

Testing Predator–Prey Theory by Studying Fluctuating Populations of Small Mammals

Stan Boutin

Department of Zoology, University of Alberta,
Edmonton, Alberta, T6G 2E9, Canada.

Abstract

Fluctuating populations of small mammals provide an excellent opportunity to study the functional and numerical responses of predators because of the wide range in prey density that occurs. I reinterpret data from six studies that have examined the role of predation in the population dynamics of voles in California, southern Sweden and western Finland, of snowshoe hares in northern Canada, and of house mice and rabbits in Australia. Most studies have measured functional responses by relying on changes in diet as reflected by scat or stomach contents. These methods are probably biased toward showing predator satiation. Contrary to previous conclusions I find that there is little evidence for non-linear (Type III) functional-response curves or predator satiation at high prey densities. Recent studies indicate that the functional and numerical responses of predators can be rapid and strong enough to initiate cyclic declines, dampen fluctuations, or even cause stable numbers. The exception to this appears to be the irruptions of mice and rabbits in Australia. I propose a general explanation for the role of predation whereby the effect of predation is largely dependent on the entire prey community. When potentially cyclic prey are a small component of the overall prey biomass, generalist predators are able to prevent fluctuations by strong functional or numerical responses. As the prey community becomes dominated by a few species that fluctuate, limit cycles predominate. Limit cycles turn into irruptive population dynamics when seasonal prey reproduction is eliminated because of extended periods of vegetation growth (vegetation flushes following drought). In the future we must test assumptions underlying the way we study predation by telemetric monitoring of prey mortality and by experimentally manipulating predation.

Introduction

The functional and numerical response of predators to changing prey densities forms the basis for our theoretical and empirical understanding of how predators and prey affect the population dynamics of each other (Holling 1959). The study of predators preying on fluctuating populations of small mammals has provided most of the empirical measures of these responses for terrestrial vertebrates (Keith *et al.* 1977; Korpimaki and Norrdahl 1989). Consequently, these studies provide important tests of the shapes of theoretical functional response curves. In addition, researchers have used functional responses combined with numerical responses as the primary method for determining the impact of predation on fluctuating populations of small mammals. The purpose of this paper is to review studies that have measured the functional response of predators that rely on a prey base made up of small mammals in fluctuating populations. Included in this would be the 3–4-year microtine cycles of Scandinavia and Arctic Canada, the 10-year snowshoe hare cycle in northern Canada, and the irruptions of mice and rabbits in Australia. It is my contention that certain conclusions have been biased by techniques and the pressure to have data fit theory. This, in turn, has led to an underestimation of the impact of predation in the dynamics of fluctuating populations of small mammals.

To determine the role of predation in affecting the population dynamics of a prey species we need to answer the following questions.

- (1) What is the proportion of the population killed by predators?
- (2) What is the proportion killed by other sources?
- (3) What is the potential reproductive rate of the prey community?
- (4) Is there any relationship between these factors and prey density or between the factors themselves?

Because it is difficult to obtain the information necessary to answer all of the above questions, researchers have adopted paradigms that allow them to agree on the important questions and acceptable assumptions. An example of these is the density-dependent paradigm (Krebs 1995), where the emphasis is on the search for density-dependent relationships because they are thought to be the key for maintenance of populations around an equilibrium. Thus, people concentrate on the shape of functional and numerical responses rather than on their magnitude. If it were possible to obtain information to answer directly the four questions I have posed, the need for paradigms would vanish, leaving us with what we want: a clear explanation of how a predator affects the prey on which it feeds. The problem is that we can only get bits and pieces of information to answer all of the questions, so we have to make assumptions about the unknown parts. The set of acceptable assumptions depends on the paradigm one adopts. In this review I examine the assumptions that have been made concerning the impact of predation on fluctuating populations of small mammals in the hope of seeing the correct path while recognising the contributions of previous work that have led to these assumptions.

Assessing the Impact of Predation by Measuring Functional and Numerical Responses

Theory

One of the most influential concepts in predator-prey theory has been that of functional and numerical responses (Solomon 1949). When combined, the responses have the potential to render the proportion of the prey population removed at different prey densities, and this can be examined for density dependence. Holling (1959) was the first to quantify the concepts formulated by Solomon (1949) into distinct forms, which he called the Type I, II and III responses. These simple curves have established some deeply rooted principles in predator-prey theory. One of the most important of these for researchers studying fluctuating prey is that all curves reach an asymptote at high prey densities. In the case of the functional response this is due to satiation through handling time or gut processing and in the case of the numerical response it is due to behavioural limitation through territoriality. This predicts that predators take a decreasing proportion of the prey population at high prey densities, which for fluctuating prey populations then means that the influence of predation should be relatively less at peak densities. There is no question that there is a theoretical prey density at which an individual predator cannot handle any more prey. However, we cannot assume that these prey densities would necessarily be reached in the field.

The second important point has to do with the shape of the curves at low-to-intermediate prey densities. Type I and II curves show a constant or decreasing slope, which means that a decreasing proportion of the prey population is taken per predator as prey density increases. The response is inversely density dependent. In contrast, the Type III curve is sigmoidal, which means that the slope increases over low prey densities, and this implies that a greater proportion of the population is taken per predator over low-to-intermediate prey densities. The reason for the sigmoidal nature of the curve is switching by the predator, whereby prey are not consumed in any quantity until they reach a certain threshold. Holling (1959) attributed the switching to learning on the part of the predator but there could be any number of reasons for the switch. The vulnerability of the prey itself may change because of physical condition (McNamara and

Houston 1987) or habitat occupancy (Wolff 1980; Hik 1995). The Type III curve is an important component of more-recent theoretical developments such as two-state predator models (Sinclair *et al.* 1990).

Because the Type III curve appeared to be the only curve that had the potential to show density dependence, some researchers have been particularly preoccupied with looking for it. However, as pointed out by Messier (1993), combining functional and numerical curves of many types can lead to density-dependent predation. Thus, classifying curves as Type I, II or III may not be as important as actually quantifying how kills per predator and predator density changes with prey density.

Methodology and Assumptions

Describing the functional response requires that the number of prey killed per predator be known. To my knowledge, this has rarely been measured directly for terrestrial vertebrates in the wild (Messier 1993). Instead, virtually all measures are based on changes in proportion of the prey in the diet. For avian predators, diet is assessed by pellet analysis or by prey remains at the nest (Rusch *et al.* 1972; McInville and Keith 1974; Korpimaki and Norrdahl 1991a). For mammalian predators it is done from scats (Erlinge *et al.* 1983) or stomach contents (Todd *et al.* 1981; Corbett and Newsome 1987; Pech *et al.* 1992). Changes in diet composition with changing prey density give a measure of the shape of the functional response but do not give the actual number of prey consumed per predator. To get this, researchers have multiplied the proportion in the diet by the daily energy requirements of an individual predator and divided this by the energy content of a single prey item. Daily energy requirements are estimated from laboratory studies, in most cases. Thus, the only factor that is actually measured in the field is diet composition.

How does the above approach affect the shape of the functional response? Changes in proportion in the diet are probably a reasonable reflection of dietary shifts over intermediate prey densities but this is less likely at high and low densities for the following reasons. At high prey density, predators could respond in a number of ways that would increase the number of prey killed per predator but not necessarily the proportion of the prey in the diet. The most important of these would be partial prey consumption and prey caching (Kruuk 1972; Keith *et al.* 1984). Optimal foraging theory would predict that predators should start to consume only the most nutritious or most digestible parts of a kill if killing is easy. These parts, in turn, would be least likely to be detected in scats or pellets. Similarly, predators may cache part or all of a kill but fail to return to it if making another kill is easy to do. Thus, even if the proportion of scats made up by a certain prey item is 100%, predators could still be increasing the number of prey they kill in the manner described above.

There are also problems at low prey densities. The proportion of scats containing a certain prey item may remain constant but the deposition rate could change such that fewer scats are produced. Consequently, kills per day would be lower than that calculated by diet composition. Alternatively, the importance of an item may be overestimated if predators scavenge old carcasses. Finally, fewer scats are found at low prey densities, which means that greater changes in proportions in the diet are required to be statistically detectable. In other words it is more difficult to detect changes in the slope of a relationship.

Some studies have tried to avoid some of the above problems. Sinclair *et al.* (1990) argued that raptors produce a single pellet per day so the number of jaw bones of mice per pellet was a direct measure of prey killed per predator per day. Pech *et al.* (1992) calculated the functional response of foxes eating rabbits by measuring the amount of rabbit in the guts of a shot sample of foxes and calculating the average amount of time a single meal would be detectable in the gut. Brand *et al.* (1976) snowtracked lynx to determine the number of snowshoe hares killed per kilometre of trail. They calculated the average distance moved in a day by assuming that the distance between resting sites was equivalent to a 24-h period and then converted the kills per kilometre to a daily kill rate.

Table 1. Studies that have measured the functional response of predators under conditions of a fluctuating prey base

Amplitude was measured as the highest divided by lowest value over the course of the study. Amplitude was calculated from density estimates or indices for the prey and the numerical response (NR) of the predator. Amplitude of the functional response (FR) was calculated from measures of kills per predator per unit time. *n* is the number of independent measures of kill rate that were made (usually years), type is the type of functional response identified by the researchers (n.r., no response) and satiation (y, yes; n, no) refers to whether the researchers argued that the curve showed asymptotic behaviour

Predator	Amplitude		<i>n</i>	Type	Satiation	Reference ^A
	Prey	Predator FR NR				
Great horned owl	20	6 3-4	10	I	y	1
Red-tailed hawk	20	2 0	10	I	n	1
Lynx	20	3 3-4	5	II	y	1
Coyote	20	77 3-6	7	III	y	1
European kestrel	50	15 23	11	I	n	2
Short-eared owl	50	33 49	11	I	n	2
Long-eared owl	50	4 19	11	I	n	2
Tengmalm's owl	50	6 26	11	I	n	3
Stoat	40	5 20	6	I	n	4
Least weasel	40	1 12	6	n.r.	-	4
Dingo	100	3 -	12	I	y	5
Fox	100	15 15	24	III	y	6
Diurnal raptors	14	2 8	14	III	y	7
Terrestrial predators	200	5 47	13	-	-	8

^A1, Keith *et al.* (1977); 2, Korpimaki and Norrdahl (1991a); 3, Korpimaki and Norrdahl (1989); 4, Korpimaki and Norrdahl (1991b); 5, Corbett and Newsome (1987); 6, Pech *et al.* (1992); 7, Sinclair *et al.* (1990); 8, Pearson (1966).

Thus, conventional methods of measuring functional responses are loaded with assumptions, and more problems are likely to exist at low and high prey densities, the two regions that have the greatest implications for the effect of predators on fluctuating prey. Given these problems, one should be careful when data are few or changes are small.

Functional and Numerical Responses of Predators with a Fluctuating Prey Base

Because small-mammal populations that fluctuate show wide variation in density, their predators should be good candidates for measuring functional responses. I found six such studies and they are summarised in Table 1. There are two important things to note. In the 13 species where the shape of the functional response was measured, seven were classed as Type I, two were Type II, three were Type III and one showed no relationship. Secondly, six of 12 cases found no satiation at high prey densities. Korpimaki and Norrdahl (1989, 1991a) present strong evidence that raptors feeding on *Microtus* populations in western Finland show linear functional responses with no satiation. They compared satiation curves to linear curves and found that satiation curves did not improve the fit significantly. The six cases that reported satiation by predators at high prey density are shown in Fig. 1. Keith *et al.* (1977) drew asymptotic curves for three predators of snowshoe hares: great horned owls, lynx and coyotes. In each case, there was no statistical comparison made of the fit obtained by a linear versus a curvilinear

relationship, and the satiation is based on a single critical point. The same can be said for the study of dingo predation on rabbits in Australia (Corbett and Newsome 1987). Foxes feeding on rabbits appear to show satiation although the data are highly variable (Pech *et al.* 1992) and the same holds for various raptors feeding on a mouse plague in central Australia (Sinclair *et al.* 1990). Thus, despite the methodological biases toward finding satiation responses as previously

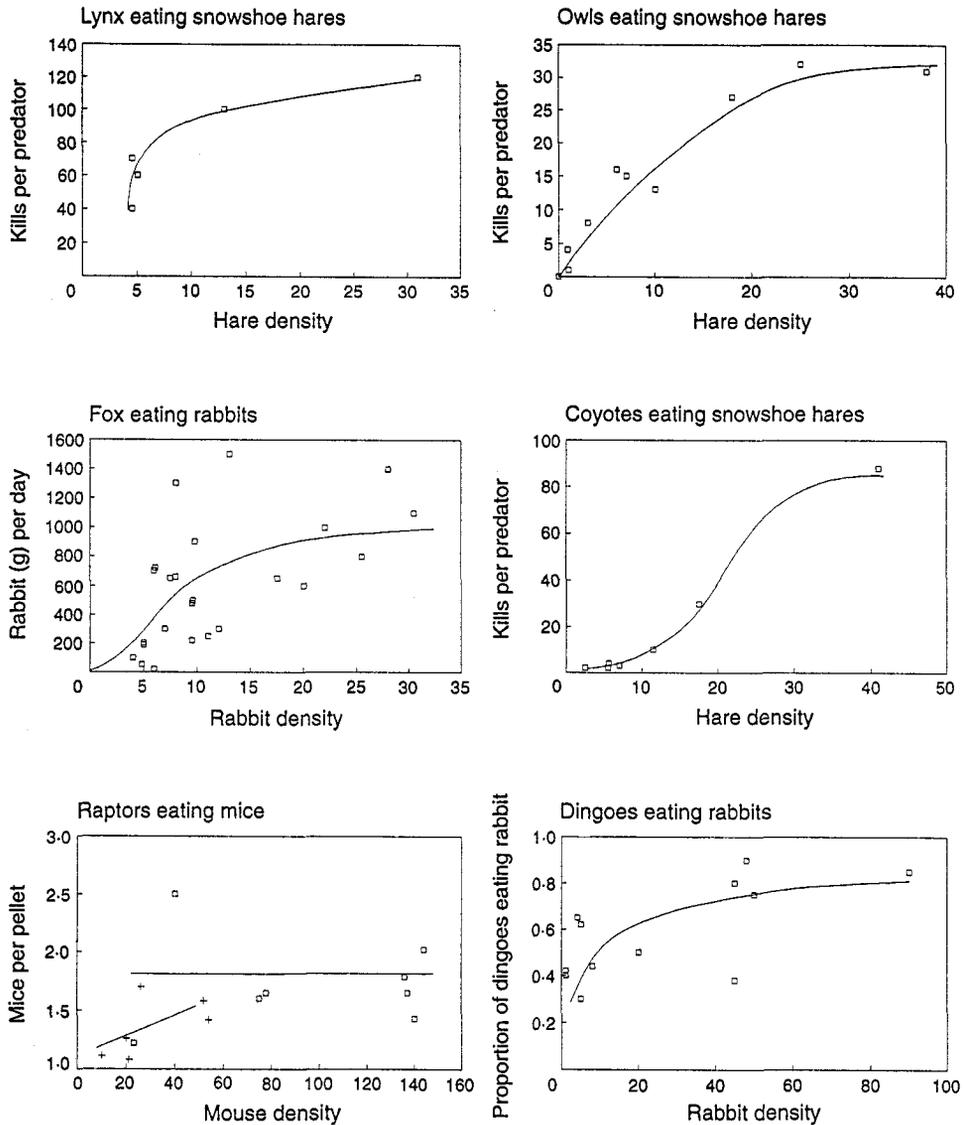


Fig. 1. Functional responses of predators experiencing a fluctuating prey base. Graphs for lynx, owls and coyotes redrawn from fig. 4 of Keith *et al.* (1977); that for dingoes redrawn from fig. 4a of Corbett and Newsome (1987); that for foxes redrawn from fig. 4 of Pech *et al.* (1992); that for raptors drawn from table 1 of Sinclair *et al.* (1990).

outlined, the studies of irruptive mouse and rabbit populations in Australia are the only strong examples of predators exhibiting functional responses that asymptote over the range of prey density observed in the wild. In addition, most of the data are inadequate to differentiate between Type II and III curves. Only Pech *et al.* (1992) has tried to do so statistically.

Table 1 also shows the amplitude of change (high/low) in functional and numerical responses that have been recorded. As expected by relative reproductive rates of predator and prey, the amplitude of numerical change of the predator over a fluctuation in prey is usually well below that of the prey. However, when functional and numerical responses are combined, the total amplitude of predator response exceeded the amplitude of prey change in 10 of 13 cases. In other words, the magnification of killing rate of the predator population from the low to the high phase of the prey fluctuation was equal to the magnification of the prey population itself. On this basis, the killing capacity of the predator population was capable of matching the increase of the prey. The problem with these comparisons, however, is that the ratio of high to low is highly dependent on the values determined at the low phase of prey density where slight errors could mean an order-of-magnitude difference in the calculated change in amplitude.

Predator Impact in Relation to Prey Density

Studies that calculated the proportion of the prey population removed, as determined by combining functional and numerical responses of the major predators in the community, are summarised in Table 2. All but one of these describe the relationship as being inversely density dependent over part or all of the range of prey densities. An example of the type of information used to reach this conclusion is shown in Fig. 2a. Keith *et al.* (1977) measured the proportion of a snowshoe hare population killed by predators over winter and concluded that predation was inversely density dependent. Fig. 2a does show that losses to predation *can* be higher at low than at high (peak) densities. However, losses to predation can also be relatively low when prey numbers are low, as shown by the two measures taken during population increase. My point is that drawing an inverse relation through these points may not be the best interpretation. The

Table 2. Proportion of the prey population removed by predation

Number of prey consumed was calculated by combining functional and numerical responses of the principal predators. Total number of prey available was determined by density estimates obtained by live-trapping in most cases. The relationship between the proportion of the prey population removed and prey density was classed as density dependent (DD) or inversely density dependent (IDD) as suggested by the authors. The number of different seasons or years in which the removed proportion was calculated is shown in parentheses

Prey	Prey dynamics	Proportion removed (%)	Relationship	Reference ^A
Snowshoe hare	cyclic	10.4–42.7	IDD (7)	1
California vole	cyclic	5–100	IDD (13)	2
Field vole	weakly cyclic	7–52	DD (11)	3, 4
Field vole	stable	10–60	DD, IDD (30)	5
House mouse	irruptive		DD, IDD (14)	6
Rabbits	irruptive		DD, IDD (25)	7

^A1, Keith *et al.* (1977); 2, Pearson (1966); 3, 4, Korpimäki and Norrdahl (1991a, 1991b); 5, Erlinge *et al.* (1983); 6, Sinclair *et al.* (1990); 7, Pech *et al.* (1992).

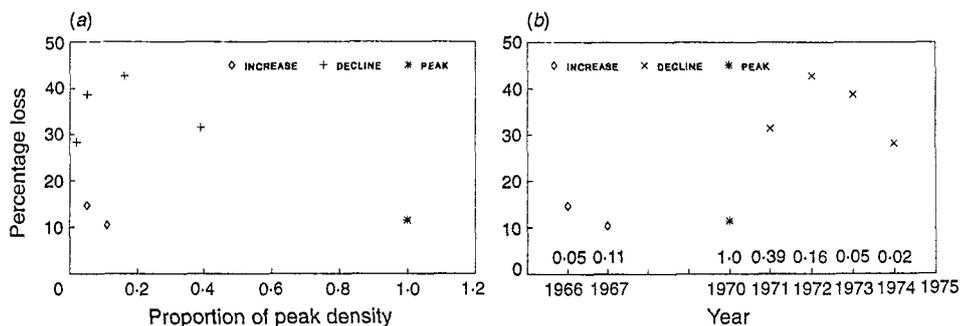


Fig. 2. Changes in the percentage of the prey population (snowshoe hares) killed by predators (a) at different prey densities and (b) in different years (with densities shown above each year for which information was available). Densities are expressed as a proportion of peak density (990 hares per 100 ha of hare habitat). Each point represents a different year and increase, peak and decline represent phases of the population cycle. Note that the proportion lost to predation was roughly constant over a wide range of prey densities during the increase and peak phases of the cycle. Rates were again constant, but three times higher, over a wide range of prey densities during the decline phase. Data are from table 1 of Keith *et al.* (1977).

same information is shown in Fig. 2b, but with the x-axis showing the years of the study rather than increasing hare density. The striking aspect of the figure is that predation was roughly constant at 10% over a wide range of low-to-peak prey densities, after which the rate jumped to 30%, where it again remained constant over a wide range of density as the population declined. Thus, prey density tells us little about predation rate and, therefore, predation rate should not be termed density dependent or inversely density dependent. Instead, predation rate is more clearly related to phase of the cycle, being three times greater during the decline. Pearson (1966) observed a similar pattern in California voles where rates were 5–15% during the increase and early peak followed by rates of 25–85% during the crash and low phases.

Predation by various raptors in western Finland is a striking contrast to the above (Korpimäki and Norrdahl 1989, 1991a). In this case the proportion of the vole population removed during the breeding season was density dependent because of the raptor's rapid numerical response through immigration. Erlinge *et al.* (1983) reported studies of non-cyclic vole populations, in which they argue that predators were responsible for the lack of cyclicity. Within any year, predation rate was inversely density dependent except at peak densities in autumn when it was density dependent. They found that predation was density dependent when comparing between three years (Erlinge *et al.* 1988).

Sinclair *et al.* (1990) and Pech *et al.* (1992) have argued that predators feeding on house mice and rabbits in Australia showed density-dependent predation over low-to-intermediate prey densities followed by inverse density dependence at high densities. They did not actually calculate the proportion of the prey population removed but compared proportional changes in mortality caused by predators and prey density to make these arguments. These studies are important because the authors claim that predation regulated prey density around a lower equilibrium. This will be discussed in more detail in a later section.

To summarise, the relationship between predation rate and prey density was highly variable. In general, the proportion of the prey population killed by predators was lower at high than at low prey densities. However, there is little evidence to indicate that rates were linearly related to density. The presence or absence of density dependence did not seem related to whether prey populations were stable, cyclic or irruptive.

The Impact of Predation at Different Phases of the Cycle

Are Predators Capable of Initiating Population Declines?

Until recently, researchers argued against the ability of predators to initiate a decline in prey numbers because the functional and numerical responses of predators were thought to show satiation at high prey densities (Keith *et al.* 1977). I have already shown that evidence for satiation is rare over the range of prey densities observed in the wild, and Table 1 shows that the amplitude change from combined functional and numerical responses can be equivalent to the amplitude of change in the prey population. Studies by Korpimäki and Norrdahl (1989, 1991a) suggest that rapid numerical responses of raptors through immigration allows these predators to track vole fluctuations rapidly and to dampen peak populations.

In contrast, Keith *et al.* (1977, 1984) argued that peak populations of snowshoe hares had to be reduced by winter food shortage before predators could remove a significant proportion of the population. They found no increase in the proportion of the population removed by predators until the year following the peak. However, Boutin *et al.* (1986) showed that predation losses, as monitored by following radio-collared prey, did increase in the peak year in the population they studied.

In the case of irrupting populations of house mice and rabbits in Australia, it seems that predators cannot initiate declines in prey numbers on their own and that drought conditions were necessary to reduce densities of these species (Newsome *et al.* 1989).

Are Predators Responsible for the Low Phase of the Population Cycle?

A characteristic feature of fluctuating populations is that numbers stay low for extended periods following the crash. This phase of the cycle remains the least understood but many argue that predators play a key role. Keith *et al.* (1977) showed that predators feeding on snowshoe hares declined in numbers more slowly than did their prey such that predator: hare ratios were very high, as was the proportion of prey killed by predators (Fig. 2b). They argued that predators must decline to very low levels before hare numbers would begin to increase. However, the proportion of the population killed by predators at the crucial transition from the low to the increase phase of the cycle is not available.

Korpimäki and Norrdahl (1991b) argued that weasel predation on voles during winter in western Finland was responsible for vole crashes and extended lows. They found that kill rates (density of predator \times percentage of *Microtus* in the diet) were inversely correlated to changes in density over winter. Henttonen *et al.* (1987) provide correlative evidence to suggest that weasels may be responsible for the crash and low phase of vole cycles in northern Fennoscandia.

Sinclair *et al.* (1990) argued that predation by raptors on house mouse populations was density dependent over low prey densities and that predation actually regulated the prey around a lower equilibrium. There have been similar arguments made for foxes preying on rabbit populations in eastern Australia (Pech *et al.* 1992). In these cases, populations escape from the predator-regulated equilibrium when increased rainfall leads to increased breeding by the prey population. Once the prey population escapes it is no longer regulated by predators and some other factor must cause prey numbers to decrease before predation becomes regulatory again. These arguments are important because it suggests that there are two possible states, a lower, predator-regulated equilibrium and an upper, food-regulated equilibrium. Some of the data that have been used to make this interpretation are shown in Fig. 3. Sinclair *et al.* (1990) chose to interpret the predation losses in reference to the density-dependent paradigm and consequently saw linear relationships between an index of predation mortality and density. An equally plausible explanation is that there are two states of predation intensity that may or may not be related to prey density: the first is a variable but high level and the second a less variable and lower level. The two states are separated somewhat in terms of where they occur in the range of prey density but there is overlap. It seems premature to make arguments about whether

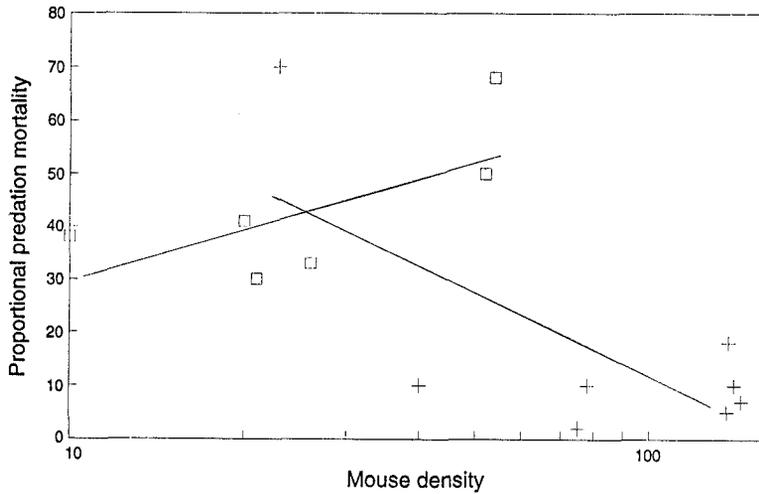


Fig. 3. Proportional predation mortality by diurnal raptors in relation to an index of house mouse density. Redrawn from fig. 6a of Sinclair *et al.* (1990). Symbols denote different phases of the mouse plague: see Sinclair *et al.* (1990) for an explanation.

predation rates are density dependent at this point, given the data and that doing so may not be necessary. The striking point of the graph is that the system appears to switch from one state to another, and the question is what causes this switch. There is some agreement that heavy rains are involved but how this relates to predation is not clear (Newsome *et al.* 1989).

The Changing Role of Predation in Stable, Cyclic and Irruptive Prey Populations

Is it possible to link the studies of predation on fluctuating populations of small mammals under some general hypothesis? In Fennoscandia, studies of predators of northern small mammals form a continuum from the non-cyclic vole populations in southern Sweden (Erlinge *et al.* 1983) to weakly cyclic vole populations in western Finland (Korpimäki and Norrdahl 1989, 1991a, 1991b) to strongly cyclic populations in northern Fennoscandia (Henttonen *et al.* 1985). Many researchers have commented on how prey cyclicality is more pronounced in northern regions, and Hanski *et al.* (1991) have suggested that generalist predators in southern areas dampen cycles created by specialist predators. In northern areas there are few generalist predators, and a stable-limit cycle between specialist predators and their prey exist. In North America, snowshoe hare cycles are less pronounced in the southern part of their range and this too has been attributed to higher densities of facultative predators and more habitat heterogeneity in the south (Wolff 1980).

Many of the above ideas can be simplified into the following general theory, which concentrates on the composition of the prey community rather than that of the predator community. The key question is what percentage does the fluctuating prey species make up of the total prey base? The study by Erlinge *et al.* (1983) of voles in southern Sweden stands out as an example of lack of cyclicality due to predation by generalist predators. In this case, voles were actually the alternative prey to predators that were living primarily on rabbits. The result was a constant high density of predators that fed opportunistically on voles, particularly in winter and spring, when all prey populations were generally depressed. During the breeding season, vole populations increased but the season was not long enough to permit them to build to numbers that were greater than could be removed by the resident predators over winter. The result was stable numbers of voles from year to year.

In western Finland, vole densities were also relatively low but, in this case, the alternative prey was the same species but in a different location. In other words, predator populations were maintained by local pockets of high vole density and predators simply switched pockets as relative densities changed. Because of the predator's mobility, prey density must be measured at a landscape level and the biomass of any single vole peak is small relative to the total area. Predator numbers are maintained on a landscape level by the vole fluctuations being asynchronous so that there are always some areas with high vole densities. As in southern Sweden, vole populations increase during the summer but not to the levels seen in more northern areas because of the high predation by raptors. The result is weakly cyclic populations of voles with dampened peaks.

In the case of strongly cyclic populations of voles in northern Fennoscandia and of snowshoe hares in Canada, the cyclic prey species is the dominant herbivore in the system and other prey are relatively scarce or difficult to catch. Consequently, predator and prey are tightly linked but, because of differences in potential for increase, time-lags develop and cycles result. Under this scenario, voles or hares do not increase until predators have declined to levels dictated by the scarce alternative prey base. As the prey increases, predators also respond but not fast enough to prevent prey increase. The key question remains as to whether the prey is eventually depressed by the predator because of a slowdown in prey reproduction or because functional and numerical responses of predators become sufficient to stop prey population increase. Once the decline in numbers begins, however, the decrease is severe because there is relatively little buffering of predation by alternative prey and because predator numbers decline more slowly than do those of the prey.

Do the irruptive dynamics of house mice and rabbits in Australia fit into this theory? Judging from the work by Corbett and Newsome (1987), rabbit forms a large part of the prey biomass available for dingoes and foxes. Other prey is relatively scarce. This would make the system more similar to that of cyclic hares and voles. Why do rabbits irrupt rather than cycle? The answer might be Newsome's Environmentally Modulated Predation Theory (Newsome *et al.* 1989). Alternative prey may be adequate to maintain predators such that they prevent increase in prey populations during drought conditions; however, rains lead to increased reproduction and a prey irruption. Predators never catch the prey during the irruption because prey can breed continuously whereas the predators seem to maintain seasonal reproduction. Instead, drought must reduce prey reproduction and abundance before predation becomes limiting or regulatory. Similar things might be happening with house mouse plagues.

The ideas I have presented above are not new. What is different, however, is the attempt to integrate previous ideas into a perspective that concentrates on the make-up of the prey community rather than that of the predator community. Because of the concentration on functional and numerical responses of predators, most studies describe the curves in terms of changes in a single prey population with the assumption that other prey densities remain constant. Information on changes in density of alternative prey are not reported in many studies nor is the percentage that the prey of interest makes up of the total prey biomass. However, it is the composition of the prey base that determines whether predators can be generalists. It is clear that all predators respond functionally to changes in prey density but the timing and reason for prey switching remains unresolved.

An Alternative Approach to Studying Predation

I have tried to show that much of our confusion about the effect of predation on fluctuating small mammals is due, in part, to the methodological problems associated with measuring the impact of predation by functional and numerical responses. Are there alternative approaches that have fewer assumptions? One possibility is to study predation by concentrating on the prey rather than on the predator. This approach uses radio-telemetry to monitor mortality rates of the

prey and to determine cause of death. This approach has many advantages over the conventional method of measuring functional and numerical responses, one of the most important being that there are statistical methods that can be used to attach variance estimates to rates. The major assumption in this approach is that the proximate cause of mortality is the most important and that mortality rates due to various agents are additive. This assumption is common to all of the studies discussed so far and multifactor experiments are required to test this.

My colleagues and I have been monitoring predation on snowshoe hares by telemetry since 1978 (Boutin *et al.* 1986; Trostel *et al.* 1987). This has spanned two population peaks and declines. These studies have produced the following important results. Firstly, we found that predation rates increased in the peak year and remained high well into the decline (Boutin *et al.* 1986). Secondly, predation rates were much higher than those determined by Keith *et al.* (1977) when they used functional and numerical responses. These results lend support to the argument that predation alone is capable of causing the hare decline. Finally, in the recent increase and peak we were able to radio-tag very small leverets and follow their fates. This produced the striking result that a previously unidentified predator, the red squirrel (*Tamiasciurus hudsonicus*), was a major source of mortality of young hares (O'Donoghue and Krebs 1992). It is possible that this source of mortality may have slowed the rate of population growth of hares enough to allow predators to force a decline over winter.

These findings point to the fact that alternative ways of studying predation will probably produce interesting results and, at the very least, provide a comparison with conventional methods that might suggest potential biases. We must begin to be more critical of the assumptions underlying how functional responses and predation impact are calculated. Finally, manipulation of predation pressure must be a more frequent experiment if we are to understand the actual mechanisms at work.

Acknowledgments

I thank my colleagues involved in the Kluane Boreal Forest Ecosystem Project for sharing their ideas. Rich Moses, Barb Thomas, A. R. E. Sinclair and two anonymous reviewers provided helpful comments on earlier drafts. This is contribution No. 54 of the Kluane Boreal Forest Ecosystem Project.

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