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Interactions between woodland rodents and their predators

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Synopsis

The interactions between woodland rodents (mainly wood mice, *Apodemus sylvaticus*, and bank voles, *Clethrionomys glareolus*, but also including ecologically equivalent species of *Peromyscus* and *Mus*) and their predators are discussed at both the individual and the population level. The hunting techniques of predators, and the anti-predator defences of the rodents, determine which and how many rodents are killed. The effects of fluctuations in numbers of rodents on the biology of predators depend largely on the predator's hunting technique and life-history strategy. The effect of the combined force of predators on the population fluctuations of the rodents depends on whether their collective functional and numerical response is sufficiently extensive and rapid; this is greatly influenced by the supply of alternative prey and the heterogeneity of the habitat. In four case studies discussed, the impact of predation was considered to be substantial in all, but the apparent effects were opposite: in two it amplified and in the other two it minimised the population fluctuations of the rodents.

Introduction

Practically all small- to medium-sized carnivores and raptors that regularly hunt on or near the forest floor will take rodents whenever the opportunity offers. Lists of the food habits of woodland owls (e.g. the tawny owl (*Strix aluco*): Southern 1954) and carnivores (the stoat (*Mustela erminea*), the weasel (*M. nivalis*), polecat (*M. putorius*), mink (*M. vison* and *M. lutreola*), marten (*Martes martes* and *M. foina*), cat (*Felis catus*) and fox (*Vulpes vulpes*): Corbet & Southern 1977) nearly always include woodland rodents in larger or smaller amounts. Various other predators are also reported to take them occasionally. A comprehensive bibliography on the subject would be long: the one compiled by Jüdes (1982) for *Apodemus* included 82 entries under the heading 'predation, pellet analysis' for 1970-80 alone. Goszczyński (1983) tabulated the estimated proportion of bank voles (*Clethrionomys glareolus*) in the diets of 14 species of vertebrate predators, citing 27 papers dated from 1954 to 1976.

Unfortunately the great majority of such reports are of casual interest only, since they tell us nothing about the consequences of the encounter for either the predators or the prey. Most are simply lists of the foods eaten by the predators, which do not qualify as studies of predation, still less as studies of the interactions between predators and prey. The conditions for such a study demand much more than this.

For the purpose of this review I have, wherever possible, concentrated on papers which meet all or most of the following criteria:

- a) study area was largely or at least partly in woodland;
- b) principal prey were species of *Apodemus*, *Clethrionomys* or ecological equivalent;
- c) at least rough density estimates were made for both predator and prey together throughout the year;
- d) at least some attempt was made to examine the biological responses causing any observed changes in density of predator and/or prey;
- e) at least a rough estimate was calculated of the intensity of predation, measured directly or by any change in prey density probably due to predation;
- f) if possible, some estimate was made as to how the above relationships might have changed with variations in prey density.

These criteria immediately exclude many well-known studies on predation in rodents, which have focussed on *Microtus* (subject of a contemporary review by Pearson 1985), or have not supplied parallel data on predators and prey together, as well as the great majority of studies on *Apodemus* and *Clethrionomys*, which mention predation only casually, if at all. On the other hand, by expanding the definition of 'woodland' to include any kind of forest, and by considering rodents ecologically equivalent to *Apodemus* and *Clethrionomys* living elsewhere in the world, a wider literature on woodland predator-prey relationships may be tapped. This paper is not a comprehensive index of what predators eat bank voles or wood mice, but a discussion of the general patterns of *interactions* between woodland rodents and their predators from selected examples, including other forest environments and other species when the available information on bank voles and wood mice is insufficient.

Research on predator-prey interactions is demanding and difficult in all habitats, but it tends to be more so in woodland than elsewhere, for a number of reasons. First, the rules of ecological energetics ensure that populations of strictly woodland rodents (and therefore also of their predators) are generally sparser, and fluctuate within narrower limits, than those of grassland and tundra species (see Fig. 2); and, since the massive deforestation caused by civilised man over the last two or three thousand years,

strictly woodland species are often less widely distributed. Material and data on undisturbed woodland predator-prey systems are therefore relatively harder to get. A further complication is that some woodland species, especially wood mice (*Apodemus sylvaticus*) may also live in hedges, copses and crops outside true woodland, and may often be caught there by non-woodland predators such as barn owls (*Tyto alba*: e.g. Buckley & Goldsmith 1975) or wide-ranging ones such as stoats (e.g. Erlinge 1981), but they provide only a small and unpredictable proportion of the food eaten by these predators. The landscapes of most intensively-settled temperate countries are a mosaic of habitats, in which the originally near-continuous woodland is reduced often to a few scattered patches. The interactions between the rodents and their predators in these forest islands are often strongly influenced by events in the more extensive farmland outside, which are, in turn, related more directly to the predator's relationships with *Microtus* and rabbits than to any attribute of the woodland rodents themselves.

Second, rodents inhabiting open country have tended to attract attention and research funds for reasons both practical (damage to farm crops and new plantations) and intellectual (the challenge of solving the mysteries of intrinsic population cycles). Understandably then, the literature on predator/prey interactions in rodents is concerned far less with the inhabitants of woodland, such as *Apodemus* and *Clethrionomys*, than with *Microtus* spp.

Predator-prey relationships can be discussed at the individual or at the population level. The outcome of an interaction between any *individual* predator and its prey is determined by the characteristics of the opponents—i.e. by the hunting strategy of the predator and the anti-predator defences of the prey. These are therefore examined in the first two sections of this review. The outcome for the *populations* they each represent is the long-term sum of the individual interactions of all the predators and prey of equivalent trophic level living together in a single community. These are examined in the next two sections. The final section lists some of the most obvious gaps in our knowledge that future students of this subject might consider.

Hunting strategies of predators

Various details of the morphology or behaviour of a predator influence its ability to catch woodland rodents. In this paper, the term 'hunting strategy' simply means the combined observable effects of these attributes in individual real predators living in the field, as distinct from in theoretical models. Characters to be considered include the functional type of each predator; the season, the time and the method it uses to search for woodland rodents; its degree of dependence on them; whether or not it tends to select between classes and species of the rodents available to it; and the effects of habitat variables such as cover, weather, and the availability of alternative prey.

Functional type

Andersson & Erlinge (1977) distinguished several functional types of rodent predators. *Specialists* are well adapted to prey on rodents, and their abundance, distribution and breeding success are strongly influenced by the density of rodents. *Generalist* predators take a greater variety of prey, and their abundance, distribution and breeding success need not be greatly influenced by the density of rodents if alternative prey are available. *Resident* predators have limited dispersal capacity, or a strong attachment to an individual territory, regardless of variations in prey density, as opposed to *nomadic* or *migratory* predators (scarce in woodland), which may congregate or disperse across large distances according to the local density of rodents. There are, of course, all shades of intermediates between these extreme types.

In Britain and Europe, two predators commonly found in contemporary woodland, the tawny owl and the weasel, both clearly belong to the resident specialist end of the range. Both may take invertebrates, young rabbits, birds, etc., and tawny owls also take moles and rats; but small rodents supply more than half their prey every year (Southern 1954; King 1980) and exert a decisive influence on their breeding success (Southern 1970; King 1983a).

In former years in Britain, and in boreal forests even now, various species of martens (*Martes* spp.) were or are widespread woodland predators belonging more to the category of resident generalist (Lockie 1961; Weckwerth & Hawley 1962; Pulliainen 1981; Powell 1982). The red fox, stoat and feral cat are also resident generalists, although none is as dependent on woodland as are the martens. Martens, stoats, foxes and cats take woodland rodents when they are abundant, or, conversely, when other prey are particularly scarce, but a dearth of woodland prey is usually much less serious for them than for the specialists.

Hunting technique

A predator's method of finding and catching its prey determines what proportion of the prey population is available to it. For example, weasels are active searching predators, locating their prey by eye and ear and only secondarily by smell (Erlinge, Jonsson & Willstedt 1974; Nams 1981); they check every covert and hole on the surface, running along a zig-zag path (Powell 1978; Pounds 1981); most individuals (especially females) are small enough to enter rodent burrows and nests (Simms 1979; Pounds 1981), so they do not have to wait until their prey are active, but can hunt whenever they are hungry. They can reach the entire population of both voles and mice regardless of, for example, weather or moonlight, the familiarity of the terrain, or the age or activity of the prey, including unweaned nestlings and adults at rest: they can kill adult *Clethrionomys*, *Apodemus* or *Microtus*

equally readily (Erlinge 1975). In parts of North America where weasels (*M. nivalis*) are absent, this niche is filled by small-sized *M. erminea* (Simms 1979).

By contrast, tawny owls normally use the ambush method of hunting, locating a moving rodent by ear and eye and dropping silently on to it from a perch (Southern & Lowe 1968). They are very largely nocturnal, and normally catch only those rodents that expose themselves at night, above ground and outside thick cover. Tawny owls hunt both voles and mice, but catch relatively more of the nocturnal wood mice (Southern & Lowe 1982); and a smaller proportion of the total population of these is available to them than to weasels. Their hunting is also more influenced by environmental conditions affecting their hearing or sight. Rain reduces the owl's capture rate, both because the sound of raindrops falling on the foliage is distracting, and because rodents make less noise running across sodden ground (Hirons 1982). On dark nights the owl's strike may be less accurate, but the greater activity of the wood mice gives them more opportunities; conversely, on bright nights the mice avoid showing themselves, but those that do can be seen more clearly and so are more easily caught (Clarke 1983). Familiarity with its territory is important to a hunting tawny owl. Lack of familiarity reduces hunting success; lack of a territory means almost certain death (Southern 1970).

The resident generalists use a variety of similar but less effective hunting methods. Cats have a feline version of the owl's 'sit-and-wait' technique; foxes can sometimes reach nests of young rodents by digging in earth; martens burrow down through snow. But an individual rodent sheltering in a hole is more secure from one of these than from a weasel, which would go in after it, or from an owl, which could probably afford to wait till it came out. Generalist predators (and even the largest male weasels) have to rely on flushing it out, by scratching or stamping at the entrance (Erlinge, Bergsten & Kristiansson 1974) and, if it is safely out of reach and refuses to move, they tend to give up, especially if there is a good chance of easier prey elsewhere. *Microtus* is a common alternative; fluctuations in numbers of *Microtus* may strongly influence the degree of attention paid by generalist predators to woodland rodents, but in heterogeneous habitats *Apodemus* and *Clethrionomys* are usually minor items by comparison (Goszczyński 1977; Erlinge, Göransson, Hansson *et al.* 1983).

The hunting behaviour of a predator is strongly influenced by the chances of encountering suitable prey, and the energy costs of searching and of attack. For example, active searching predators such as weasels, stoats, martens and foxes use up a lot of energy while hunting, and cannot afford to waste any opportunity to secure an easy meal. Their killing behaviour is triggered by the sight of prey—especially if it is moving (Powell 1978; Pounds 1981)—regardless of whether they are hungry or not. If they are

not, the prey is cached. This loose link between the predatory instinct and satiation is sometimes called 'surplus killing', as if it were unnecessary, even reprehensible: but it is better regarded as a useful adaptation, an insurance policy against future bad hunting days. Foxes certainly can remember the location and even the contents of these caches (Macdonald 1977). The habit is strongly developed in the mustelids of boreal and cool-temperate areas, where supplies of prey are unstable and stored meat would remain fresh for long periods (Rubina 1960; Parovshchikov 1963; Pulliainen 1981; Oksanen 1983).

Selection of prey

Studies of the diets of predators that have access to a variety of prey sometimes report that prey species of different sizes or habits are not eaten in the same proportion as they appear in traps (Lockie 1961; Moors 1975; Erlinge 1981). This implies that predators select some particular prey species more often than others, either those that are more likely to be found or caught, or those that are for some reason actively preferred by the predator. Other field studies have reached the opposite conclusion. The relative proportions of *Microtus*, *Clethrionomys* and *Apodemus* in the diet of Swedish weasels reflected their relative abundance in the habitats sampled (Erlinge 1975); and variation in known diet between six resident male weasels at Wytham was clearly explicable in terms of the habitat of their home ranges and the seasons during which they contributed scats to the analysis (King 1980).

However, field studies are not usually competent to detect selection between alternative prey, because there are too many unknown or uncontrolled variables. Enclosure experiments, though artificial to some extent, allow the observer to manipulate the conditions of the interaction more closely. For example, Nams (1981) analysed the prey-selection mechanisms used by the small Canadian ermine (*Mustela erminea*) hunting *Clethrionomys* and *Peromyscus* in a 900 m² outdoor enclosure in boreal forest. The predatory sequence was broken down into five steps, at each of which there is a certain probability for each prey type (species, sex) that the predator will continue to the next step. Selection by the predator can be demonstrated if these probabilities differ between prey types. Nams defined the steps as: (1) encounter (do predator and prey meet?), (2) detection (can the predator identify the prey?), (3) choice (does it attack?), (4) capture (can it make a kill?), (5) consumption (does it eat the kill?).

Nams (1981) concluded that the six ermine he tested tended to eat *Clethrionomys* proportionately more often than *Peromyscus*, mainly because of selection at step (1). *Clethrionomys* were more often encountered, because the ermine searched the micro-habitats they used (e.g. close to fallen logs) more often than those used by *Peromyscus* (see also King 1980). He com-

Table 1. Number of wood mice and bank voles caught by tawny owls and by traps in relation to cover type in Wytham Wood.

	Grid squares dominated by cover type				Total	χ^2	P
	Sparse		Dense				
	A	B	C	D			
Number of squares	27	25	30	38	120		
Number of rodents							
<i>A. sylvaticus</i>							
caught by traps	156	143	158	169	626	} 17.1	< 0.001
owls	30	17	13	8	68		
<i>C. glareolus</i>							
caught by traps	159	282	394	531	1366	} 6.2	> 0.05
owls	9	26	31	26	92		

From Southern & Lowe (1968).

mented that in the wild there is probably no real preference for a particular kind of prey, but that selective hunting in profitable microhabitats could well be real. Pounds (1981) confirmed by radio-tracking that the preferences of wild stoats and weasels for hunting in certain habitats closely reflected the distribution of prey. Southern & Lowe (1968, 1982) used the much more laborious method of mapping the distribution of numbered rodent leg-rings recovered from owl pellets in relation to the distribution of vegetation cover-types in the owl's territories (Table 1). They showed that the owls tended to catch wood mice proportionately more often than did the traps on open ground, and much less often than the traps in the dense cover: they caught bank voles in the same proportions as did the traps in all four cover types. Overall, they caught relatively fewer bank voles and more wood mice, probably because more mice often braved the open ground where the owls could most easily catch them. However, the owls caught both sexes and all size classes of mice and voles in the same proportion as did the traps.

Selection at step (2) (detection) is influenced more by the behaviour of the prey than the predator (see below): selection at steps (3) and (4) (the predator's ability to attack and kill) will depend on the predator's hunting technique, discussed above. Finally, there is selection at step (5), when the predator, having found and caught its prey, has the choice of whether to eat, cache or abandon it. Controlled food preference tests have given, as might be expected, different results. Foxes have a definite three-rank hierarchy of preferences, in the order *Microtus*—woodland rodents—insectivores (Macdonald 1977). Weasels in a 30m² enclosure agreed with the foxes in rejecting shrews, but did not distinguish between *Microtus* and woodland rodents, eating them in the order they were caught (Erlinge 1975). Nam's Canadian ermine were not offered shrews, and disagreed with the weasels in not always eating *Peromyscus* and *Clethrionomys* in the order that they

were caught (they avoided eating female *Peromyscus*). As Nams (1981) pointed out, surplus dead prey will probably be cached whether they are palatable or not, but when the cache is revisited the most palatable ones will be eaten first. Shrews, disliked by most individual carnivores, are often ignored (King 1980; Erlinge 1981) or discarded, or accumulate untouched in the den or cache (Rubina 1960).

Anti-predator defences of prey

Woodland rodents are too small to put up any serious physical defence against a predator once they are found. Their only practicable defences are therefore to avoid detection, and failing that, to minimise the consequences of being detected.

To avoid detection, both mice and voles make full use of the cover provided by their habitat or by darkness. *Clethrionomys* is active by day, but always in or under thick vegetation (Southern & Lowe 1968); *Apodemus* and *Peromyscus* are nocturnal and avoid bright moonlight (Wolton 1983; Clarke 1983). When foraging, rodents may not be able to stay under cover all the time, but resident animals soon learn the distribution of refuges and safe pathways between feeding sites on, above and below the ground. This three-dimensional familiarity with their home ranges is in itself an important means of avoiding attracting the attention of predators. For example, Montgomery (1980) suggests that swift, silent movement along arboreal runways allows rodents (more often *Apodemus* than *Clethrionomys*) to avoid noisy disturbance of leaf litter that would be heard by tawny owls. Conversely, the resident *Peromyscus* observed by Jamison (1975) were more alert than transients, and often detected the arrival of the predator (*M. erminea*) and escaped before it detected them.

Once detected, the commonest fugitive reaction is to bolt for a hole, and this is easiest for resident rodents living on familiar territory, which know the positions of all possible refuges and the routes to reach them from any direction: also, they can often throw off a pursuing weasel by dodging through cover and around obstacles on the way. In enclosure experiments, the rodents with the longest experience of moving about among the refuges provided were the best able to escape from predators (Metzgar 1967; Smirin 1975; Table 2). Wood mice often react to the presence of a predator by climbing, leaping or freezing, and thereby escape more readily than voles from sight-oriented predators such as weasels, stoats (Erlinge, Bergsten *et al.* 1974; Erlinge, Jonsson *et al.* 1974) and owls, especially in poor light (Clarke 1983).

It is curious that *Apodemus*, unlike *Microtus*, does not change its behaviour in response to the pungent scent of the musk of weasels or stoats (Stoddart 1976; Gorman 1984). Individual *Apodemus* have as much to fear from

Table 2. Defensive advantage of residential status for *Peromyscus* hunted by *Mustela erminea* in an enclosure.

Status of <i>Peromyscus</i>	Mean times (in seconds) from 19 trials per class			Mean number of escapes
	Total time to capture	Search time	Chase time	
Male residents	241.0	170.5	176.1	1.09
Male transients	62.5	87.6	8.4	0.18
Female residents	215.7	83.8	218.4	2.27
Female transients	53.0	63.5	14.8	0.27
Male and female residents	228.3	127.2	197.3	1.68
Male and female transients	57.8	75.5	11.6	0.23
<i>P</i>	< 0.05	NS	< 0.05	

From Jamison (1975).

these predators as have *Microtus*, so the reason for their indifference to (or inability to detect) this potentially important cue for escape is unknown. However, once it reaches the security of its underground burrow systems, a wood mouse is relatively safe. The burrows excavated by Jennings (1975) all had a 'ring-road' plan with multiple entrances, which may provide at least a chance of escape from weasels; also they were sometimes blocked with soil and leaves, which would help to keep weasels out. The nest chambers were all under the roots of trees, which would deter digging foxes and badgers. Bank voles also have burrows to shelter in, but in enclosure experiments they tend to be more easily flushed out of them than wood mice; once in the open they can seldom move far before they are caught (Pounds 1981).

The effort of avoiding detection becomes, sooner or later, more costly than the alternative, which is to provide for the consequences of failing to avoid it. *Apodemus* and *Clethrionomys* tend to have a relatively low survival rate matched by the capacity to make a large reproductive effort early in life. In such species, often called opportunists or 'r-strategists', individuals invest in producing their offspring quickly rather than in their own defence and survival (French, Stoddart & Bobek 1975; Fleming 1979). The annual turnover of local populations of woodland rodents is normally high, with density varying from substantial peak to local extinction; predators can take a heavy toll without visible effect, since individuals removed are quickly replaced (Smyth 1968; Sullivan 1977). These demographic defences against predation are extremely successful; small rodents are the universal staple food of northern vertebrate predators and yet remain widespread and abundant.

Effects of woodland rodents on their predators

The distribution, density and population dynamics of predators and their prey are, of course, strongly correlated. Although predators are scarcer than

Table 3. Sizes of home ranges of male *Mustela nivalis* in woodland and in grassland, in relation to the density of rodents available as prey.

	Grassland (young pine plantation)	Mature deciduous woodland (Wytham)
Home ranges of male weasels (ha)	1-5	7-15
Home ranges observed	10	7
Principal prey species	<i>Microtus</i>	<i>Clethrionomys</i> , <i>Apodemus</i>
Density of prey/ha	111-543	21-39
Approx. biomass of rodents per weasel at lowest rodent density	28-139	31-66
at highest rodent density	136-679	57-123

From King (1975).

prey, it is easier to demonstrate the influence of prey on predators than vice versa. This is largely because the supply of food is usually the most important single factor regulating a population of predators, whereas, so far as we know at present, predation is less often such an overriding consideration for a population of prey. For example, *Microtus* provides a more variable, feast-or-famine food resource for predators, compared with woodland rodents; during the feast years, grassland weasels can live well on a much smaller territory than would support a weasel in woodland (Table 3). From such straightforward observations one may conclude that the density of rodents has a strong general influence on territory size (and density) of weasels. However, it is much more difficult to demonstrate the effect of weasel predation on the density of rodents (see below).

A substantial increase in numbers of rodents commonly stimulates both functional and numerical responses in all the local predators, whether rodents are their normal prey or not. But the consequences of this initial reaction vary between predators with different hunting and life-history strategies, as two contrasting examples will show.

Tawny owl

A population of tawny owls living in a deciduous woodland at Wytham, near Oxford, was closely observed from 1947 to 1959. These owls do take some field voles (*Microtus agrestis*), rabbits (*Oryctolagus cuniculus*) and moles (*Talpa europaea*), and this ability to survive on other prey when rodents are scarce makes it possible for individual resident owls to retain their territories for many years (Hirons 1976). However, the decisive control over the owl's breeding success is exerted by the density of woodland rodents, as documented by Southern (1970), Southern & Lowe (1968), and Hirons (1976, 1982). Basically similar, but less detailed, results have been

reported for tawny owls living in a pine forest near Berlin by Wendland (1972). When rodents were exceptionally scarce (10 per 12 acres (2/ha) in May/June) none of the 31 pairs of owls in Wytham even attempted to breed; but as rodent density increased, the proportion of pairs that at least started on the breeding cycle also increased. When the number of rodents reached about 100 per 12 acres (20/ha) in May/June, about two-thirds of the resident owl pairs attempted to breed, and they averaged just under one fledged young per pair (i.e. about 20 a year over the whole study area). However much the density of rodents increased beyond that level, the proportion of pairs breeding and the mean number of young fledged per pair reached no higher (Table 4).

Key factor analysis of Southern's data (re-analysed by Smith 1973) showed that the most important source of loss of potential productivity was the failure of some pairs (ranging from 30 per cent to 100 per cent each year) to attempt to breed; the second, varying inversely with the first, was post-fledging, or over-winter loss of young birds; the third was that a high proportion of eggs (33–77 per cent each year) failed to hatch. The first and third of these factors were re-examined by Hirons (1976, 1982) in the same study area in 1971–74. He showed that food supply (i.e. rodent density) was the key to both. The nutritional condition (fat deposits and body weight) of the owls in early spring determined the maturity of the gonads; undernourished owls were not capable of breeding. During incubation, sitting females that could not obtain enough food from their mates or from fat reserves had to leave the eggs in danger of chilling in order to hunt for themselves. However, the proportion of owlets hatching that successfully fledged was similar in good and bad years, because by the end of incubation the parent birds could supply the chick's needs from alternative prey, which are more readily available later in the season (Hirons 1976). The effects of rodent density on breeding success are therefore implemented before or around the time of laying.

Fluctuations in the density of rodents were therefore very largely responsible for determining the variable reproductive output of the Wytham owls. Other considerations, e.g. the local knowledge and hunting skill of individual owls, the combination of cover types on their territories, and wet weather during incubation, contributed to the variation in breeding success but were secondary to rodent density. But rodent density had no short-term influence on the density of the owl population. This is because the second of the three key factors controlling the owls (post-fledging mortality) was strongly density-dependent. Surplus juveniles produced in good years emigrated or died—which, as the Wytham data show, usually amounts to the same thing. The resident adults are long-lived, and most keep their territories for six to 10 years, breeding only in the good seasons. Despite wide fluctuations in the density of rodents at Wytham the equilibrium number of

Table 4. The breeding success of tawny owls in Wytham in relation to the density of woodland rodents.

	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959
Rodents/12 acres in May/June	—	—	42	77	61	152	56	74	25	69	362	10	276
Owl pairs resident	17	20	20	20	21	24	24	26	30	32	32	31	32
attempting to breed*	(11)	(13)	(18)	17	12	17	15	18	4	21	20	0	22
Young fledged	20	20	26	25	6	21	20	17	4	24	20	0	28
Mean young per pair	1.2	1.0	1.34	1.2	0.3	0.9	0.8	0.7	0.1	0.8	0.6	0	0.9

Abbreviated from Southern (1970).

* Figures prior to 1950, when nest boxes began to be used extensively, are suspect

owls holding territories has remained remarkably constant since the middle 1950s (Table 4 and Hirons 1976).

Weasel and stoat

The weasel and the stoat are unlike the tawny owl in being less strongly territorial, less restricted to woodland, and short-lived. Like the owl, both can take a variety of prey, but always concentrate on rodents when they are available, and the breeding success of a population of either species is closely correlated with rodent density. Various studies have demonstrated a predictable link between the density fluctuations of stoats and weasels and those of the locally dominant small rodents, usually *Microtus* and/or *Arvicola* (e.g. Tapper 1979; Debrot 1983; Delattre 1983; Erlinge 1983; King 1983a and references therein). Erlinge (1981, 1983) caught on average more juvenile female stoats per breeding female in grassland areas where preferred prey (water voles, *Arvicola terrestris*) were common, although the difference was not statistically significant, because there was great local and individual variation in breeding success even in the 'best' habitat.

Because woodland is a minority habitat in most countries where weasels and stoats have been studied in the northern hemisphere, it is difficult to find an extensive wooded study area where these wide-ranging small mustelids can be observed in sufficient numbers and their interactions with woodland rodents examined free of influence by the outside (non-woodland) world. In Wytham, studies of weasels by King (1975, 1980) and G. F. Hayward (unpublished) were done by live trapping on small areas and over short time periods, and both authors could expound at length on the problems of analysing the small samples of data that resulted. Neither obtained any detailed field observations on the factors determining the breeding success of Wytham weasels. In the South Island of New Zealand, however, extensive forests of southern beech (*Nothofagus*) still remain relatively untouched by man, and in them stoats, feral house mice (*Mus musculus*, which, broadly speaking, occupies the niche of *Apodemus*) and ship rats (*Rattus rattus*), all introduced, are common. Their interactions are clearer than in most habitats, because of the relatively simple composition of *Nothofagus* forest and the scarcity, both of other mammalian predators or prey, and of native raptors (King 1981, 1983b; King & McMillan 1982). In such favourable circumstances it is possible to examine a particularly simple woodland rodent-predator relationship on the scale required for mammals and now no longer possible in Britain or most of Europe.

In three forests in the South Island, studied in 1972-81, the breeding success of the female stoats (number of independent young produced) was closely correlated with the density of mice in spring (Table 5), just as it is in tawny owls, but by an entirely different mechanism. Female stoats have no

Table 5. The breeding success of stoats in the Eglinton Valley, Fiordland, in relation to the density of forest rodents.

	Antipodean summer seasons					
	1973-4	1974-5	1975-6	1976-7	1977-8	1979-80
Density index of mice						
November (spring)	4.3	4.3	3.8	20.9	6.8	12.8
February (summer)	0.5	4.3	6.7	24.0	3.9	3.9 ⁽³⁾
Density index of stoats						
spring	—	0.24	0.15	0	0.64	—
summer	—	1.46	0.70	5.43	1.42	5.49
Fecundity of stoats (mean corpora lutea per female) ⁽¹⁾	9.6	10.2	9.7	9.7	10.2	—
Number of females	16	16	24	7	35	—
Density index for independent young stoats in summer ⁽²⁾	—	1.26	0.60	4.89	0.43	4.82

From King (1981, 1983b). Compare with Table 4.

(1) Kruskal-Wallis analysis of variance $H = 2.86$ (incl. 1972-3), NS.

(2) Relationship between density indices of young stoats in summer and of mice in the preceding spring $r_s = 0.72$, $P < 0.05$ (Eglinton plus adjacent Hollyford Valleys pooled).

(3) This peak population was cut short early, see Fig. 1.

opportunity to adjust their initial reproductive effort to the chances of success, since prolonged and obligatory delayed implantation separates ovulation from parturition by 9-10 months. The mean ovulation rate does increase in good rodent years, but this is probably a simple physiological response to good nutritive condition, and the chances are strong that most of the extra ova will be 'wasted', in the sense that they will not directly lead to any increase in number of young produced next year. However, a female stoat invests far less energy in one ovum than a female tawny owl does in one egg, so the enforced commitment a year in advance, and a modest physiological extravagance, are not serious disadvantages. The important processes of adjusting litter size to food supplies begin just before implantation in late winter (August). They operate by reducing, to various degrees, the proportion of the already fixed number of potential young to pass through the later stages of the breeding cycle, although the relative importance of failures at the blastocyst, embryo and nestling stages is unknown. Rodent density is the principal arbitrator at all stages, but it has been proved only at the beginning and at the end (King 1981, 1983a, b).

Comparisons

In both owls and stoats, many females respond to exceptionally low rodent density by failing to breed at all; in both, high rodent density is the signal for maximum reproductive effort (Table 6). Both responses lead by different pathways to the same result—the saving of resources in bad years and the

Table 6. Effect of fluctuations in woodland rodents on breeding success and density of two types of predator

	Tawny owl	Stoat
Type of predator	"K-strategist"	"r-strategist"
Response to abundant prey	Maximum fecundity	Normal fecundity, maximum productivity
Response to scarcity of prey	Zero fecundity	Normal fecundity, zero productivity
Mortality of independent young related mainly to	Density of adults	Density of prey
Effect of good season on predator density	Little or none	Strong but temporary

largest possible number of independent young in good years. In both, the mortality of these newly independent young is very high, but is controlled by different factors. The sum total of all these reactions may have a strong temporary effect on the density of a local population of stoats, which are typical 'r-strategists' (King 1983a) whose characters include the capacity for large reproductive effort, short lives and unstable populations; whereas they have very little effect on the density of a resident population of tawny owls, which are typical 'K-strategists' with the opposite characters.

Effects of predation on woodland rodents

Populations of rodents are affected by many different external and internal factors, some of which are much easier to measure, e.g. food supplies or incidence of wounds (taken as a measure of aggressive behaviour), than is predation. To make a reasonable estimate of predation pressure on rodents requires exhausting fieldwork on two populations or communities—the predator and the prey—an immediate doubling of the workload which, except in the simplest ecosystems, can be avoided only by extrapolation from the literature, often with misleading results (e.g. Golley 1960) data-sharing between independent studies in the same area (e.g. King 1980) or team work (e.g. Erlinge, Göransson, Hansson *et al.* 1983; Erlinge, Göransson, Högstedt *et al.* 1984; Ryszkowski, Goszczyński & Truszkowski 1973).

One of the main external factors controlling populations of woodland rodents is the seeding pattern of the trees under which they live, especially in forests where masting tree species are dominant (Jensen 1982). Heavy seed-falls in autumn are followed by improved juvenile survival, over-winter breeding and a large increase in rodent density by the following summer, accompanied by predictable changes in age structure and an early termination of breeding and/or recruitment of young mice into the resident population (Jensen 1982; King 1982; Flowerdew 1985; Alibhai & Gipps 1985). Woodland predators could, in the right circumstances, diminish and/or

abbreviate these post-seedfall peak populations; but some pattern of increase, crash and subsequent period of low density is inevitable from the reactions of the rodents to the seed fall, whether predators are present or not, and the interval between the increase phases is controlled entirely by the trees. By contrast, the interaction between predators and rodents in non-forest habitats may amplify, extend, or eliminate the population cycles of *Microtus*, according to the species composition of the predator community, the supply of alternative prey, and the heterogeneity of the environment (Erlinge, Göransson, Hansson *et al.* 1983).

The total impact of predation on a population of rodents is the sum of all the functional and numerical responses of all the predator species present. These responses vary in intensity with season and year, and, where alternative prey are scarce, they commonly lag behind changes in the population density of the rodents. The combined total effect is to increase the number of rodents killed; but the result for the rodent population depends on whether the increase in predation is proportionate to the increase in rodents, and at what season this increase in predation is applied. The problems of estimating so many variables at once are huge, as the following examples show.

The impact of resident specialist predators in continuous woodland

In Wytham woods, Southern & Lowe (1982) and King (1980) attempted to estimate the effects of predation by tawny owls and weasels on a mixed population of wood mice and bank voles. Other predators were not considered, because they were shot on sight (fox), naturally scarce (stoat and diurnal raptors), or did not eat rodents (badger, *Meles meles*: Kruuk 1978), so the combined efforts of the owls and weasels should account for most losses of rodents to predators. In both studies, usable data for predator and prey together were obtained over relatively short (1.75 and 1.2 years) periods which did not coincide (owls 1954–56, weasels 1968–69), and led to results that are 'approximate and full of assumptions' (Southern & Lowe 1982: 99), but, for the present purposes, no better ones are available.

Southern & Lowe (1982) estimated the density of wood mice and bank voles every two months from October 1954 to June 1956, by capture-mark-recapture on an area of 48.6 ha, which included all or part of 11 owl territories. The analysis concentrated on bank voles in two territories, which totalled 20 ha. They searched a total area of 81 ha for owl pellets, of which they found 649 on the two territories (23 per cent of the total expected from the four adult birds). By comparing the proportion of marked to unmarked bank voles in the traps and in the pellets, they calculated that 20–30 per cent of the standing crop of bank voles per two months was taken by the owls (Table 7). This, as Southern & Lowe (1982) remark, is no small drain on the

Table 7. Estimated impact of tawny owls and weasels on the standing crop of bank voles in Wytham.

Month	Tawny owls		Month	Weasels	
	Est. total voles ⁽¹⁾	% killed per 2 months		Est. total voles ⁽²⁾	% killed per month
1954 Oct.	983	15	1968 Sept.	536	4
Dec.	2630	17	Oct.	429	2
1955 Feb.	—	—	Nov.	375	10
Apr.	121	34	Dec.	402	20
June	201	24	1969 Jan.	590	13
Aug.	244	15	Feb.	563	9
Oct.	232	18	Mar.	563	3
Dec.	783	21	Apr.	563	2
1956 Feb.	538	19	May	670	3
Apr.	391	33	June	536	3
			July	750	—
			Aug.	804	5
			Sept.	616	7
			Oct.	482	20

From Southern & Lowe (1982); King (1980).

(1) On 49 ha in Great Wood

(2) On 27 ha in Marley Wood (c. 2 km from Great Wood)

population. Wood mice were scarcer and less amenable to calculation than bank voles, and the data on them could be used only for subsidiary comparison; but they suggested an even greater impact by owls on wood mice—either because the owls prefer wood mice, or wood mice are relatively more vulnerable because of their preference for more open habitats, or both.

King (1975, 1980) live-trapped weasels in another part of Wytham Woods (27 ha) from March 1968 to June 1970, and found that, for most of that time, one to four male and one to three female weasels were resident, occupying home ranges of roughly 7–15 ha and 1–4 ha respectively. Data on the density of bank voles and wood mice on a 1.5 ha triangular trapping grid at one end of the weasel study area were kindly supplied by Flowerdew (1971, 1972) for the period September 1968 to December 1969 inclusive. A total of 344 samples of weasel scats were collected (which were estimated to represent 11 per cent of the total number of meals taken by the resident weasels during the study period); 89 bank voles and 34 wood mice were found in them. The total number of rodents living in the whole wood, and the total number killed per month by the weasels (assuming two rodents a day killed by male weasels and one a day by females, constant at all observed rodent densities), were estimated by extrapolation from the figures provided by Flowerdew and the scat analyses. This somewhat crude method yielded comparable removal rates for both rodent species, averaging 8–10 per cent per month (range 1–20 per cent) varying with season according to

the number of resident weasels, although, as before, the best data were for bank voles (Table 7).

For various reasons (listed in King 1980) these figures were considered to over-estimate the proportion of voles killed by weasels, and yet in most sample periods weasels accounted for only a small proportion of the total number of bank voles that Flowerdew (1971, 1972) calculated to have disappeared (12–55 per cent). There is plenty of room, therefore, to add in the large number of voles removed by the tawny owls. The relative importance of predation by the owls, as calculated from Wooster's (1938) formula, was greater than that of the weasels, and the owls probably accounted for a higher tally of rodents per year than did the weasels. Hence the conclusion by Southern & Lowe (1982) that . . . 'it certainly looks as if tawny owls and weasels between them are, at times, formidable predators on the bank vole'. It would be interesting to know how the combined impact of weasels and owls would vary through a substantial fluctuation in numbers of rodents; but the studies by Southern & Lowe (1982) and King (1980) were too short and too hampered by assumptions (e.g. that the daily food requirements of the predators were constant across the modest range of prey densities each observed) to produce a decisive answer to this question. However, at very high densities the rodents were probably able to 'escape' from control by the owls (Table 4), whereas at very low density the owls had no choice but to continue hunting (unlike the weasels, which disappeared—G. F. Hayward unpubl.). Hence, Southern & Lowe (1982: 99) suggested that the total effect of predation on the voles was inversely density-dependent, and 'could help to produce the kind of fluctuations [of rodents] recorded'. The difficulties and frustrations of predator-prey studies are well illustrated by the fact that, despite the massive amount of ecological field work done in Wytham since 1947, no stronger statement than this can be made.

Less laborious field methods can be carried on for longer, and, in forests dominated by masting species of trees, will eventually span the enormous rise and fall of a post-seedfall irruption of forest rodents. For example, in two *Nothofagus* forests in Fiordland National Park, New Zealand, King (1983b) made two replicate sets of observations of two successive post-seedfall peaks of feral *Mus musculus*, in 1976–77 and 1979–80 (Fig. 1), confirmed by less complete observations in other forests (King 1981). Most seed fell in autumn (March–June) and the density indices of mice began to increase in late winter and early spring (August–November): but because the timing of the breeding cycle of stoats is invariable and fixed by daylength, no numerical response by the predators was possible until mid-summer (December). (An immediate functional response was probable but unimportant, because only small numbers of adult stoats were present between August and December.) Then an extra-large cohort of young stoats appeared, of roughly the same size (five to six stoats per 100 trap-nights, i.e.

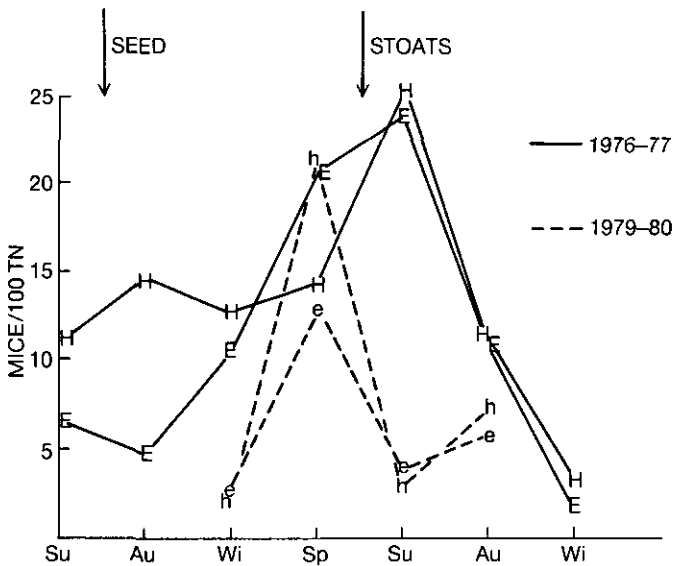


Fig. 1. Density indices for mice (*Mus musculus*) (captures per 100 trap-nights in 36-station index lines, 50 m spacing) through two beechmast years in the Eglinton (E,e) and Hollyford (H,h) Valleys, southern New Zealand (see also Table 5). The beech mast falls in late summer and autumn (arrow marked 'seed') and lies on the ground over winter. The annual crop of young stoats, which after a seedfall may be very large, appears abruptly in the forest in early summer (late November to January: arrow marked 'stoats'). In 1976-77 all stoats were removed at first capture; in 1979-80 they were live-trapped and released. In 1979-80 the seedfall was larger (and the winter index of mice probably underestimated) and the peak cohort of young stoats as large as in 1976-77; but the expected peak of mice was cut short in both valleys, presumably by predation. (After King 1983b.)

two to five times greater than in normal summers) in both areas and both years, although in the first summer their density index was calculated by monthly Fenn (breakback) trapping and in the second by intensive live-trapping.

The effect on the mice of this large influx of new predators was not estimated directly; but the density index for mice reached much higher levels (to 24 mice/100 trap-nights) in 1976-77, when stoats were being constantly removed every month, than in 1979-80, when captured stoats were released alive. The 1976-77 mouse index also remained high for some three months longer. In both years the same result appeared in both forests. King suggested that these observations amounted to strong circumstantial evidence that the immediate and large numerical response of stoats, plus a lesser functional response, applied together *at the time* the mice were numerous and already reducing the number of recruits added to their population

(King, 1982) could have had a considerable effect in dampening the population fluctuations of the mice.

The impact of a broad range of predators in heterogenous habitats

In the extensive agricultural lands of central and northern Europe, only isolated patches of forest cover remain, surrounded by a sea of non-forest habitats occupied by *Microtus*, *Arvicola* and rabbits, and a range of both specialist and generalist predators. At least two major research programmes have attempted to estimate the impact of predation on the population dynamics of field rodents; these have involved teams of workers covering large areas—including, incidentally, the forest patches. In Poland, the total area was 32 km², of which 12 per cent was wooded (Ryszkowski *et al.* 1973; Goszczyński 1977); in southern Sweden, it was 40 km², which was 'interspersed with copses of deciduous trees and pine plantations' (Erlinge, Göransson, Hansson *et al.* 1983; Erlinge, Göransson, Högstedt *et al.* 1984). Ten species of raptors and carnivores were observed for four years (1975–78) by the Polish team, and nine for four years (1975–78) by the Swedish team. Woodland rodents composed only a minor portion of the diets of these predators; nevertheless, they could at times be subjected to an intense predation pressure.

In Poland, *Microtus arvalis* was abundant in the summer of 1971 (Fig. 2) and predators accounted for only 33 per cent of the total mortality of forest rodents, and 20 per cent of that of *Microtus*; but as the *Microtus* declined, the impact of predators on both field and woodland rodents increased. By the winter of 1972/73, when the density of *Microtus* was down to under 10/ha, the predators were accounting for 95 per cent of the mortality of forest rodents and 89 per cent of *Microtus*; six months further into the low phase, these figures were 97 per cent and 100 per cent. The pooled density of forest rodents was high (43/ha) in the autumn of 1971, when all the predators were feasting on *Microtus*, including tawny owls and martens which normally caught mainly forest rodents. By the following year the situation was reversed, and the predators which normally took mostly *Microtus* (e.g. foxes, buzzards (*Buteo* sp.) and cats) joined the tawny owls and martens in hunting for woodland rodents, whose density in autumn 1973 was only 11/ha. The capacity of the combined force of predators to switch to woodland rodents when *Microtus* was scarce meant that the intensity of predation on wood mice and bank voles living in that area was variable and determined more by the population phase of the *Microtus* cycle than by the density of predators.

The Swedish team did not study a woodland area as such, but a 40 km² area of heterogenous grassland including 800 ha of old fields (half each on peat and mineral soils) and 2900 ha of grazed fields. The density, pregnancy

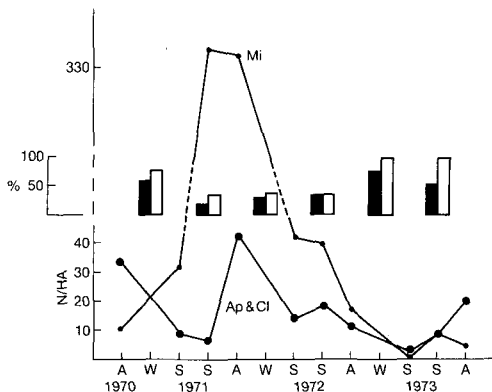


Fig. 2. Relationship between the density fluctuations of *Microtus* (small symbol, Mi), and of woodland rodents (large symbol: Cl, *C. glareolus*, Ap, *A. flavicollis* and *A. agrarius*) in forest and shelterbelts scattered through the rural landscape near Turew, Poland. Histograms show the proportion of the forest rodent population killed (black) and the proportion of their total mortality due to predation (white). (After Goszczyński 1977).

rate and litter size of *Apodemus sylvaticus* in these three habitat types was estimated by removal trapping in early June, early August and mid-September of 1974–77 inclusive. The number of *Apodemus* eaten by the combined force of predators was estimated throughout the year in 1975 and 1976. Presenting these figures as averages, the predation rate was calculated to be almost 30 per cent of the standing crop in June, when the mouse population was low, dropping to 10–15 per cent in August and September, when the mouse population was rising (Fig. 3). Like the Wytham studies, these results are full of assumptions. For example, the density of mice was not measured during the non-breeding season (October to April), but it was assumed to decrease steadily. The proportionate consumption by predators during this part of the year, estimated by calculating the known number of mice eaten as a proportion of the extrapolated number present, fell within the range of measured figures for the summer months. The total annual production of *Apodemus* on the study area was estimated to be about 20,000 individuals; predators removed 25,679 mice in 1975 and 17,413 in 1976. This effect was independent of the large *Microtus* population living in the same fields, which did not display the classic three- to four-year cycle

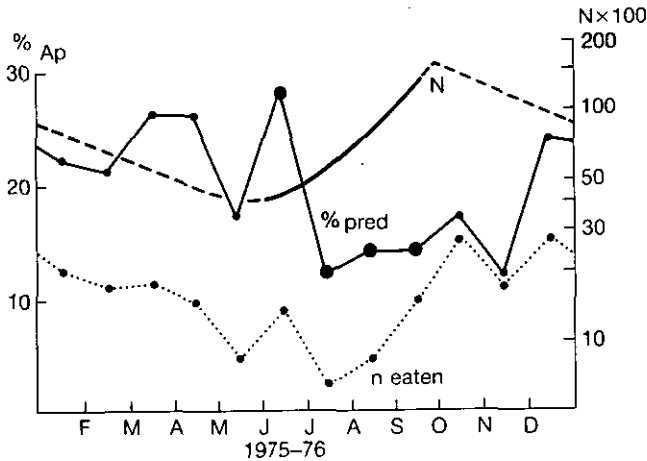


Fig. 3. Estimated number of *Apodemus sylvaticus* eaten by the total force of predators living in open country in southern Sweden (dotted line). The density of *Apodemus* available was estimated by trapping three times a year between June and September (solid black line); during the rest of the year, mostly the non-breeding season, the density was assumed to decrease steadily (dashed line). The predation rate (thin solid line) was calculated by expressing the number of mice eaten as a percentage of the estimated (large symbols) or assumed (small symbols) population available. (After Erlinge, Göransson, Hansson *et al.* 1983).

observed in Poland, because, Erlinge, Göransson, Hansson *et al.* (1983) suggest, it is suppressed by predation.

Comparisons

The results of the studies outlined in this section are contrasted in Table 8. Estimates of the total impact of predation calculated, to various degrees of accuracy, in four areas, show that there is no simple, general answer to the question: what is the impact of predation on forest rodents? In two areas the effect appeared to be a dampening of the rodent population fluctuations, but by completely different means. In Sweden, a large diverse and stable community of generalist predators living in a heterogenous habitat, mainly on rabbits, may have removed the entire annual production of *Apodemus* by a rapid *functional* response; whereas in Fiordland, a virtually single-species population of specialist predators living in continuous forest with limited alternative prey was apparently able to curtail a post-seedfall peak population of feral *Mus* by a rapid *numerical* response, assisted by changes in the dynamics of recruitment among the mice. In the other two areas, both relatively small patches of woodland surrounded by farmland, the effect appeared to be an enhancement of the rodent population fluctuations, in both cases largely due to considerable variation between years in the intensity

Table 8. Estimates of the impact of predation on woodland rodents in four study areas.

	Wytham Wood, England	Turew, Poland	Revinge, Sweden	Fiordland, New Zealand
Area	525 ha	32 km ²	40 km ²	35 and 40 km transects
Years studied	1954-1956, 1968-70	1970-73	1975-78	1972-81
Principal woodland predators	Tawny owl Weasel	Tawny owl Marten Fox	Tawny owl Fox Cat	Stoat
Other predators present	Few	Many	Many	Very few
Woodland prey (small rodents only)	<i>C. glareolus</i> <i>A. sylvaticus</i>	<i>C. glareolus</i> <i>A. flavicollis</i> <i>A. agrarius</i>	<i>C. glareolus</i> <i>A. sylvaticus</i> <i>A. flavicollis</i>	<i>Mus musculus</i> <i>Rattus rattus</i>
Alternative prey	Scarce	Present	Abundant	Scarce
Effect of predation on variations in prey density	?Increase	Increase	Dampen	?Dampen
Sources	Southern & Lowe (1982) King (1980)	Goszczyński (1977) Ryszkowski <i>et al.</i> (1973)	Erlinge, Göransson, Hansson <i>et al.</i> (1983) Erlinge, Göransson, Högstedt <i>et al.</i> (1984)	King (1981, 1983b) King & McMillan (1982)

of predation, but again, for different reasons: in Wytham, the rate of predation on bank voles inside the wood was to some extent inversely density-dependent, and in Poland, it depended more on the population dynamics of *Microtus* outside the woodland than on either the predators or their prey inside it.

The four studies can also be contrasted in another way, which has the particularly interesting effect of rearranging the above partnerships. Two of them concluded that the impact of predation must be substantial, since it probably accounted for the total production (Sweden) or the total disappearance (Wytham) of the rodent populations. The other two documented a reduction in rodent density, apparently due to predation and achieved by a *strong functional (Poland) or numerical (Fiordland) response set off by factors external to the woodland prey and predators themselves.*

However, none of the four studies cited has presented a really conclusive case. The Swedish and Wytham data are not proof of control of rodents by their predators, since there is no information on what the density or the productivity of the rodents would be in the absence of predators; the Fiordland and Polish data are not proof of control, as neither could eliminate other possible explanations of the reduced density observed. The case for or against predation as a factor controlling the populations of woodland rodents is therefore still open. Further progress depends largely on improvements in the accuracy of future estimates of predation rate. None of the studies reviewed here was free of debatable assumptions; none could *prove* that the observed effects on the rodents were due to predation and not to changes intrinsic to the rodents themselves; and none was able accurately to estimate whether the observed changes in consumption rate by predators were more or less proportionate to changes in rodent density, measured over a sufficient span of years and densities. This information is the key to any argument concerning control of rodent populations by predators, and it is usually not available, because proof of it in the field is extremely hard to come by.

The future

One of the useful functions of a review is to provide some signposts for future research. The most obvious ones suggest themselves from the above discussion, and they are largely technical. Theoreticians and field observers have always been able to ask plenty of searching questions: the difficulty is to find the means of obtaining the critical data to answer them.

(1) The problems of estimating the mean and range of variations in numbers of prey available to predators, both absolutely and also in the same terms as each of the predator species perceives them (which will be different

for predators of different hunting strategies) continue to undermine the credibility of even the best-organised studies. Important questions are: how to allow for errors arising from the unequal responses of both predators and rodents to all census techniques; the unequal certainty of detection of remains of prey of different ages and species; 'surplus killing' (rodents removed from the population but not appearing in the predator's diet); the continual additions to and subtractions from the standing crop due to recruitment, dispersal and mortality of rodents other than that due to predators; and the possible intercompensations between these variables and predation pressure. (Incidentally, Pearson (1985) also concludes that progress in understanding predator-prey relationships in *Microtus* is slow because adequate methodology is lacking.)

In general there should be more emphasis on rigorously controlled field experiments or carefully planned observations in manageable but realistic situations. An obvious approach would be to compare the population dynamics of rodents on predator-free islands and on the adjacent mainland. This has been done, but not with specific reference to the effects of predation (e.g. Sullivan, 1977; Adler & Tamarin, 1984).

(2) In contrast to even 10 years ago, it is much more widely accepted nowadays that the interactions between predators and prey are profoundly important for *both* parties—predators are no longer believed merely to mop up the 'doomed surplus' in the Erringtonian sense, although there are no doubt still situations where they do do that. But, although it is easy to demonstrate functional and numerical responses in predators, or even to calculate that the impact of predation must be heavy, these data are not proof of control. Advances in techniques that would permit closer, assumption-free examinations of the difference between situations where some degree of control of woodland rodent populations is apparently possible (e.g. in Revinge and Fiordland, although for opposite reasons) and those where it seems less likely (e.g. Wytham, Turew) might help to remove some of the nagging doubts concerning methodology that still somewhat devalue all existing predator-rodent information. Still, what we have provides plenty of food for thought, and hypotheses to test. Closer co-operation between developing ecological theory, well-designed field experiments, advances in technique and well-organised team field work (of the kind pioneered by Erlinge and his co-workers) could lead to exciting advances in the near future.

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