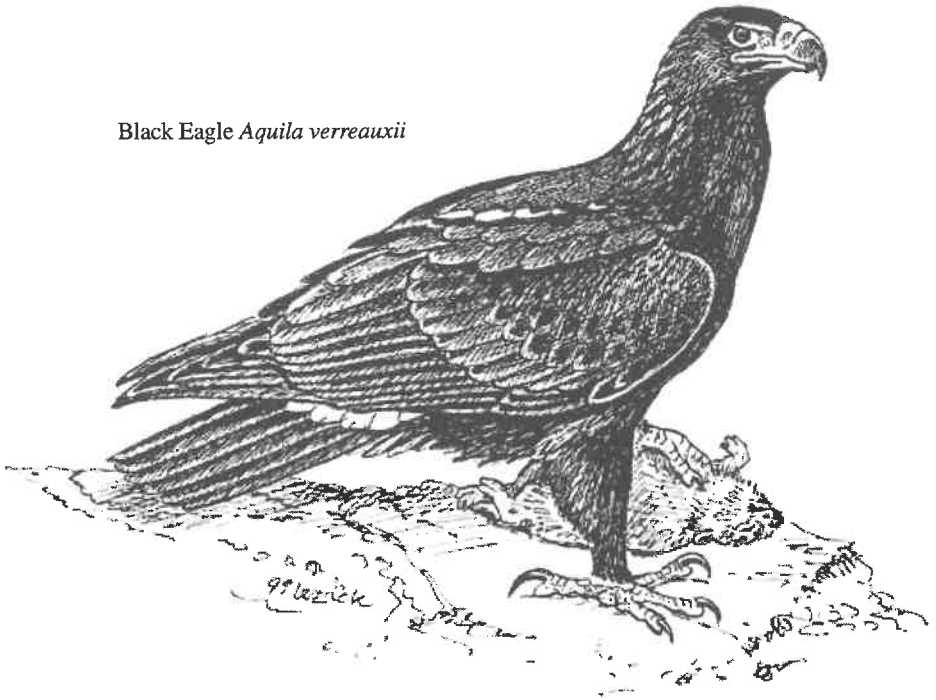


Part 7

Predation and Feeding Ecology

Black Eagle *Aquila verreauxii*



Conveners:

Ian Newton & Rob A. G. Davies

Effects of Predators on their Prey: some generalisations

I. Newton

ABSTRACT

1. To reduce the breeding numbers of a prey species, mortality from predation must be additive to other mortality, and not merely 'compensatory', replacing other forms of death, such as starvation.
2. In any study of predation it is helpful to distinguish effects on prey breeding numbers from effects on prey post-breeding numbers. It is on breeding numbers that the immediate future of the prey population depends, but post-breeding numbers may be important to game hunters.
3. Predation might eliminate some prey species from particular areas, or it might lower prey breeding density below the level that would occur in the absence of predation, cause marked fluctuations in prey breeding density, or have no obvious effects on prey breeding density.
4. From studies in Britain, the Sparrowhawk has been found to have no obvious effects on the breeding densities of some common woodland prey species.

INTRODUCTION

Because many raptors eat other birds and mammals, their predation often causes conflicts between people interested in the raptors and those interested in the prey species. Yet there have been relatively few studies of the impacts of raptor predation on prey populations (for examples, see Kenward 1977, Kenward *et al.* 1981, 1991, Perrins & Geer 1980, Newton *et al.* 1997). In this paper, I make some general points about predation and summarise some empirical evidence for the effects of predators on bird populations. Not all examples concern raptors and emphasis is placed on those aspects not covered by other papers in this session, notably those of Thirgood & Redpath (this volume) and Davies (this volume).

SOME GENERAL POINTS

1. Additive and compensatory mortality.

Practically all animals are subject to predation at some stage of their lives, whether juvenile or adult. Many bird species, for example, suffer heavy predation at the egg and chick stages, and some

also at the fledgling and adult stages. In some bird species, predation is the major cause of loss at all stages of the life cycle, accounting for almost every nest that fails and almost every adult that dies. Yet, despite the prevalence of predation, it is not easy to assess its effects on prey population sizes. The numbers of many bird and mammal species can more than double each year through breeding so that, if they are to remain stable from year to year, more than half the individuals present at the end of one breeding season must die before the next, if not from predation then from something else. For predators to reduce a breeding population below the level that the habitat would otherwise support, at least part of the mortality they inflict must be 'additive' to other mortality, and not simply 'compensatory', replacing other forms of death. Whether losses from predation are subsequently offset by improved reproduction or by improved survival (or both) among remaining individuals, depends on whether these aspects vary in a density-dependent manner, increasing with reduction in density.

2. Predation and the annual cycle.

The numbers of individuals in any population that is exposed to predation must be reduced, at least temporarily, because some individuals die earlier than they would in the absence of predation. Inevitably, then, predators influence the dynamics of prey populations, and could reduce their average level over the year as a whole. But the important question is whether the predation to which many species are subject throughout the year reduces their overall breeding numbers. In any seasonally-breeding species, like almost all birds and mammals, the start of breeding is when numbers are at their lowest in the year, after most mortality on adults has occurred but before reproduction begins. If predation does not reduce breeding numbers, it has no effect on numbers entering the next generation and is not limiting in the long-term. It is thus irrelevant to the long-term persistence of the population at that level.

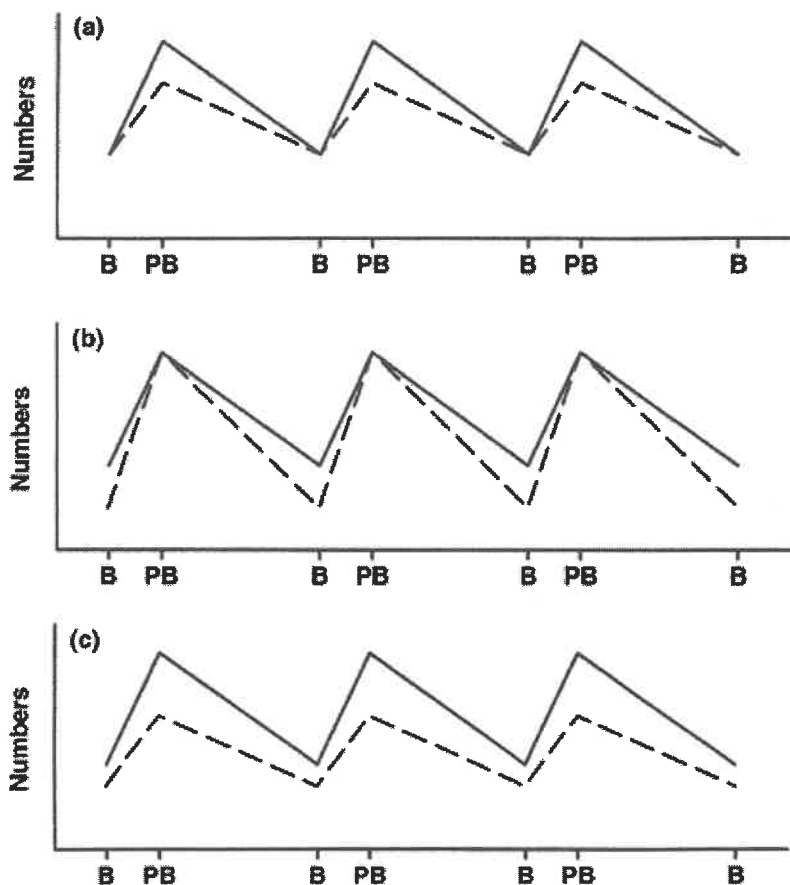
Game managers have a different perspective because they are interested in producing birds and mammals for human hunters to kill. They are thus concerned, not only with maintaining breeding stocks from year to year, but also with producing as large a post-breeding population as possible. Any predation or other mortality which lowers the production of young might reduce the numbers of game birds and mammals available for hunters, even though it may have no effect on breeding numbers. It is not contradictory, therefore, that predation might reduce the size of the post-breeding population peak each year, but have no impact on the pre-breeding low.

In assessing impacts of predation, much hinges on the fact that the annual cycle of most birds and mammals falls into two distinct phases, a breeding season when numbers increase because reproduction exceeds mortality, and a non-breeding season when numbers decline because only mortality operates.

In general, we can envisage three scenarios involving predation effects in the annual cycle of any bird or mammal species (Figure 1).

- (1) Predation reduces the post-breeding numbers below what would otherwise occur, but not the breeding numbers. This scenario requires total compensation in over-winter survival.
- (2) Predation reduces the breeding but not the post-breeding numbers below what would otherwise occur. This scenario requires total compensation in reproductive output.
- (3) Predation reduces both breeding and post-breeding numbers below what would otherwise occur. In this scenario, compensation is insufficient to offset the full effects of predation.

Figure 1. Models showing possible effects of predation on the annual cycle of numbers in seasonal-breeding prey species. Solid line - no predation effects, dashed line - with predation effects. For further details, see text. From Newton 1998.



Successive annual cycles in bird numbers (B-breeding, PB-post-breeding)

MAIN IMPACTS OF PREDATORS ON PREY

The following are the major types of impact that predators have been found to have on their prey (see also Kenward 1986, Newton 1993, 1998):

1. Annihilation of prey.

The only documented examples known to me concern generalist predators, such as rats and cats, introduced by human action to offshore islands (Newton 1993, 1998). Because of their isolation, the avifaunas of oceanic islands have mostly evolved in the absence of mammalian predation. Many island bird species are tame, show no escape response to predators, and may nest in unprotected sites; some species are also flightless. For these reasons, some endemic island bird-species have proved highly vulnerable to introduced predators because they had no natural defences. Such predators are held responsible for at least 40% of the extinctions of endemic island birds known to have occurred in the past 400 years (King 1985). Clearly, this special situation is of limited relevance in the context of continental areas where most predator and prey species have persisted together for thousands or millions of years.

2. Lowering of prey breeding numbers.

The ability of predators to hold prey breeding density well below the level that could occur in the absence of predation is exemplified by research on the Grey Partridge *Perdix perdix* and Red Grouse *Lagopus l. scoticus* in Britain (Potts *et al.* 1980, Potts 1986, Thirgood & Redpath, this volume), and also by predator removal studies on a range of other gallinaceous birds and waterfowl (discussed in Newton 1993, 1994, 1998). Such limitation usually involves density-dependent predation on either eggs, chicks or adults, that regulates breeding numbers at a level lower than the habitat and food-supply would otherwise permit.

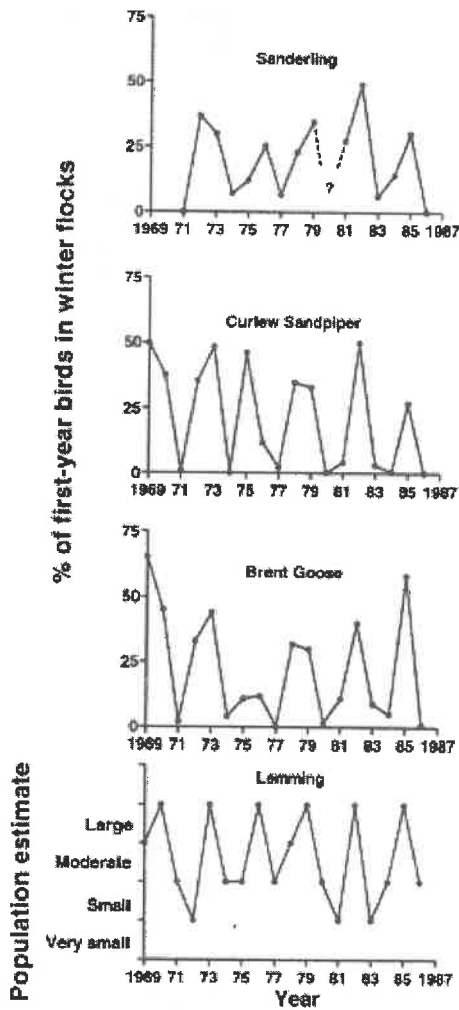
3. Oscillations in prey numbers.

Many grouse species, especially in northern latitudes, undergo cycles of abundance in which successive peaks and troughs in numbers occur at fairly regular intervals (Elton 1942, Lack 1954, Keith 1963, Keith *et al.* 1977). In boreal North America, for example, Ruffed Grouse *Bonasa umbellus* and others fluctuate in approximate ten-year cycles, in parallel with similar cycles in Snowshoe Hare *Lepus americanus* numbers. In much of boreal Europe, Hazel Grouse *Bonasa bonasia* and others fluctuate in 3-5-year cycles, in parallel with the numbers of voles. Moreover, some species, such as Willow Ptarmigan *Lagopus lagopus*, may follow a 3-5 year cycle in parts of Europe and a ten-year cycle in parts of North America (Watson & Moss 1979, Bergerud *et al.* 1985).

Predation is one of several hypotheses proposed to explain cycles in grouse numbers (Watson & Moss 1979), with predators causing regular crashes in the prey, which are followed by recoveries. In seeking causes of the cycles, however, it is important to separate the primary prey species (voles or hares) from the secondary (scarcer) ones (grouse). The evidence for predators causing the cycle is much stronger for the secondary species than for the primary (mammalian) ones. The supposed mechanism is as follows: as the numbers of herbivorous mammals rise over a period of years, so do the numbers of the predators that depend on them. Then, when mammal numbers crash, the abundant predators switch their emphasis to grouse and other birds (eggs, chicks or adults), reducing their numbers, and eventually themselves declining through starvation, emigration and non-breeding (Hagen 1952, Lack 1954, Keith 1974). This then enables both mammal and grouse numbers to rise again to start another cycle, and the remaining predators to shift their emphasis back to mammals. In these circumstances, grouse breeding numbers can be said to be limited by predation, at least in the decline phase of the cycle. Another likely effect of avian predators is in helping to synchronise the fluctuations in their prey over wide areas, as their movements lead them to concentrate at any one time in localities with the highest prey densities. What causes the cycles in mammal numbers is a more controversial question, but it is probably not predation.

On this basis, ten-year cycles in the numbers of Ruffed Grouse *Bonasa umbellus* in North America have been attributed to predators, such as Goshawks *Accipiter gentilis*, switching their attention to grouse in years when the primary prey (Snowshoe Hares) decline (Keith & Rusch 1988). Similarly, 3-5 year cycles in the nesting success (and hence numbers) of certain bird-species in northern Eurasia have been attributed to predators switching to birds in years when their rodent prey decline. This switch gives regular years of heavy nest predation in a wide range of bird-species, from passerines (Dunn 1977, Järvinen 1985, 1990, Orell 1989, Högstad 1993, Viestola *et al.* 1996) to waterfowl and waders (Pehrson 1976, Roselaar 1979, Summers & Underhill 1987). The pattern is exemplified in Brent Geese *Branta b. bernicla* and two shorebird species which nest on the Taimyr peninsula of Siberia and winter in western Europe (geese) or southern Africa (shorebirds), where the proportion of young in winter flocks has tended to fluctuate in synchrony and on a 3-year cycle, in inverse relation to lemming numbers (Figure 2). In these studies, therefore, predation by specialist predators was seen as an important cause of cycles in the numbers of avian prey. In contrast, in a study by Thirgood & Redpath (this volume) predation by generalist predators proved capable in preventing a cyclic increase in Red Grouse and holding their numbers at a low level.

Figure 2. Proportion of first-year birds in wintering populations of various bird species that breed in arctic Siberia, in relation to the numbers of lemmings on the breeding grounds in different years. High production of young in Sanderling *Calidris alba*, Curlew Sandpiper *C. ferruginea* and Brent Goose *Branta bernicla* occurred about every three years when lemming numbers were also high, providing alternative food for predators. From Summers & Underhill 1987.



4. No effects on prey breeding numbers.

In some bird and mammal species, predation might remove so few individuals that it has no discernible effects on breeding numbers. In other species, which are subject to substantial year-round predation, the losses involved could be fully compensated by reductions in other losses. This might happen, for example, when total mortality is density-dependent and ‘pre-determined’ by the extent to which numbers exceed the available territories or other resources, giving rise to the idea of a ‘doomed surplus’ (Errington 1946, Jenkins *et al.* 1964). An example of a system in which a raptor has been found to have no apparent effects on the breeding numbers of its prey is discussed below.

A CASE STUDY: SPARROWHAWKS AND THEIR SONGBIRD PREY

The Sparrowhawk *Accipiter nisus* is one of the commonest raptors in Europe, nesting in woodland and hunting small birds, in both woods and open country. It can remove a large proportion of prey individuals each year, yet seems to cause no obvious depression of breeding densities (Tinbergen 1946, Perrins & Geer 1980, Newton 1986, McCleery & Perrins 1991, Newton *et al.* 1997). This was shown incidentally over much of Europe around 1960, when Sparrowhawks were eliminated from large areas through the use of organochlorine pesticides, recovering and recolonising years later when organochlorine use was reduced (Newton 1986). During the period of Sparrowhawk absence, woodland songbirds were not noticeably more numerous than before or after.

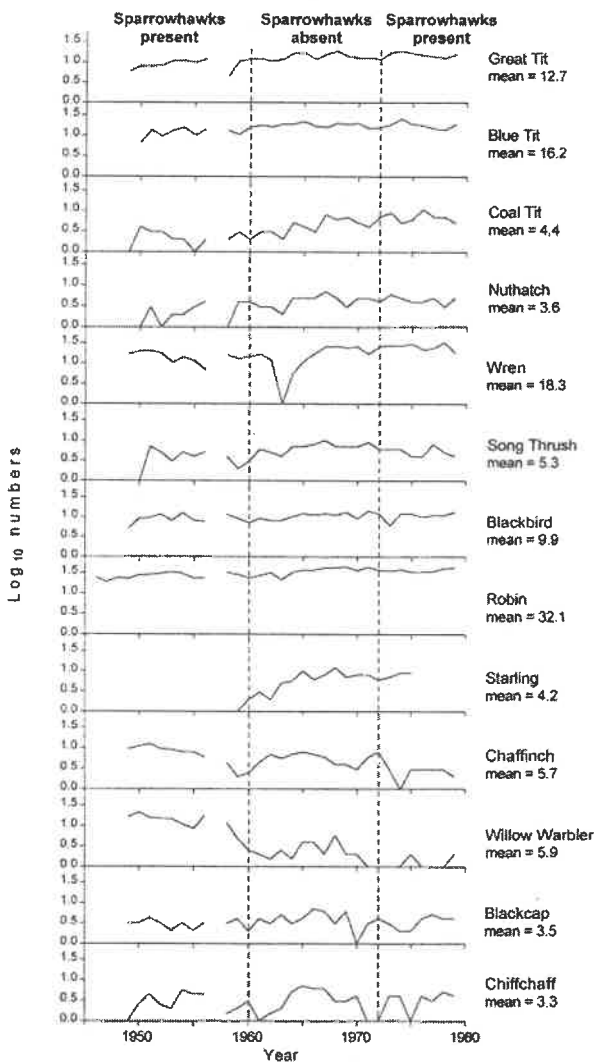
Table 1. Means of annual numbers of various songbird species in a 16 hectare oakwood plot during three successive periods when Sparrowhawks were present, absent or present respectively. From data in Bevan (1976) and Kettle (1982), based on counts of singing males.

SD - standard deviation, SE - standard error. The terms increasing, decreasing and no significant trend refer to long term trends over the whole 34 year period (see Table 2).

Species	1946-59		1960-72		1973-79	
	Mean	SD SE	Mean	SD SE	Mean	SD SE
Increasing						
Great Tit (<i>Parus major</i>)	9.0	± 2.4 (0.77)	13.8	± 2.5 (0.71)	16.0	± 2.2 (0.82)
Blue Tit (<i>Parus caeruleus</i>)	11.8	± 2.9 (0.96)	18.0	± 2.1 (0.57)	18.6	± 3.9 (1.46)
Coal Tit (<i>Parus ater</i>)	2.3	± 0.9 (0.30)	4.4	± 2.0 (0.55)	7.1	± 2.2 (0.83)
Nuthatch (<i>Sitta europaea</i>)	2.1	± 1.4 (0.43)	4.3	± 1.3 (0.36)	4.6	± 1.0 (0.37)
Wren (<i>Troglodytes troglodytes</i>)	14.8	± 4.3 (1.37)	17.0	± 8.1 (2.26)	25.7	± 5.1 (1.92)
Song Thrush (<i>Turdus philomelos</i>)	3.7	± 1.9 (0.62)	6.6	± 1.9 (0.53)	5.3	± 1.5 (0.57)
Blackbird (<i>Turdus merula</i>)	8.7	± 2.6 (0.79)	10.5	± 2.1 (0.60)	10.7	± 2.3 (0.87)
Robin (<i>Erithacus rubecula</i>)	26.8	± 4.3 (1.18)	30.1	± 7.6 (2.09)	36.3	± 3.4 (1.27)
Starling (<i>Sturnus vulgaris</i>)	0.1	± 0.3 (0.10)	6.3	± 3.0 (0.82)	8.3	± 1.2 (0.67)
Decreasing						
Chaffinch (<i>Fringilla coelebs</i>)	8.0	± 3.1 (0.98)	5.6	± 1.8 (0.51)	2.6	± 0.8 (0.30)
Willow Warbler (<i>Phylloscopus trochilus</i>)	13.8	± 4.7 (1.48)	2.3	± 1.6 (0.45)	1.0	± 0.8 (0.31)
No significant trend						
Blackcap (<i>Sylvia atricapilla</i>)	3.0	± 0.7 (0.21)	3.9	± 1.7 (0.47)	3.4	± 1.1 (0.43)
Chiffchaff (<i>Phylloscopus collybita</i>)	3.1	± 1.6 (0.49)	3.3	± 2.1 (0.58)	3.6	± 1.3 (0.48)

This was apparent, for example, in a single 16 ha oakwood, on Bookham Common, Surrey, where all breeding birds were counted every year during 1949-1979 (except for 1957). These counts covered both the decline and the recovery periods of the Sparrowhawk, which bred in the wood up to 1959 (inclusive) and again from 1973 (Beven 1976). This gave three periods for comparison: 1947-59 (hawks present), 1960-72 (hawks absent) and 1973-79 (hawks present). The 1960s corresponded with the period when Sparrowhawks were scarcest in the general area, reaching their lowest numbers around 1964.

Figure 3. Counts (log values) of various songbird species in an English oakwood each year during three successive periods when Sparrowhawks were present, absent and present respectively. Mean values show average numbers of singing males (untransformed values) present each year over the whole period. None of the species shown was significantly most numerous in the middle period when Sparrowhawks were absent. From Newton *et al.* 1997.



Thirteen songbird species were judged sufficiently numerous for analysis (Newton *et al.* 1997). In nine such species, significant variation occurred between the mean counts for the three successive periods (Table 1). In seven species, this was attributable to a sustained increase over the whole period, and in two species to a sustained decrease. These trends occurred regardless of Sparrowhawk numbers, and coincided with changes in the internal structure of the wood (less understorey and more canopy) (Beven 1976). Not a single species was present in significantly greater numbers in the middle period when Sparrowhawks were absent from the wood and at their lowest numbers in the surrounding area (Table 1, Figure 3). One species, the Starling *Sturnus vulgaris*, colonised the wood after Sparrowhawks ceased to nest there, but remained in good numbers after they returned. In the Wren *Troglodytes troglodytes*, the main noticeable effect was the hard winter of 1962-63. Hence, these data gave no evidence that Sparrowhawks had any negative impact on the breeding densities of woodland songbirds.

How is it that Sparrowhawks had no obvious impact on counts of singing males in the study area? Four explanations seem possible: (a) the proportions taken from the wood were too small to be detectable in the overall counts; (b) killed birds were quickly replaced from a non-territorial surplus so that the numbers of territorial (singing) birds in the wood were maintained in the face of continuing predation; (c) the census plot represented optimal habitat for most species in which their densities were maintained by continual immigration from suboptimal habitats where the effects of predation might have been more apparent; or (d) when Sparrowhawks were absent, songbird mortality from other causes (including other predators) increased in compensation. In retrospect, it is not possible to separate these possibilities, but evidence for the existence of surplus birds, able to take the places left by removed territorial ones, has been obtained for a wide range of bird species, including several of those discussed here (Newton 1992).

Some additional findings emerged from a detailed study of hawk predation on box-nesting tits in a 320 ha wood near Oxford (Geer 1978, Perrins & Geer 1980):

- (1) Within 60m of each successful hawk nest, both the occupancy and the success of nest boxes were depressed, compared with boxes further away. This was attributed to the hawks eating more of the tits near their own nests than elsewhere in the wood. Findings were consistent between years, even though the locations of hawk nests changed from year to year. However, the effects of this localised high predation on the overall tit population of the wood was immeasurably small.
- (2) The hawks ate many fledgling tits, removing an estimated 34%, 18% and 33% of young Great Tits in three different years, and 27%, 18% and 27% of young Blue Tits. More than six young tits per pair (including failed pairs) were raised in these years, but only about one chick per pair was needed to replace the annual losses of adults in order to maintain the population at constant level. Hence, many young tits must have died from predation or other mortality causes at other times of year.
- (3) Great Tit and Blue Tit breeding numbers fluctuated greatly from year to year, but in general the numbers of nest boxes occupied each year were no higher in the period when hawks were absent than when they were present. These results thus gave no evidence that Sparrowhawks, despite their predation, depressed the breeding populations of these tit species.

These various findings for tits could probably be generalised to many other prey species, in that the main effects of Sparrowhawk predation were to: (1) change the seasonal pattern of mortality; (2) reduce the size of the post-breeding peak in the population; and (3) change the main agents of death; all without causing any noticeable decline in breeding numbers. In practice, this meant that, instead of dying mainly in winter from food shortage, for example, potential prey individuals died at all seasons, and largely from predation.

Despite the long-term findings from woodland birds, some people writing in the popular press in Britain have claimed that increasing numbers of Sparrowhawks (in recovery from organochlorine impacts) have caused declines in farmland birds. There is no doubt that most farmland bird-species

have declined in the past 30 years (some species by more than 50%, Fuller *et al.* 1995), but these declines have coincided with a period of agricultural intensification which has enormously reduced the habitat and food-supplies available for most farmland bird-species. In fact, all studies of declining species on farmland have excluded predation as a significant causal factor (Newton 1998).

CONCLUDING REMARKS

Among animals in general, predator-prey relationships vary from closely-coupled interactions at one extreme, in which the numbers of prey and predators are inter-dependent, to neutral feeding links at the other extreme which are of no consequence for the population dynamics of either consumer or consumed. In between are prey-controlled dynamics in which the numbers of prey influence the numbers of predators but not vice versa, and predator-controlled dynamics in which the numbers of predators influence the numbers of prey but not vice versa. Studies of predation by raptors are relatively few in number, and while some raptors had no obvious effects on prey breeding numbers, others helped to hold prey breeding numbers below the level they would otherwise achieve, or contributed to cyclic fluctuations in prey numbers.

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