prey densities, the numerical response.

Most predators exhibit a positive numerical response, becoming more abundant as the density of their preferred prey increases. Two independent mechanisms underlie this pattern, predator aggregation and enhanced reproduction. First, predators often aggregate in areas where prey abound. This is a behavioral response of predators to prey that results in a short-term change in the spatial distribution of predators. The local density of the wolf spider *Pardosa littoralis*, for instance, can be dramatically enhanced over a three-day period when prey are experimentally added to its habitat (Döbel and Denno 1994). Likewise, a significant increase in the number of ladybird beetles (e.g., *Hippodamia convergens*) in response to artificially enhanced aphid densities can be detected within as little as one day following aphid manipulation (Evans and Toler 2007). However, it is important to keep in mind that the spatial and temporal scale at which predators detect and respond to changes in the abundance of their prey can vary. For example, some predators may distinguish among individual

plants, whereas others distinguish among patches of plants (Schellhorn and Andow 2005). Thus the appropriate spatial scale at which to assess predator aggregation and the numerical response may vary among predators. Second, if prey density remains high for an extended period of time, predator populations may build as a consequence of increased reproduction. For example, the number of eggs produced by ladybird beetle females has been shown to increase with an increase in aphid abundance (Dixon and Guo 1993). Unlike the aggregation of predators that happens relatively quickly in response to changes in prey abundance, the reproductive numerical response is only exhibited after a lag that can be equal to the generation time of the predator. Thus, predator aggregation and enhanced reproduction can both account for the numerical response of a predator to increased prey density, although at different time scales.

7.5 Prey–predator dynamics

Given that predators both affect and respond to changes in prey abundance, it is not surprising that reciprocal interactions between prey and predators can determine the long-term population dynamics of each (Gilg *et al.* 2003). Historic support for the view that a coupled prey–predator interaction can drive population cycles came from an analysis of ~100 years of fur-trapping records by the Hudson Bay Company in boreal Canada. An analysis of the number of lynx and snowshoe hare pelts showed spectacular periodicity with peaks and valleys of abundance occurring at roughly 10-year intervals. When hares were numerous, lynx increased in numbers, reducing the hare population, which in turn caused a decline in the lynx population. With predation relaxed, the hare population recovered and the cycle began anew. It should be noted, however, that there is controversy over the singular role