10 PREDATION

Lectures by A. R.E. Sinclair

10.5 The behavior of predators

We must first understand how predators respond to their prey in order to interpret predator-prey interactions. We ask three questions. How do predators respond to: (i) changes in prey density; (ii) changes in predator density; and (iii) differences in the degree of clumping of prey? We look at these in the following three sections.

10.5.1 The functional response of predators to prey density

The response of predators to different prey densities depends on: (i) the feeding behavior of individual predators, which is called the functional response (see also Section 12.4, 12.5), and (ii) the response of the predator population through reproduction, immigration and emigration, which is called the numerical response (see also Section 12.5) (Solomon 1949). We deal with the functional response first.
Understanding of the functional response was developed by Holling (1959). If we imagine a predator that: (i) searches randomly for its prey; (ii) has an unlimited appetite; and (iii) spends a constant amount of time searching for its prey, then the number of prey found will increase directly with prey density as shown in Fig. 10.2a. This is called a
For the lower range of prey densities some predators may show an approximation to a Type I response, such as reindeer feeding on lichens (Fig. 10.3), but for the larger range of densities these assumptions are unrealistic. For one thing, no animal has an unlimited appetite. Furthermore, a constant search time is also unlikely. Each time a prey is encountered, time is taken to subdue, kill, eat and digest it (handling time, $h$). The more prey that are eaten per unit time ($N_a$), the more total time ($T_t$) is taken up with handling time ($T_h$) and the less time there is available for searching ($T_s$) (i.e. search time declines with prey density ($N$)).

Thus, handling time is given by:

$$T_h = h N_a$$

and total time is:

$$T_t = T_h + T_s.$$  (10.2)

The searching efficiency or attack rate of the predator, $a$, depends on the area searched per unit time, $a'$, and the probability of successful attack, $p_c$, so that:

$$a = a' p_c.$$  (10.3)

The number of prey eaten per predator per unit time ($N_a$) increases with search time, search efficiency, and prey density, so that:

$$N_a = a T_s N.$$  (10.4)

Substituting equation 10.1 and 10.2 into 10.4 we get:

$$N_a = a(T_t - h N_a) N$$

or:

$$N_a = (a T_t N) / (1 + a h N).$$  (10.5)

This is Holling's (1959) "disc equation" which describes a Type II functional response, where $N_a$ increases to an asymptote as prey density increases (Fig. 10.2a).

When there are several prey types (species, sex or age classes), the multispecies disc equation for prey type $i$ eaten per predator is then:

$$N_{a_i} = \frac{(a_i T_t N_i)}{(1 + \sum_j a_j h_j N_j)}$$  (10.7)

where the sum is across all prey types eaten.

The Type II functional response can be constructed from the parameters of the disc equation estimated from observations. Searching efficiency is the product of $p_c$ and $a'$. The probability of capture is usually low, about 0.1 - 0.3 in most wildlife cases (Walters 1986). The area of search, $a'$, can be approximated from [distance moved \times width of reaction field or detection distance]. Handling time per prey item, $h$, can be obtained from direct observation or from maximum feeding rates because maximum rate = $1/h$. Examples of such calculations are given in Clark et al. (1979) and Walters (1986).

The important effect of the Type II response is seen when numbers eaten per predator are re-expressed as a proportion of the living prey population alive (Fig. 10.2b). The Type II curve shows a decreasing proportion of prey eaten as prey density rises. Fig. 10.4a illustrates the Type II response of European kestrels (Falco tinnunculus) feeding on voles (Microtus spp.) in Finland (Korpimäki and Norrdahl 1991). The functional responses of herbivores are not as well known as those of carnivores but where measured they appear to be Type II as in Fig. 10.4b for bank voles (Clethrionomys glareolus)
feeding on willow shoots (Lundberg 1988). Deer and elk show Type II functional responses to their food supply. Dale et al. (1994) report Type II responses of wolves preying on caribou.

**FIGURE 10.4 a, b Type II Functional Response (top) and Fig. 5 Type III (bottom)**

Holling found a third type of functional response (*Type III*, Fig. 10.2). The number of prey caught per predator per unit time increases slowly at low prey densities, but fast at intermediate densities before levelling off at high densities, producing an S-shaped curve. When those eaten are expressed as a proportion of the live population, the
proportion consumed increases first, then declines. Hen harriers (*Circus cyaneus*) in the United Kingdom show a Type III functional response (Fig. 10.5) to changes in red grouse (*Lagopus l. scoticus*) populations (Redpath and Thirgood 1999).

The S shape of this curve is attributed to a behavioral characteristic of predators called *switching*. If there are two prey types, A being rare and B being common, the predators will concentrate on B and ignore A. Predators may switch their search from B to A, thus producing an upswing in the number of A killed when A becomes more common. There is often a sudden switch at a characteristic density of A. Birds have a *search image* of a prey species such that they concentrate on one prey type while ignoring another. As the rare prey (A) becomes more common, birds (such as chickadees (*Parus* spp.) searching for insects in conifers) will accidentally come across A often enough to learn a new search image and switch their searching to this species.

In practice, it is often difficult to determine whether there is a Type II or III response because the differences occur at low densities of prey and measurements are usually imprecise. The most robust evidence comes from determining whether predators ignore prey until there is a sizeable prey density available: that would indicate a Type III response.

10.5.2 *Predator searching*

The success with which predators catch prey depends upon the density of the predator population. Predators usually react to the presence of other individuals of their own kind by dispersing. Mammal and bird predators are usually territorial and evict other individuals once the space has been fully occupied. These examples are forms of "interference" as we discussed in Section 8.6.2.

Interference progressively reduces the searching efficiency of the predator as predator density increases. The drop in searching efficiency caused by crowding lowers the asymptote of the functional response curve. Interference also has a stabilizing influence on predator numbers because it causes dispersal once predators become too numerous. Both interference behavior of predators and antipredator behavior of prey result in non-linear predation rates as predator populations increase. Sometimes this can result in a decrease in predation rate at higher predator levels (Abrams 1993).

10.5.3 *Predator searching and prey distribution*

Prey usually live in small patches of high density with larger areas of low density in between; in short, prey normally have a clumped distribution. This can be seen in the patchiness of krill preyed upon by whales, of insects in conifers searched for by chickadees, of seeds on the floor of a forest eaten by deermice, of caribou herds preyed upon by wolves, and impala herds hunted by leopards (*Panthera pardus*).

Searching behavior of predators is such that they concentrate on the patches of high density. By concentrating on these patches, predators have a regulating effect on the prey because of the numerical increase of predators by immigration (see Section 10.6).
10.6 Numerical response of predators to prey density

We define the numerical response of predators as the trend of predator numbers against prey density (see also Section 12.5) for other ways of looking at this). As prey density increases, more predators survive and reproduce. These two effects, survival and fecundity, result in an increase of the predator population, which in turn eats more prey. An example of this is Buckner and Turnock's (1965) study of birds preying on larch sawfly (*Pristiphora erichsonii*) (Table 10.2). As prey populations increased, the number of birds eating them also increased by reproduction and immigration. When plotted against prey density predator numbers increased to an asymptote determined by interference behavior such as territoriality (Fig. 10.6). Territoriality results in dispersal so that resident numbers stabilize. Wolves at high density have high dispersal rates, around 20% for adults and 50% for juveniles (Ballard et al. 1987; Fuller 1989). In New Zealand, the response of feral ferrets (*Mustela furo*) and cats to an experimental reduction of their primary prey (European rabbits) was a rapid long distance dispersal (Norbury et al. 1998). Extreme long distance dispersal (800km) of lynx has been observed in northern Canada when numbers of their primary prey, snowshoe hares, collapse.

FIGURE 10.6 Numerical response curve

*Resident numbers stabilize.*
Table 10.2. The predation rate on larch sawfly in areas of tamarack (*Larix laricina*) (high density) and mixed conifers (low density). Bird predators include new world warblers and sparrows, cedar waxwing (*Bombycilla cedrorum*) and American robin (*Turdus migratorius*). (After Buckner and Turnock 1965).

<table>
<thead>
<tr>
<th>Density</th>
<th>High Density (N/km²)</th>
<th>Low Density (N/km²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sawfly larvae</td>
<td>528 * 10⁴</td>
<td>9.88 * 10⁴</td>
</tr>
<tr>
<td>Sawfly Adults</td>
<td>50.75 * 10⁴</td>
<td>1.16 * 10⁴</td>
</tr>
<tr>
<td>Birds</td>
<td>58.1</td>
<td>31.1</td>
</tr>
<tr>
<td>%Predation larvae</td>
<td>0.5</td>
<td>5.9</td>
</tr>
<tr>
<td>%Predation adults</td>
<td>5.6</td>
<td>64.9</td>
</tr>
</tbody>
</table>

The initial increase in numerical response may or may not be density-dependent. However, because of the asymptote, the numerical response at higher prey densities can only be depensatory (inversely density dependent). This means it has a destabilizing effect on the prey population, by either driving the prey to extinction or allowing it to erupt. This is an important characteristic of populations and it is illustrated in Buckner and Turnock's (1965) study: the proportion of sawfly eaten by birds in the high prey density area was lower than that in the low density area (i.e. predation was depensatory and, therefore, could not keep the sawfly population down). The conditions when regulation can or cannot occur are discussed in the Section 10.7.

10.7 The total response

We can now multiply the number of prey eaten by one predator (*Nₐ*, the functional response) with the number of predators (*P*, numerical response) to give a total mortality, *M*, where:

\[ M = Nₐ P \] (10.8)

The instantaneous change in prey numbers is:

\[ \frac{dN}{dt} = -Nₐ P \] (10.9)
and an approximation for changes in prey number, over short intervals when prey populations do not change too much (<50%), is given by:

\[ N_{t+1} = N_t + N_t e^{-NaP/Nt} \]  

(10.10)

where \( N_t = N \) in equation 10.6 (Walters 1986).

If we express this total mortality, \( M \), as a proportion of the living prey population, \( N \), we can get a family of curves, as shown in Fig. 10.7, which depend on whether or not there is density-dependence in the functional and numerical responses. If there is density-dependence (for example from a Type III functional response) then we have a curve with an increasing (regulatory) part followed by a decreasing (depensatory) part. These are called the total response curves and examples are shown for some of Holling's small mammals (Fig. 10.8a) and for wolves eating moose (Fig. 10.8b) (Boutin 1992).

FIGURE 10.7 Theoretical total response curves (solid lines) for (a) Type III and (b) Type II, in relation to the net recruitment rate of prey (dotted line)
10.7.1 Regulatory effects of Predation

In Fig. 10.7 these total response curves have been superimposed on the per capita net recruitment rate of prey \(\frac{dN}{dt}\) (1/N). For the case where we have density-dependence (Fig. 10.7a) there are several stable equilibria (A, C, C') where prey net recruitment is balanced by total predation mortality. The point B is an unstable equilibrium where any perturbation to the system (from weather for example) will result in the prey declining to A or increasing to C. In practice B is never seen and is regarded as a boundary between domains of attraction towards A or C.

Curve (i) illustrates the case where predators can regulate the prey population under the complete range of prey densities and hold the prey at a low density A. One possible example of this occurs where both wolves and grizzly bears (Ursus horribilis) prey upon moose in Alaska (Ballard et al. 1987; Gasaway et al. 1992). Wolves appear to keep moose densities at low levels (<0.4/km²). When wolves were removed in a culling operation, the mortality of juvenile moose caused by bears increased so that moose numbers remained at the low level. Moose are kept at similar low levels by the density-dependent predation from wolves in Quebec (Messier and Crete 1985). Red foxes can regulate some small marsupials in desert regions of Australia and some medium sized...
marsupials in large Eucalypt forests of Western Australia (Sinclair et al. 1998). The combined predation of two raptor species, the hen harrier (*Circus cyaneus*) and peregrine falcon (*Falco peregrinus*), on red grouse in Scotland and England was density dependent in winter and was probably regulating the prey (Thirgood et al. 2000). Regulation was due at least partly to the Type III functional response referred to earlier (Redpath and Thirgood 1999).

Curve (ii) can occur when prey are regulated by intraspecific competition for food. Predators then kill malnourished animals and the effect on the prey population is depensatory rather than regulatory. This may be occurring on Isle Royale in Lake Superior where wolves cannot increase sufficiently to regulate the moose population (Fig. 10.9). Moose appear to be regulated by food (Peterson and Vucetich 2003) and wolf predation is merely depensatory (Fig. 10.9). Similar depensatory predation is exhibited in the total response of wolves depredating moose in the Findlayson valley (data in Hayes and Harestad 2000).

**FIGURE 10.9** Wolf numbers (dotted line) follow moose numbers (solid line) on Isle Royale, showing that wolves eat moose that starve from lack of their own food.
FIGURE 10.10 (a) The increasingly negative rate of increase of British Columbia mountain caribou indicate the inverse density dependent effects of wolf predation. (b) % predation by mammals (raccoons) and birds (crows) on small birds is a function of habitat patch size (which is a function of prey population size), also showing inverse density dependent predation.

Curve (iii) is the special case where both A and C are present and we have multiple stable states. This situation has been suggested for a few predator-prey systems. One example is that of foxes feeding on rabbits in Australia (Pech et al. 1992). Foxes were experimentally removed from two areas and the rabbit populations increased in both as would be expected from any of the curves in Fig. 10.7, and so by itself the increase in prey tells us little about the nature of predation. However, when foxes were allowed to return to the removal areas there was some evidence that rabbits continued to stay in high numbers rather than return to their original low densities. This result suggests that we have curve (iii) and not (i) or (ii): the interpretation is that rabbit populations, originally at A, were allowed to increase above the boundary density, B, so that when foxes reinvaded the experimental area rabbit numbers continued towards C.
The "forty mile" caribou herd of Yukon may have exhibited behavior characteristic of multiple stable states (Urquhart and Farnell 1986). Traditionally, this herd, whose range is on the Yukon-Alaska boundary, numbered in the hundred of thousands -- one estimate by O. Murie in 1920 being 568,000. In the 1920s and 1930s, goldminers and hunters killed tens of thousands. After the Second World War, when the Alaska Highway and associated roads were built, hunting increased further. By 1953 numbers were estimated at 55,000 and by 1973 there were only 5000 animals left. Although wolf numbers declined along with their prey, as one might expect, the proportional effect of predation was thought to be high. After 1973 hunting of caribou was restricted and during 1981-83 wolf numbers were reduced from 125 to 60. Thereafter, wolf numbers returned to pre-reduction levels. Although caribou numbers increased marginally to 14,000 during the wolf reductions, they have remained at approximately this level since the early 1980s. Despite the lack of accurate population estimates the density changes shown by the "forty mile" herd are so great (almost two orders of magnitude) that it is reasonably clear there has been a change in state from a high level determined by food to a low level determined by predators. The wolves may have been able to take over regulation because hunting could have reduced the caribou population size below the boundary level, B.

Another example of two states may be seen in the wildebeest of Kruger National Park, South Africa (Smuts 1978; Walker *et al.* 1981). In this case high numbers of wildebeest were reduced by culling. When the culling was stopped numbers continued to decline through lion predation, suggesting the system had been reduced below point B. A herbivore-plant interaction with two stable states is seen in Serengeti woodlands (Dublin *et al.* 1990b; Sinclair and Krebs 2002). Woodland changed from high to low density in the 1950s and 1960s by severe disturbance from fires. In the 1970s elephant browsing was able to hold woodlands at low density despite a low incidence of fires. Then, poaching removed elephants in the 1980s and trees have regenerated in the 1990s. Elephant numbers are rebounding in the 2000s but they cannot reduce tree density.

10.7.2 Destabilizing effect of predation

Fig. 10.7b shows the case where predators have no regulatory effect but can cause the extinction of the prey species if prey numbers are allowed to drop below B. Predation mortality is greater than prey net recruitment below B so that the prey population will decline to extinction. The conditions for this situation occur when there is no switching by predators (i.e. there is a Type II functional response), there is no refuge for the prey at low densities, and predators have an alternative prey source (their primary prey) to maintain their population when this (secondary) prey species is in low numbers.

Various mechanisms have been modelled by Gascoigne and Lipcius (2004). The inverse density dependent effect of predation on secondary prey (i.e. greater proportional predation as numbers decline) was shown experimentally using hens eggs in sooty shearwater (*Puffinus griseus*) nests in New Zealand. Smaller colonies of nests experienced higher proportional egg predation from rats and mustelids that were dependent on other primary prey such as European rabbits (Jones 2003).

Low densities of the secondary prey could be produced by reduction of habitat (as has occurred with many endangered bird species), or hunting. For example, wolves prey upon mountain caribou in Wells Gray Park, British Columbia during winter, but not in
summer when caribou migrate beyond the range of wolves (Seip 1992). Recruitment for this herd in March is 24-39 calves/100 females. In contrast, caribou in the adjacent Quesnel Lake area experience predation year-round and the average recruitment is 6.9 calves/100 females. This population suffers an adult mortality of 29% (most of which is caused by wolves), well above the recruitment rate, and so the population is declining. Wittmer et al. (2005) have shown that the predation rate increases as caribou density declines causing the populations to decline even faster (Fig. 10.10a) as predicted in Fig. 10.7b. Moose are now the primary prey in this system and maintain the wolf population. However, moose have only recently entered this ecosystem, having spread through British Columbia since the 1900s as a result of logging practices, so that previously wolves would not have had this species to maintain their populations at low caribou numbers. One interpretation, therefore, is that before the arrival of moose, caribou were probably the primary prey of wolves and the system was stable at either A or C. Moose have now become the primary prey, caribou have become the secondary prey, and they may be vulnerable to local extinction (Hayes et al. 2000). Similar caribou declines have been recorded in central Canada (Rettie and Messier 1998).

Habitat fragmentation for passerine birds breeding in deciduous forests of North America is thought to be the primary reason for the major decline in their populations (Wilcove 1985; Terborgh 1989; 1992). The interior of large patches of forest provide a refuge against nest predation from raccoons (Procyon lotor), opossums (Didelphis virginiana) and striped skunks (Mephitis mephitis), and parasitism from brown-headed cowbirds (Molothrus ater). Fragmentation of the forests reduces this refuge because nests are now closer to the edge of the forest where there are more predators and nest parasites. Predation rates are inversely related to forest patch size which must be related to total prey population (Fig. 10.10b). In large forest tracts nest predation is only 2%, in small suburban patches it is close to 100% and well above the recruitment rate. Since small fragmented forest patches are the norm in much of North America, many populations of bird species may be in the situation shown in Fig. 10.7b where the density is left of the boundary B and declining to extinction.

A similar result was observed in southern Sweden with forest fragments embedded in an agricultural landscape. Andren (1992) recorded the impact of various species of the crow family as predators of artificial nests placed in the forest. Two species, the European jay (Garrulus glandarius) and raven (Corvus corax) were confined to forest and were absent from small fragments, so their impact declined with fragmentation. Jackdaws (C. monedula) and black-billed magpies (Pica pica) were largely in agriculture. The hooded crow (C. corone) lived in agriculture but invaded forest patches causing increased predation along forest edge and within small fragments.

In Kruger National Park, the expansion of zebra (Equus burchelli) populations into dry habitats when water holes were constructed in the middle of last century allowed lions to move into those areas. Consequently, rare secondary prey, such as roan antelope (Hippotraus equinus) and tsessebe (Damalisus lunatus) have been driven towards extinction (Harrington et al 1999).

Cougar (Puma concolor) appear to be having an inverse density dependent effect, destabilizing bighorn sheep (Ovis canadensis) populations in the Sierra Ladron of New Mexico, U.S.A. These effects occur because cougar prey primarily on domestic cattle, which therefore subsidize the cougar population in this area (Rominger et al. 2004).
introduction of exotic predators and their exotic primary prey in Australia and New Zealand have caused declines and extinctions of endemic marsupials and birds. Thus, red foxes that depend on European rabbits and sheep carrion are able to drive black-footed rock-wallabies (*Petrogale penicillata*) and other marsupials to extinction in Australia (Kinnear et al. 1998; Sinclair et al. 1998). In New Zealand, stoats (*Mustela erminea*), black rats (*Rattus rattus*) and brush-tailed possums (*Trichosurus vulpecula*) that depend upon exotic house mice (*Mus domesticus*), a variety of exotic passerine birds, and fruits are driving endemic birds such as kokako (*Callaeas cinerea*) and yellowheads (*Mohoua ochrocephela*) to extinction (King 1983; Murphy and Dowding 1995); experimental reductions of these predators have allowed an increase in the endemic birds (Elliot 1996; Innes et al. 1999).

10.9 **Summary**

Some of the important points for conservation and management that we can derive from this discussion of predation are as follows.

1. Predator and prey populations usually coexist. Prey may be held at low density by predator regulation or at high density by intraspecific competition for food or other resources, and here predators are inverse density dependent.

2. It is possible that both systems may operate in the same area, leading to multiple stable states. This may be generated by a Type III functional response or by a density-dependent numerical response at low prey densities. The system may move from one state to another as a result of disturbance. Such dynamics may occasionally underlie the outbreak of pest species and the decline of species subject to hunting.

3. Conversely, there are situations where the prey population could go extinct, particularly with a Type II predator functional response, no refuge for prey, and alternative food sources for the predators. This is important in conservation where habitat changes may reduce refuges; introduced pests such as rats may provide alternative prey for predators of rare endemic species; or invading prey such as moose or white-tail deer assume the role of primary prey and so cause the original prey to become vulnerable to extinction as secondary prey.

4. Which of the above occurs depends on the ability of the predator to catch prey and the ability of the prey to escape either by using a refuge or by reproducing fast enough to make up the losses. A very efficient predator defined by a high predator/prey ratio will hold the prey at low density.