8

Predation and wildlife populations

> *If there are any marks at all of special design in creation, one of the things most evidently designed is that a large proportion of all animals should pass their existence in tormenting and devouring other animals.*
>
> **J.S. Mill (1874; cited by Taylor 1984:1)**

> *The large, ferocious gray or buffalo wolf, the sneaking, snarling coyote, and a species apparently between the two, of a dark-brown or black color, were once exceedingly numerous in all portions of the Park, but the value of their hides and their easy slaughter with strychnine-poisoned carcasses of animals have nearly led to their extermination.*
>
> **P. Norris (1881), Second Superintendent of Yellowstone National Park**

Introduction

With its gore, its excitement, and its brutal finality, predation has always fascinated humans. Biologists have built on the core intrigue of predator–prey dynamics, co-opting the term **arms race** – widely used to refer to how human armies inevitably escalate technology to keep up with each other – to describe the evolutionary changes in both predators and prey (Dawkins & Krebs 1979). For wildlife prey we see speed, poisons, coloration, armor, alertness, and deception, matched on the field of battle by similar traits in the predator.

As wildlife population biologists, an understanding of predation is important because the public is vocal and curious about what happens to predators and prey, and because predation plays such an important role in population dynamics. Some of the most controversial issues in wildlife and conservation biology hinge on the extent to which predators affect prey numbers. As one recent example of a theme that has played out all over the world for centuries, on January 12, 2006 the *Idaho Statesman* newspaper reported that the Idaho Department of Fish and Game "plans to kill up to 75% of the wolves in the Lolo elk zone to bolster struggling elk herds there."

Do wolves and other predators control or adversely affect their prey, so that killing the predators will in fact bolster the abundance of their prey? Similarly, in the context of invasive species (Chapter 11), would a predator biocontrol agent successfully reduce the numbers of a pest or invasive species? Might native species be driven inadvertently toward extinction by the introduced biocontrol predator?

To help shed light on these questions, this chapter focuses on the effect of predators on prey dynamics and, to a lesser extent, the effect of prey on predator numbers. I will emphasize concepts, avoiding a plunge into the sea of predator–prey models, including the famous Lotka–Volterra predator–prey equations of heuristic value to general ecology, but of less practical value in an applied population biology text.

Finally, before jumping in we must define two key terms. First, the concept of predators **controlling** prey. Taylor (1984) has noted that the word control has been used in predator–prey discussion to mean almost anything and, therefore, nothing. When I refer to predators controlling prey I will specify particular outcomes, such as predation regulating prey numbers and affecting fluctuations around an equilibrium, or acting to limit prey at low numbers, including extinction[1].

The second term to define is what is meant by **predation**. Do herbivores prey on plants, do decomposers prey on dead animals, or granivores on seeds? Is a parasite or disease a predator? Is it predation if an animal kills one of its own species in a fight? For the purposes of this chapter I will focus primarily on animals killing and consuming animals, recognizing that even in this narrow definition there can be surprises: the main killer (and consumer) of pre-weaning snowshoe hares are not big-fanged carnivores, but rather red squirrels and ground squirrels (O'Donoghue 1994).

Does predation affect prey numbers?

As you might expect, the best short answer to this question is sometimes or that it depends (Box 8.1). We don't have to look very far to see examples where predators limit prey population size – potentially all the way to extinction – or cause oscillations in prey abundance to be either exacerbated or dampened. Some of the most spectacular examples of control by predators are with recently introduced predators, both when they arrive and after they are removed. Cats, rats, brown tree snakes, and foxes have caused devastating extinctions around the world when they arrive in a new area. Indeed, 40% of the extinctions of birds on islands have been caused by predation by introduced animals (Estes et al. 2001).

One reason why native prey – particularly on islands – can be so badly affected by introduced predators is that the prey are a big step behind in the arms race, lacking the adaptations necessary to escape or even to fear the predators. The loss of antipredator behaviors, leading to **ecological naiveté** of prey on islands, could arise either

---

[1] Recall from Chapter 6 that **regulation** refers to maintaining numbers within some equilibrium range through density-dependent processes while limiting factors determine the actual equilibrium numbers and may be density-dependent or -independent.

Box 8.1 Do predators in New Zealand affect two species of shearwaters?

This chapter is all about why predators have demographic effects on some prey populations but not others. An instructive case involves two species of shearwater, burrowing petrels of conservation concern in New Zealand, where the management concern is whether control of exotic predators would be a more efficient path to recovery than reducing browsing damage by introduced mammals or establishing new breeding sites.

Predators of shearwaters in New Zealand include, most prominently, stoats (a type of weasel otherwise known as ermine) introduced to New Zealand in the 1880s, as well as other introduced mammalian predators such as rats and cats. The main factors that affect how the Hutton's and sooty shearwaters are affected by predators include the following.

- The location of colonies affects the suite of predators. Hutton's shearwaters nest above the snowline, and stoats are their only substantial predator. By contrast, sooty shearwaters nest close to sea level and must contend with a suite of introduced predators including not only stoats but also cats and rats.
- Size of existing colonies affects the impact of predation. The two remaining colonies of Hutton's shearwaters contain about 110,000 and 10,000 breeding pairs. Because predator (stoat) numbers are limited by a lack of prey over the winter (when shearwaters and many other species are gone), the predation rate is fairly dilute. On the other hand, sooty shearwater colonies are perhaps 90–9% smaller, so kills can have a much larger impact.

Therefore, predation on sooty shearwaters has led to low and highly variable breeding success and adult survival. To increase sooty shearwater abundance, the only real management solution is aggressive reduction of the whole suite of predator species, including not only stoats but also cats and rats. By contrast, the relatively low predation rates on Hutton's shearwater indicate that even if all stoats could be killed, population growth for this prey species would be marginally affected, indicating that the best management strategy for Hutton's shearwaters would be to control destructive browsing by introduced mammals and to establish alternative breeding sites (Cuthbert et al. 2001, Cuthbert & Davis 2002, Jones 2002).

from the chance loss of key traits when an island is founded by a few individuals or from relaxed selection on anti-predator behaviors that are potentially expensive to maintain (Blumstein & Daniel 2005). Quammen (1996:205–6) gives examples:

> *Loss of wariness is sometimes manifest as ingenuous nesting behavior: In the Galapagos, the blue-footed booby puts its eggs onto a bare patch of ground, unprotected, unconcealed, not even cushioned by a cradle of vegetation. Another form of ingenuous nesting involves building a nest in plain view on a tree limb, where it can easily be raided by a climbing predator. The Mariana crow practices that sort of reckless behavior on the island of Guam. A more cautious bird might at least conceal the nest, or place it beyond reach at the end of a thin branch, or suspend it in an elaborate woven pouch, as the tropical oropendolas*

> *do. But oropendolas are mainland species, surrounded by predators and obliged to be more cautious. Boobies can be boobies ... These animals aren't imbecilic. Evolution has merely prepared them for life in a little world that is simpler and more innocent than the big world.*

When they have evolved together, predators and prey interact on more equal footing, but still prey density or fluctuations can be affected by predation. The classic cycles of snowshoe hare in North America are driven at least in part by predation (Krebs et al. 1995), as are the regular, widespread cycles of northern small mammals (Korpimäki & Norrdahl 1998). More surprisingly, mammalian carnivores often kill other carnivores (**intraguild predation**), accounting for up to 68% of known mortalities in some species and at times limiting numbers (Palomares & Caro 1999).

A more subtle, but potentially pervasive line of evidence for effects of predators comes from changes more than one trophic level removed from a top predator. **Mesopredator release** (Soulé et al. 1988) occurs when mesopredators (mid-level predators) are regulated by top predators through either predation or competition. If the top predator is removed, a top-down **trophic cascade** can occur, whereby the mesopredators increase in number and in turn decrease abundance of their prey. A classic example has been documented in southern California, where intensive urbanization has destroyed most of the native sage-scrub habitat (Crooks & Soulé 1999). With the decline or absence of coyotes from this system, both native mesopredators (striped skunk, raccoon, and grey fox) and exotic mesopredators (especially domestic cats) were released from predation and competition from coyotes (the cat response also occurred because without coyotes around owners tended to let their cats outside more often). The resulting high numbers of mesopredators cascaded into both higher prey mortality (cats around a single moderately sized canyon killed more than 500 birds, nearly 1000 rodents, and over 600 lizards per year), and reduced abundances of scrub-breeding birds. Trophic cascades initiated by vertebrate predators in terrestrial systems are fairly common in nature (Schmitz et al. 2000).

Despite the range of examples where predators do reduce numbers of their prey, we also see plenty of places in the wild where prey continue to persist and even flourish with predators in their midst. To foreshadow a theme of the chapter, prey are active participants in the life and death process, evolving and behaving to reduce their chances of being killed. Even predator-naïve animals can harbor innate reactions of caution that can reduce vulnerability to novel predators. For example, the last population of the rufous hare-wallaby on the Australian mainland was destroyed by a fire and foxes in 1991 so the species persisted only on two islands off the coast; however, captive-breeding efforts showed that hare-wallabies can be trained to avoid cat and fox predators, which they will be exposed to when reintroduction programs begin (McLean et al. 1996). At a population level, the death of prey individuals, no matter how massive or macabre it may seem to us, does not necessarily result in a smaller prey population; consider that roughly one-third to one-half of all bird nests are destroyed by predators, but the decline of bird populations following such predation is certainly not inevitable (Côté & Sutherland 1997).

In short, predators and prey are entwined in a dance of evolution and population response. The best generalization we can make on population response is that predation can certainly regulate and help limit numbers of prey, but is unlikely to drive prey populations to extinction unless introduced species are involved or the prey population is small and fragmented or otherwise affected by other recent perturbations (Macdonald et al. 1999). To extend this generalization, we will closely examine three main factors that determine whether a predator will limit or regulate prey in any particular case: the predation rate of the predator on the prey (in turn a function of predator and prey numbers, and the number of prey killed per predator), the degree to which the predation can be compensated for by the prey, and which individuals are killed. Considering these factors will move us away from the relatively empty question of whether predation affects prey numbers and toward the more interesting and useful question of whether predators in a particular setting are likely to affect the dynamics of their prey.

Factors affecting how predation impacts prey numbers

Percentage of the prey population killed

Prey face a world that is "red in tooth and claw" (as Lord Tennyson put it), populated by predators that can respond to an increasing number of prey by increasing their own numbers and by killing more per predator per unit time. Therefore, the total number of prey killed will be a product of both the number of predators (the predator numerical response) and how many prey each individual predator kills (the predator functional response). The **predation rate**, or percentage of the prey population killed per unit time, is

$$\text{Predation rate} = \frac{\text{Number of prey killed}}{\text{Prey abundance}} 100 \qquad (8.1)$$

Thus, in this section I first discuss the predator numerical and functional responses, which collectively determine the number of prey killed, then merge those with prey abundance to explore the implications for predation rates.

Numerical responses of predators

The **numerical response** reflects the change in number of predators as prey abundance changes; more precisely, it is the equilibrium numbers of predators present at a given prey density (there could be a time lag between current prey numbers and the eventual equilibrium predator number). Within a population, the numerical response will be a function of the predator's birth and death rates, which we know can be captured as λ or r.

In addition to the numerical response mounted from within the predator population, more rapid numerical increases in a predator's population can be driven by an

aggregative response, whereby predators converge from elsewhere to consume prey. Aggregative responses are of special interest in the agricultural-pest arena, because the numerical response of, say, an avian predator to an outbreaking insect pest will be too slow to be effective, whereas an aggregative response may lead to a very rapid increase in local predator density. To cite one such case, Carolina chickadees rapidly congregate in woodlands with greater densities of leaf-mining moths, aiding in suppression of the moth (Connor et al. 1999).

Predicting and interpreting numerical responses becomes more complicated when there is more than one predator or prey. With several predator species, reducing the abundance of one predator (say through predator control) could actually increase the numerical response of other predators due to trophic cascades or relaxed competition. This seems to be what happened in New Zealand when attempts to remove stoats to protect nesting birds (Box 8.1) increased introduced rat numbers (one prey of stoats), which in turn increased predation on sooty shearwaters (Lyver et al. 2000).

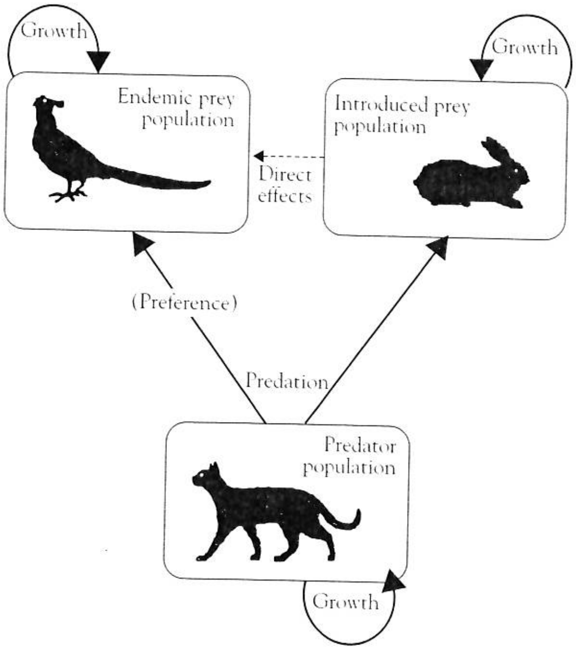
Multiple prey species can strongly affect the numerical response of predators on prey. Because some prey species are better able to increase or sustain their numbers in the presence of predation, they may facilitate a numerical response in the predators that results in a decrease of other prey species. Thus, what seems like competition between alternate prey species may actually be **enemy-mediated apparent competition** (Chaneton & Bonsall 2000), where prey species affect each other's abundances through their effects on the numerical response of a shared predator. For example, woodland caribou in Canada are exposed to multiple native predators (especially wolves, cougars, and bears) that in turn are supported by multiple prey (especially moose and deer) that do quite well in the human-modified landscape. The incidental take of caribou by the abundant subsidized predators reduces caribou population growth (Wittmer et al. 2005).

A special form of enemy-mediated apparent competition, termed **hyperpredation** (Smith & Quin 1996), occurs with the introduction of both a predator and an introduced prey that is able to sustain or increase its numbers in the face of predation. The introduced species might seem to be merely a competitor with natives – say, rabbits introduced to an area with native rodents, lizards, or birds – but through hyperpredation it could also drastically impact the native prey by sustaining much higher numbers of the shared predator than could be supported by the native species alone (Box 8.2). Even if the native prey is only a by-catch of secondary importance to the predator, the predator's numerical response – subsidized by the introduced prey – can devastate the native prey.

Interestingly, with cats and cat food humans are introducing to native systems both a hyperpredator and its introduced prey. Cat food can maintain both domestic and semi-feral farm cats at densities far higher than native carnivores (Woods et al. 2003, Kays & DeWan 2004). In Great Britain the cat population of approximately 9 million is about 20 times that of stoats and weasels and more than 30 times that of foxes. Cat numbers in the USA total perhaps 80–100 million owned, stray, or feral cats. Given that each cat kills anywhere from tens to hundreds of wild birds and mammals each year, allowing cats to roam free unleashes the fury of their numerical effects on native wildlife.

Box 8.2 Introduced rabbits lead to hyperpredation by cats on native species

Rabbits have been introduced – usually intentionally – to hundreds of islands worldwide. They adapt well to most conditions, eat a variety of plants, and have exceptionally high population growth rates. Rabbits certainly have well-known direct effects on both the vegetation and on other grazing species that are competitively inferior. Less well appreciated and probably more insidious, however, are the indirect effects they can have on native wildlife via apparent competition and hyperpredation (Smith & Quin 1996, Courchamp et al. 1999, 2000, Norbury 2001). Consider the response of feral and domestic cats (*Felis silvestris catus*) to a bountiful food source of rabbits, captured in the figure.



Introduced rabbits affect other herbivores both directly and indirectly by sustaining predators. From Courchamp et al. (1999).

Cats have caused local extinctions of native birds and mammals throughout the world (Mack et al. 2000, Risbey et al. 2000). Often feral cat numbers are limited by seasonal lows in prey abundance, and they may be limited in space by intervening areas with few native prey. However, when rabbits arrive and increase in numbers across the landscape, cats can prey on them whenever and wherever native prey are sparse, initiating a vicious numerical response. Here are just two of many documented examples.

- On the sub-antarctic island of Macquarie, introduced cats persisted with parakeets for more then 60 years. However, within 20 years of rabbit introduction the parakeet was extinct because rabbits increased cat numbers, even as the only indigenous land birds present during winter (parakeets, rails, and a teal species) declined.

(Continued)

Box 8.2 Continued

- In New Zealand, both cats and introduced stoat populations are supported by rabbits, and highly endangered native grand and Otago skinks suffer elevated predation as a result. The effects are worst when rabbit density fluctuates, because the sustained predator community switches to skinks most ferociously when rabbit numbers temporarily decrease.

The moral of the story is to deal with not only the predators, but also with the rabbits. Control of rabbits needs to be sustained, because if it is tentative, allowing rabbits to bounce back in repeated pulses, the predator suite could switch to native fauna during rabbit lows and cause even more damage.

Awareness of enemy-mediated apparent competition can lead to better management decisions that may not be obvious (Box 8.2). If an introduced predator is demolishing the native fauna, and its abundance is subsidized via hyperpredation on an introduced prey species, removing the predator would be easier if the introduced prey were simultaneously removed. Likewise, removing only an introduced competitive prey species as a means to increase a native species could cause more harm than good if an associated hyperpredator is not simultaneously removed. A classic case involved proposals to remove feral pigs from the California Channel Islands (USA), both because the pigs have badly damaged the islands' native vegetation, and have supported through hyperpredation increased numbers of introduced golden eagles, which in turn have caused the precipitous decline of endemic and endangered island foxes. Although the pig removal would seem to be a straightforward and sensible plan, eradicating pigs without also reducing the eagles could actually trigger fox extinction because eagles will likely kill more foxes as pigs decline (Courchamp et al. 2003).

Functional responses of predators

The functional response, or **kill rate**, describes the number of prey killed per predator per unit time. As the prey numbers increase, kill rate could respond (or not) in many different ways. Although predator–prey theorists have categorized a variety of functional responses (Jeschke et al. 2002), we will focus on the two most likely for wildlife predators, named by Holling (1959) as **Type 2 and Type 3 functional responses**[2]. These are shown on the two panels on the left of Fig. 8.1; Type 2 has a hyperbolic curve whereas Type 3 shows a sigmoidal increase.

For any functional response, the kill rate must always flatten at a maximum because there is limited time available for hunting and killing. In particular, **search time** is required to locate prey, and **handling time** to pursue, kill, and eat the prey. The functional response can also be limited by **satiation** where a full stomach takes away motivation to eat more. However, the functional response can exceed what would be

---

[2] We're ignoring Type 1, a straight-line relationship between prey density and functional response, for which it is hard to come up with biologically realistic mechanisms.

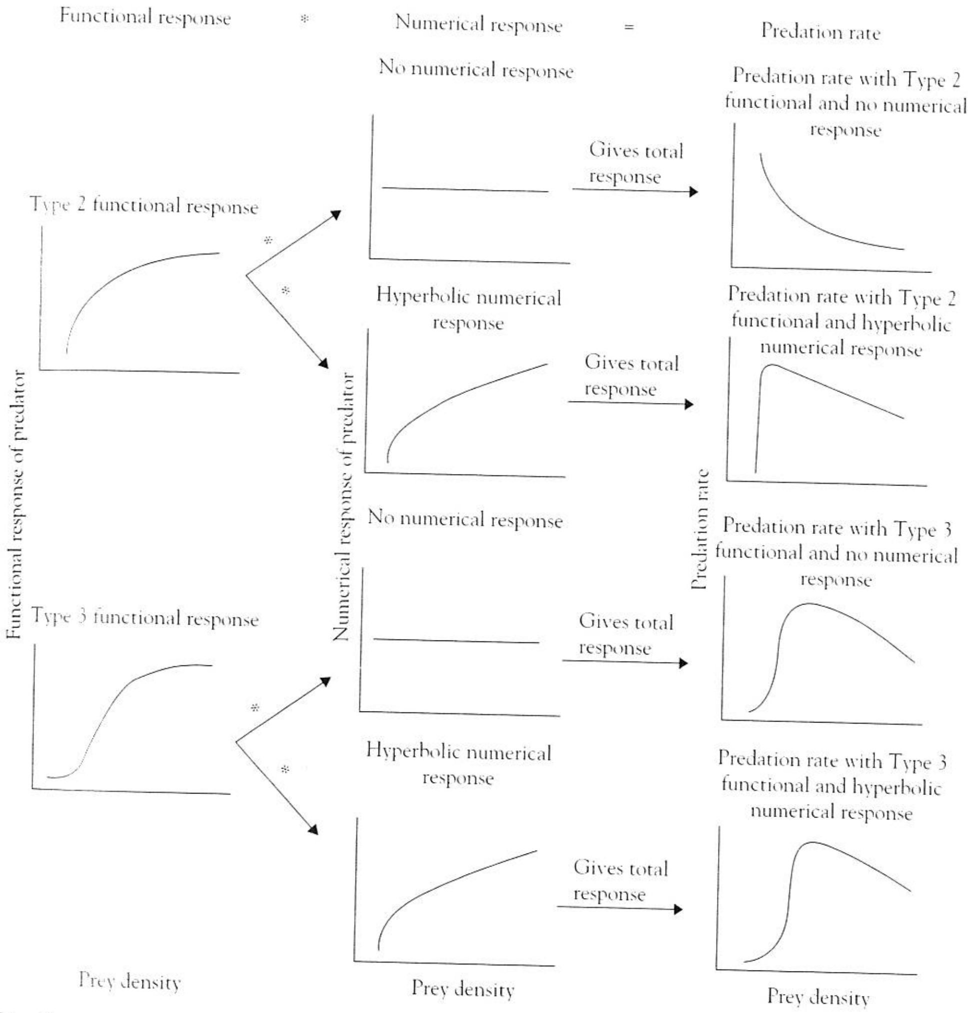


Fig. 8.1 How a predator's functional and numerical response can combine to affect predation rate on a prey population, using as examples curves derived from analyses on wolves and moose (Messier 1994, 1995). The left-hand panels are functional response curves (moose kills per wolf per 100 days) that are either Type 2 or Type 3. Each functional response is multiplied by a numerical response (middle panels; wolves per 1000 km^2) that is either constant (unresponsive to density) or a hyperbolic increase resulting from local births and/or an aggregative response by the predator. The right-hand panels show the predation rate (percentage of moose population killed by wolves per year).

expected based on the energy needs of the predator (Kruuk 1972, Short et al. 2001): four or fewer red foxes killed up to 230 adult black-headed gulls in one night, eating fewer than 3% of them; in two separate instances in Australia a single introduced fox killed 11 wallabies and 74 penguins over several days, eating almost none of the victims; up to 19 spotted hyenas killed 82 Thomson's gazelle and badly injured 27 more in one night, eating only 16% of the kill.

Such seemingly heinous acts by predators raise intense emotions in humans because the gratuitous killing can seem to be an immoral waste of life. Why do predators do it? In some cases, when predators encounter easily accessible domestic prey or arrive in a system with naïve wild prey they initiate **surplus killing**, whereby animals are killed but not eaten. The **henhouse syndrome**, leading to surplus killing, is an almost inevitable result of a high-performance predator confronted with an easy target (see Box 8.3). A textbook case of **partial prey consumption** that comes with surplus killing can be found in brown and black bears eating salmon, where bears consume less of each fish when more fish are available. Furthermore, all fish and fish parts are not equal: unspawned fish – with higher muscle quality – are eaten more than spawned-out fish, and high-energy parts like brains and eggs preferentially consumed (Gende et al. 2001).

In addition to surplus killing via the henhouse syndrome, **excessive killing** beyond immediate energetic needs may be an adaptive strategy for foraging over a longer time period. One striking illustration can be found with least weasels (Jedrzejewska & Jedrzejewska 1989) that killed and consumed bank vole prey approximately in proportion to their energetic needs each day during the summer and fall, but killed (and cached in their nests) more than they needed as the Polish winter cold descended; when temperatures got really cold weasels stopped hunting and instead ate out of their cache, a highly adaptive trait facilitating survival through cold winters (not unlike the nuts in a squirrel's hoard). Similarly, coyotes in the Yukon of Canada cache entire carcasses of nearly half of their snowshoe hare kills in early winter, and return to eat most of

Box 8.3 The henhouse syndrome: surplus killing by predators

The behavioral programming of the act of predation can lead to the killing of far more prey than necessary to fulfill energetic demands. Often called the **henhouse syndrome** because it can happen when a predator gets into a chicken coop, such surplus killing arises from the ethology of predation. Each of the four behaviorally distinct behaviors involved in predation (search, pursue, kill, and consume) are independently reinforced (Kruuk 1972). That is, the animal is rewarded not just by completing the whole predation act – eating the prey – but also by successfully carrying out each of the four behavioral components independently. (Think about why this must be true: for a young predator to learn its craft, where most early attempts fail to culminate in a prey in the belly, there must be positive reinforcement, or psychological encouragement, for performing each stage on the way to consuming the prey item.) A decrease in time spent performing any one or more of these behaviors will elevate the functional response. Normally, each step is time-consuming because the arms race adaptations of most prey challenge predators at each step of the search–pursue–kill–consume process. But if the predator is presented with an unusual case where search and pursuit are made ridiculously easy – say the prey is penned or ecologically naïve – the predator can simply perform the act of killing again and again and again. The predators are not morally bereft, nor are such killers a case of problem or rogue individuals. For a predator faced with available prey, trivial costs of killing, and little risk of injury, there simply is no adaptive reason why it should stop killing, regardless of whether the prey are eaten.

them over the next few months of deep winter even when they are covered by half a meter of snow (O'Donoghue et al. 1998). Of course, a carcass killed but not eaten by a predator is not wasted in an ecological sense because scavengers and decomposers will consume it. In fact, some scavengers depend on excess kill, as when common ravens treat gunshots as a dinner bell and fly towards the sound with the expectation of finding a 70-kg elk gut pile to scavenge from a successful hunter (White 2005).

Even with surplus or excessive killing, the required search and handling time will still determine an upper limit to the functional response. Likewise, the overall shape of the functional response curve is also determined by search and handling time, along with satiation. For example, the tapering of kill rate (see the whole Type 2 curve and the right-hand side of the Type 3 curve in the left-hand panels of Fig. 8.1) can arise from a decreasing motivation to hunt as the belly becomes full, or from less time available as a higher and higher proportion of the predator's time is taken up by handling. The left-hand side of the Type 3 curve, showing an increasing kill rate with increasing prey density, can be driven by additional factors. As prey increase from very low numbers, predators increasingly learn how to recognize, subdue, and consume the prey, developing a **search image** to increase kill rate. A newly acquired search image can cause the predator to switch to a prey as it becomes more numerous. Another mechanism leading to the increasing kill rate in the Type 3 curve is prey behavior: if prey use camouflage, or safe hiding places that are limited in number, both strategies will result in a larger proportion of prey taken as their numbers increase.

How do functional responses affect predation rate on the prey, independent of the predator's numeric response? For a fixed predator density (see the flat horizontal lines showing no numerical response in the middle panels of Fig. 8.1), a Type 2 kill rate (functional response) creates positive density dependence in prey survival; as prey numbers increase so too does prey survival because predation rate decreases. The positive relationship between prey survival and prey numbers tells us that at low or declining prey density, a Type 2 functional response can create strong Allee effects (Sinclair et al. 1998, Gascoigne & Lipcius 2004; see Chapter 6). On the other hand, a Type 3 functional response will tend to relieve declining prey from predation pressure at very low prey densities by facilitating higher survival (lower predation rate). If, however, a large prey population under predation with a Type 3 functional response collapses due to poor environmental conditions (perhaps a drought or heavy snow), its ability to increase may be compromised by the negative density dependence in prey survival at low to medium densities (i.e. as prey density increases, predation rate increases and prey survival declines; Fig. 8.1). Thus the prey could be stuck in a **predator pit**, a low density from which they cannot recover unless predation rates dramatically decline.

The functional response curves distill predator responses as a function of prey density (and so are often called **prey-dependent models**). A countercurrent to functional response curves plotted against prey density has emphasized that the kill rate depends on lots of things other than prey numbers. Certainly this is true; as we have seen, kill rate can be affected by context – evolutionary background and age structure as well as habitat and weather conditions – and also by other species including alternate prey and predators. One alternative way of capturing some of these other influences on functional response has been to plot kill rate not against prey number but rather against the ratio of prey to predator population sizes (Abrams & Ginzburg 2000). Such **ratio-dependent predator–prey models** can be useful complements to the traditional ones based only on prey density, helping us to understand the factors other than prey numbers that affect kill rates in wild populations (Vucetich et al. 2002).

Ultimately, the shape of the functional response curve for any predator–prey system is a manifestation of how well the predator and the prey are doing in the arms race[3]. Prey strive to minimize the functional response by defense and camouflage, while predators improve their search image and decrease travel and processing time between kills. Of the hundreds of examples that could be given of behavioral and morphological responses by prey to reduce functional response in the arms race with predators, one of my favorites is that the black tips on the relatively long tails of weasels confuse aerial predators and deflect attacks away from vital parts of the weasel (Powell 1982). In short, the concept of functional response is a useful heuristic component of interpreting predation rate, and improved methods allow it to be estimated, with variance, from field data (Hebblewhite et al. 2003, Joly & Patterson 2003).

Total predation rate

Next let's explore the combined effect of functional and numerical responses to determine the total number of prey killed at different prey densities, or overall predation rate (eqn. 8.1). Of the many possible combinations of numerical and functional responses that lead to different predation rates, I chose for Fig. 8.1 a few examples that could be reasonable for a wolf/moose predator–prey system (Messier 1994, 1995). Although I've avoided units to make Fig. 8.1 less busy, let's work through an example of how the predation rate (shown by the right-hand side of Fig. 8.1) is calculated from predator functional and numerical responses (the left-hand and middle panels of Fig. 8.1), and prey number. Suppose:

- moose density = 2 moose/km^2
- wolf functional response = 2.73 moose killed/wolf per 100 days
- wolf numerical response = 41.9 wolves/1000 km^2 = 0.0419 wolves/km^2
- total kill = 2.73 * 0.0419 = 0.114 moose killed/km^2 per 100 days.

Thus, the **annual predation rate** would be total killed per 100 days * 3.65/2 moose = 0.21, or 21% of the moose in the area killed by wolves per year. (You should try it with different numbers to convince yourself that you could draw the predation-rate curves in Fig. 8.1 if you were given the moose density and the wolf functional and numerical response values.)

As already discussed, a Type 2 functional response without a numerical response can cause the predation rate to increase as prey numbers decrease, leading to an Allee effect, often called **destabilizing** because the predation rate gets worse and worse as

---

[3] Although, as a generality, functional responses similar to Type 2 are probably most common for wildlife populations (Gascoigne & Lipcius 2004).

prey populations get smaller and smaller (Fig. 8.1, upper right-hand panel). When a Type 2 functional response is accompanied by a positive predator numerical response (Fig. 8.1, right-hand panels, second row), the total predation rate is low at very low prey numbers (leading to high prey survival) but destabilizing at higher prey numbers. Importantly, if the hyperbolic numerical response is moved upward, as would be expected in a multi-prey system where the predator could sustain itself at reasonably high numbers independently of the prey being considered, then the total predation rate curve becomes destabilizing at all prey densities (Messier 1995). Thus, potentially severe Allee effects (destabilizing positive density dependence) due to predation are likely when the functional response is Type 2, and when the predator numbers are limited by factors other than the prey in question (Sinclair et al. 1998, Gascoigne & Lipcius 2004).

For an endangered prey population, the theory just discussed implies that hyperpredation and multiple native prey can allow predators to persist at high numbers even when the endangered prey is nearly extirpated, thereby initiating further decline of the prey. For example, the apparent competition on woodland caribou described above means that the incidental take of caribou by predators whose numbers are subsidized by other prey will cause the small caribou populations to suffer proportionately worse predation mortality (Wittmer et al. 2005). Similarly, smaller populations of native skinks in New Zealand are less able to sustain the losses from a suite of introduced predators sustained by rabbits (Norbury 2001).

So predators can kill a lot of prey through numerical and functional responses, and that can lead to a high predation rate. But, perhaps counterintuitively, a high predation rate does not necessarily mean that predators will limit prey population growth. Why not? There are two reasons. First, mortality due to predation may be compensated for. Second, which age or stage class gets killed matters for prey population growth. We'll explore each of these next.

Compensation of predation rate

When Paul Errington started observing predation on muskrats and bobwhite quail in the mid-1940s, the theory of predation in wildlife biology was simple: predators kill prey, so the removal of predators should mean more prey. Errington (1946) challenged that dogma. Behaviors such as territoriality may limit population size for many prey, making certain individuals (e.g. social subordinates) vulnerable to dying from disease or starvation if they are not killed by predators. Errington (1956) called these individuals the "doomed surplus," surely one of the most compelling phrases of ecological jargon of all time. Taylor (1984:28) notes that "by reducing predators to the ecological equivalent of garbage collectors, Errington undoubtedly served to forestall the conscious eradication of a number of carnivorous birds and mammals from North America."

Although it may be disconcerting to think about a doomed surplus in a population, the phrase makes it easy to realize that mortality due to predation may be at least partly **compensatory**. The mortality arising from predators killing the doomed surplus will be compensated for with lower mortality from other sources, say due to weather. Thus predation merely replaces other forms of mortality, leading to no net loss in prey numbers. In symbols, the annual survival rate under predation at some time t (S_t) is the same as the survival rate in the absence of predation (S_0). In a classic example, red grouse in Scotland that do not obtain territories in the autumn absorb nearly all of the mortality for the population. When a territory holder does die, a nonterritorial bird quickly takes its place, keeping density steady even when predators remove a large number of grouse (Jenkins et al. 1964). Compensation in survival can only go so far, because predation mortality can only be fully compensatory if it does not exceed other nonpredation-related mortality sources.

So with compensatory mortality, realized annual survival (S_t) is unaffected by predation rate. By contrast, if predation operates as an **additive** form of mortality, survival becomes a product of both not being killed by predators ($1-M_P$) and surviving everything else (S_0):

$$\text{Realized survival under additive predation} = S_t = S_0(1-M_P) = S_0 - S_0M_P \qquad (8.2)$$

Errington was insightful enough to realize that mortality due to predation could be compensated for not only by other forms of mortality, but also by increases in other vital rates such as reproduction or immigration into a depredated population. Some of the most obvious examples of increasing reproduction to compensate for predation come from multiple clutches in birds. Mallard ducks are a notable example, as they rarely double brood (produce a second clutch after hatching ducklings), but if their nest is depredated they typically renest, and can do so up to five times in one season if nests are preyed upon repeatedly (Hoekman et al. 2005). Compensation for predation also occurs by immigration. For instance, despite humans killing more than 50% of an introduced red fox population each year as part of an effort to protect endangered birds in California the foxes persisted, in part because up to half of the population was immigrants coming in from neighboring populations (Harding et al. 2001). Because compensation of predator mortality can occur not only through survival (when the doomed surplus are taken) but also through increased reproduction and immigration, populations with compensation can sustain high predation rates.

The extent of compensation of predator mortality becomes of intense management interest when evaluating the efficacy of predator control, because compensation for predator mortality undercuts the utility of predator control (Côté & Sutherland 1997, Banks 1999). However, the greatest interest in compensation of predator-caused mortality centers on harvest of wildlife by humans as predators. Therefore, I will wait until Chapter 14 to explore compensatory mortality further, with lots more examples. For now, I'll leave you with the general understanding that predation rate alone cannot predict whether predators will reduce the numbers or dynamics of a prey population; fully compensatory predation will not affect prey at all, even if predation rate is high, while fully additive mortality from predation will decrease survival rates. Predation will rarely be fully additive or compensatory, but rather occurs on a continuum.

Having established two of the factors determining the effect of predators on their prey – the predation rate and compensation – we will next explore the third main factor, the age or stage of the prey killed.

Who gets killed

For predicting effects of predators on prey populations, which age class gets killed becomes important for three reasons. First, all age classes are not equally killable, so available age classes can affect the functional response. For example, American pronghorn on the National Bison Range of Montana currently face a single substantial predator, the coyote, which kills approximately 90% of fawns in their first year but cannot kill adults (Byers 1997)[4]. Second, age classes differ in the extent to which the predation mortality can be compensated; for instance, hatchling mortality in birds might be relatively easily compensated for by multiple additional clutches, whereas there may be less latitude to compensate for adult mortality.

Finally, as we have seen, all age classes and vital rates are not created equal in their effects on prey population growth. We can assess whether a given predation rate is likely to affect the prey λ value by calculating reproductive values and performing sensitivity analyses, as in the last chapter. Of course, we would keep in mind that a large mortality for an age class with a small effect on prey λ value could affect the prey as much as or more than a smaller change in a rate with a large effect on prey population growth. But the bottom line is that, depending on the age class killed, a high proportion of prey killed will not necessarily affect population growth even if the prey is unable to compensate for the predation mortality.

In short, sound estimates of vital rates can be married to projection-matrix models to gain management insights into effects of predation on particular stages. A good example expands the shearwater case study (Box 8.1). Using a matrix-projection model and an LSA-style approach incorporating uncertainty to explore how the λ value of Hutton's shearwater would vary across management changes, Richard Cuthbert and colleagues (2001, 2002) found that small changes in adult survival affect population growth more than even fairly large changes in chick or fledgling survival. Because stoats prey on chicks more than adults, and the highest mortality risk for adults occurs away from the breeding ground where stoats are, the management recommendation was to divert attention away from stoat predation on chicks and instead focus on minimizing the smaller level of stoat predation on adults and on other adult mortality sources such as by-catch of shearwaters from ocean fishing. Thus the sensitivity analysis ties back to the argument that reducing numbers of introduced stoats will be a relatively inefficient management option for the conservation of this shearwater species (Box 8.1).

Other examples abound where the effects of predators have been elucidated by formal analysis of which age or stage of prey is being killed. Although cheetah cubs are heavily preyed upon by lions and hyenas, an LSA sensitivity analysis incorporating both mean vital rates and their likely changes under management found

---

[4] Byers (1997) makes a compelling case that the remarkable adaptations of adult pronghorn for speed (approaching 100 km/h) are a "ghost of predation past," when Pleistocene predators including cheetahs and hyenas would have preyed on adults. The return of wolves to the pronghorn range may once again impose predation on adult pronghorn.

that management focusing solely on reducing predation on cubs would be less effective than actions to increase – even slightly – survival of adults (Crooks et al. 1998). Likewise, the short-necked turtle in Australia is beginning to endure high predation from introduced red foxes; although the effects of fox predation on nests appear horrific, with rates exceeding 95% in some areas, the turtles would actually be better served by management to reduce adult mortality, which is much lower than nest predation but contributes more to turtle population growth (Spencer & Thompson 2005). Finally, you may recall from Chapter 7 that breeding-ground vital rates for mallards, which are often driven by predation, influence population growth more than do vital rates in the nonbreeding season, which includes harvest by hunters.

Summary

The question of whether predators control prey is huge in applied wildlife population biology, with implications ranging from whether predator reduction will protect introduced endangered prey or increase ungulate prey for hunters, to whether introduced predators are likely to decimate their prey. To answer the question with a broad yes or no is ecologically naïve. Rather, we can answer the question for any particular case by assessing three primary details.

First, we need to know the predation rate, or percentage of the prey population killed by predators. The predation rate is the number of prey killed divided by prey abundance; the number of prey killed is the product of the numerical and functional response. The numerical response describes the number of predators as prey numbers change. Multiple predator species can complicate the numerical response because reduction of one predator could increase the numerical response of other predators due to competitive release or trophic cascades. Multiple prey also complicate the predator numerical response through apparent competition or hyperpredation, where one prey sustains high numbers of a predator which in turn affects another prey species (as a special form of apparent competition, hyperpredation tends to involve an introduced predator and prey affecting native prey).

The other component affecting the number of prey killed is the functional response, or kill rate. Defined as the number of prey killed per predator per unit time, the kill rate is limited by satiation and limits in time available to search for and handle prey. The kill rate may well exceed immediate energetic requirements, however, if surplus killing occurs or if kills are cached to be used over longer time periods. Complex behaviors and feedbacks between predator and prey determine the shape of the functional response curve, with predator learning and prey escape behavior playing roles. A Type 2 functional response curve could create an Allee effect in small prey populations, decreasing survival as prey numbers decrease; by contrast a Type 3 response would tend to stabilize small prey numbers. Ratio-dependent models are an alternative to functional response plotted against prey density.

Even for a certain predation rate, two other details must be known to determine whether predation will affect a prey's population dynamics. First, we must know whether the predation mortality is compensated for. Compensation occurs via lower mortality in other parts of the year, lower mortality in other life stages, and/or by increased reproduction or immigration. If predation mortality is compensated for, then predation is unlikely to affect prey density or fluctuations, whereas additive predator mortality is more likely to affect prey numbers.

Finally, the effect of predators on a prey population will depend on who gets killed. Because all age or stage classes are not equal in their vulnerability to predation, in their ability to compensate for mortality, or in their effect on population growth rate, massive predation can occur on certain age classes with very little impact on population growth. Alternatively, small additive mortality rates from predation imposed on age classes with high reproductive value and/or making up a large proportion of the population can substantially lower population growth.

Predation is awe-inspiring, bone-chilling, and a major driver of population dynamics for many wildlife species. The predation rate by age class and the extent to which mortality due to predation can be compensated will vary over time and space, affected by weather, habitat changes, parasites and diseases, and other factors. By measuring these factors over space and time, the effect of a predator on a prey can be resolved.

Further reading

Errington, P.L. (1946) Predation and vertebrate populations. *Quarterly Review of Biology* **21**, 144–77; 221–45. A true classic, filled with insights that continue to be timely even now.

Taylor, R.J. (1984) *Predation*. Chapman and Hall, New York. This slim volume rings with an engaging style that packs in an enormous amount of theory, math, and applied thoughts on predation.