

Population limitation in birds: the last 100 years

Ian Newton

ABSTRACT Over the past 100 years, much has been learned about what limits the numbers of birds, and many field experiments have been conducted to check ideas. Such understanding is essential for the effective conservation or other management of bird populations. All the main factors likely to affect bird numbers, whether food or nest sites, predators, pathogens or competitors, have been found to limit the numbers of one species or another. The same species may be limited by different factors in different areas or in different years. Some species may be limited by a combination of factors, which interact in their effects on population levels. Long-term trends and/or year-to-year fluctuations suggest that some migratory bird populations are limited primarily in their breeding areas, and others primarily in their wintering areas. Other aspects of population regulation are also discussed, including demographic factors (births, deaths and movements), and the role of territorial and other aggressive behaviour in the limiting process.

Introduction

Everyone with an interest in birds must have wondered why some species are rare, while others are common; why some are increasing, while others are decreasing; or more generally why each species is as numerous as it is, and not more or less so? An understanding of what limits bird numbers is not only an important subject in its own right, but it is central to all bird management, whether for the purposes of conservation, recreational hunting or pest control. In the last 100 years, there has been enormous growth in our understanding of the factors that affect bird numbers and also huge population changes in many species.

At the start of the 20th century, so little had been written about bird populations that it is hard to say what scientists thought about the subject. They clearly accepted that hard winters and predation (including human hunting) were important in reducing bird numbers, and were aware that disease and starvation were of potential significance. However, they knew little about the relative importance of these different factors, or about the behavioural components of density regulation, such as territorial and other dominance behaviour. In addition, many of the concepts that we now take for granted were unheard of then. The only long-term data available on bird numbers resulted from game bags, and perhaps not surprisingly the first detailed study of bird populations in Britain concerned the Red Grouse *Lagopus l. scoticus*, aiming to discover the cause of periodic crashes in numbers (Lovat 1911).

It was not until well into the century that detailed 'population studies' of non-game species began, involving year-on-year assessments in particular study areas of breeding numbers and nest success, and even later that such findings were related to external variables such as weather and food supply. From the nineteen-fifties, field experiments on bird populations became more frequent, providing tests of the importance of different limiting factors. At the same time, more and more data were collected on an ever-expanding range of species, both by professionals working in universities or research institutes, and by amateurs who in Britain mostly acted under the aegis of the British Trust for Ornithology (BTO). In consequence, the scientific literature on bird populations mushroomed, from a worldwide handful of relevant studies in the first decade of the century to thousands in the last decade. But during this time,

to my knowledge, only three books were written specifically on the limitation of bird numbers, two by David Lack (1954, 1966), and then my own book towards the end of the century (1998), although chapters on bird populations appeared increasingly in more general books and in symposium volumes (eg Perrins *et al.* 1991). In this paper, I shall attempt to review the main issues involved in the study of population limitation in birds, highlighting aspects that have proved controversial or confusing. Some of the findings from literature reviews that are cited here are taken from Newton (1998), where the original references may be found.

Setting the scene

The numbers and distribution of any bird species are clearly limited by the amount and distribution of suitable habitat. This is self-evident and I shall say no more about habitat as such, but concentrate on the factors that limit densities within the habitats occupied. Within the scientific literature, most discussion of bird numbers is based on breeding densities. There are good biological reasons for this. Bird numbers vary during the course of a year but it is normally at the start of breeding that annual numbers reach their lowest point, and it is on breeders that all future additions to the population depend. Moreover, while birds are breeding they are at their most conspicuous and most closely tied to fixed localities, making them easier to count reliably than at any other season. Of course, we have to count some birds, such as arctic-nesting waterfowl and waders, in their wintering areas, but for most bird species our entire knowledge of population trends is based on counts of breeders. In discussing population limitation, therefore, breeding numbers (or densities) are implied here, unless stated otherwise.

It is also important at the outset to distinguish between the external (environmental) factors that influence populations and the internal (demographic) features that change with change in numbers. External factors include resources (notably food supplies) and natural enemies (notably predators and pathogens). Internal demographic features include the rates of births and deaths, immigration and emigration – the net effects of which mediate the influence of external factors to determine population trend. Thus a population may be said to decline because of a reduction in food supply or an increase in mortality, but in this example the food-supply is the ultimate (external) factor influencing trend, and the mortality is the proximate (internal) factor through which the trend is brought about. In the past, failure to distinguish between the external and internal factors led to much confusion over the ‘causes’ of population changes.

Systematic bird ringing over the past century has revealed much about the demographic parameters of bird populations, notably birth and death rates. But if we studied populations by demography alone, we could never understand what ultimately determines their average level, and why this level varies greatly between areas or through time. Two populations of the same species may have identical rates of births, deaths and movements, and yet persist indefinitely at quite different densities. To understand the differences in population mean densities, or change through time, we need to study the external factors. It is also the external factors that have to be altered by management before a change in population level can be achieved. During a period of population change, we can expect that the birth rate, death rate or movement pattern will be different from that during a period of population stability.

External limiting factors

Few would argue with the fact that, within suitable habitat, food and other resources could provide a ceiling on bird numbers. No species can increase beyond its food supply. A key question is therefore which species or populations are currently limited by food or other resources and which are held below this level by natural enemies, whether predators, parasites, pathogens or competitors.

Food supplies

Evidence for limitation by food supply comes from those species that show spatial or temporal changes in densities which parallel similar changes in food supplies. One of the earliest studies was by Reinikainen (1937), in Finland. He travelled the same route (on skis) in March for 11 years, recorded the numbers of Common Crossbills *Loxia curvirostra* he encountered, and estimated the cone crops of spruce. The number of Crossbills seen each year was strongly correlated with the size of the spruce crop, the highest numbers of birds being 20 times the lowest, with an increase of this order occurring from one year to the next (fig. 1). The year-to-year changes in Crossbill numbers in this locality, as elsewhere, were caused mainly by movements, the birds settling each year according to available food supplies. An example of spatial variation in breeding density, linked with spatial variation in food supplies, is provided by Golden Eagles *Aquila chrysaetos* in different parts of Scotland (Watson *et al.* 1992; fig. 2). Regional variations in the density of breeding eagle pairs matched regional variations in their main source of food, namely sheep and deer carrion. Unlike the Crossbills, these differences were consistent from year to year.

Some years ago, I searched the ornithological literature for such correlations, and found 36 studies (involving more than 36 species) in which year-to-year changes in bird densities were correlated with year-to-year changes in food supplies and 28 studies (involving more than 28 species) in which spatial variations in densities were associated with spatial variations in food supplies (Newton 1998). Moreover, in 16 additional studies, a long-term or sudden change in a bird population was associated with a long-term or sudden change in food supply. While correlations such as these do not prove causal relationships, they indicate that links between bird numbers and their food supplies are widespread. Examples include many types of birds, from passerines and pigeons to raptors and seabirds (Newton 1998).

Some birds eat such a wide range of foods that it is not readily possible to measure their total supply. Their breeding densities have sometimes been related not to food as such, but to some determinant or correlate of food-supply, such as rainfall (in arid regions) or soil fertility. Thus, in northern Europe, songbirds generally breed at greater density in woods growing on rich soils than on similar woods on poor soils, and waterbirds are generally more diverse and abundant on nutrient-rich than on acidic, nutrient-poor lakes (fig. 3; von Haartman 1971). One likely reason is that the food organisms eaten by birds also depend on the general productivity of soil or water.

More compelling evidence that food supply can limit bird breeding densities has come from experiments in which additional food was provided artificially and the response of the population was measured. Most such experiments have involved tits, which are comparatively easy to study in this way: they are resident in the same areas year round; they eat food (such as peanuts) which can be readily provided; and their subsequent breeding numbers can be measured in the same area by counting the numbers of nests in boxes, which can be provided in excess. The most substantial feeding experiment of this

type spanned several successive winters in The Netherlands (van Balen 1980). It was based on two areas of similar woodland 7 km apart; extra food was provided in one, while the other acted as a control where the tits had natural food alone. Before winter feeding began, Great Tit *Parus major* breeding numbers in the two areas were similar and fluctuated more or less in parallel from year to year (fig. 4a). After feeding began, breeding densities in the two areas diverged and no longer fluctuated in parallel. Over several years, breeding numbers in the experimental area averaged 40% higher than those in the control area. However, the impact of the supplementary food varied between years depending on the Beech *Fagus sylvatica* mast crop, which was the most variable major component in the natural food supply. Comparison of numbers in the experimental area in the years before and after food provision indicated that the extra feeding doubled the population in poor Beech years but made little difference in good Beech years (fig. 4b). The fact that the extra food had most effect in years when natural food was scarce provided further evidence that winter food supplies influenced the local breeding densities of Great Tits.

Other experiments on tits, covering two or three winters, gave variable results. In some areas, two species had access to the supplementary food and, if each of these is counted as a separate experiment, then, compared with control areas, eight out of 15 winter feeding experiments led to obvious increases in subsequent breeding density while seven did not (Newton 1998). The same species responded to food provision in one area but not in another, and in the same area and year, one species responded while another did not (Krebs 1971). Where a response to food provision occurred, tit breeding density increased by up to 100% compared with that in control areas; and where the birds were ringed, the increase in breeding density was found to result from both increased local survival and increased immigration, affecting mainly first-year birds (Krebs 1971; van Balen 1980; Jansson *et al.* 1981). Similarly, in the Song Sparrow *Melospiza melodia* on Mandarte Island, British Columbia, seed provision in one winter led to improved survival, especially of juveniles, and to an increase in subsequent breeding density (38%) (Smith *et al.* 1980). Overall, of 26 studies involving 14 bird species (tits and others), 15 led to increased breeding density following food provision, whereas 11 showed no measurable change, compared with numbers in control areas (table 1). Evidently, breeding densities in some of these populations were limited by food supplies in the years concerned, but not others.

Nest sites

Some bird species require special places to put their nests, such as tree cavities, cliffs or islands in lakes – places that are not abundantly available in all landscapes. That such special nest sites can limit the breeding densities of some species is clearly evident from observation. For example, in much of their range, Peregrine Falcons *Falco peregrinus* are limited to nesting in areas where cliffs are available as nest sites; they are absent from other areas lacking cliffs, but where prey are no less plentiful. The fact that in some regions Peregrines have begun to nest on cliff-surrogates, such as quarries and buildings, only adds weight to the argument. Similarly, Barn Swallows *Hirundo rustica* naturally nest in caves, but have adapted to barns and other buildings, a habit which has enabled them to spread over huge areas previously unavailable to them, greatly increasing their population sizes. The same holds true for some other hirundines and swifts (Apodidae) in various parts of the world (e.g. Erskine 1979). In most places, population expansion resulting from human colonisation would have occurred long before there were ornithologists to record it, but it was well documented in North America during the spread of European people and their buildings in the nineteenth century (Bent 1942).

The limitation of breeding density by nest-site shortages has frequently been shown by experiment. Most such experiments have involved species which nest in tree cavities but cannot normally excavate their own holes. Such species readily accept appropriate nest boxes, but in assessing effects on populations, one has to be sure that local breeding pairs have actually increased in numbers and not merely shifted to boxes from natural sites.

The results of 46 careful studies on nest-site provision are listed in table 1. They included 25 different species, from songbirds to ducks and raptors. In 96% of these studies, breeding density of one or more species increased after box provision, suggesting that limitation by shortage of nest sites was widespread among these hole nesting birds. Density increases of between two- and four-fold were frequent, and in some studies of between five- and twenty-fold. Perhaps not surprisingly, increases were greater in species that defended little more than the nest site, such as Pied Flycatcher *Ficedula hypoleuca* and Tree Sparrow *Passer montanus*, than in species such as tits that held large territories and thereby limited the settlement of other pairs. Following box provision in an area of Finland, Pied Flycatchers *Ficedula hypoleuca* increased from virtual absence to more than 2,000 pairs per km², a greater density than all other species put together (von Haartman 1971).

Several studies (notably on Pied Flycatchers) showed that numbers increased abruptly the year after boxes were installed, implying that large numbers of potential occupants were generally available. Without the boxes, these birds would presumably not have bred but would have remained as part of a large non-breeding contingent unable to breed because of shortage of sites. Other studies showed that, following box provision, numbers increased slowly over several years, implying that no more than a small surplus was present in any one year, and that reproduction or continued immigration contributed to the longer-term increase. Whatever the species and its rate of increase, numbers eventually levelled off, regardless of the number of extra boxes provided. The implication was that, once the shortage of nest sites was rectified, another factor took over to limit numbers at a higher level. Evidence from various tits and raptors showed that this second factor was food supply. In such species, then, densities in different areas were limited either by nest sites or by food supply, whichever was in shortest supply (Newton 1979).

Cavity nesters are not the only birds that have responded to the experimental provision of nest sites. Increases in the breeding densities of other species have been noted followed the provision of baskets or artificial stick nests in trees (Village 1990), rafts (as island substitutes, Crawford & Shelton 1978), pylons (as tree-substitutes, Steenhof *et al.* 1993), and suitable buildings (as cliff substitutes, Newton 1979). It thus seems that shortage of nest sites can limit the distribution and density of a wide range of bird species. However, many nest-box experiments were in young, managed woods, deficient in old and dead trees, and the situation may be different in older, more mature woods that have more cavity-bearing trees. Moreover, studies which did not lead to an increase in breeding density were perhaps less likely to be published, so we should perhaps not over-generalise from these findings.

For many bird species, then, we have clear evidence that population levels are influenced by resources, whether food or nest-sites. For other species, the evidence suggests that breeding numbers are held below the resource limit by natural enemies, whether predators, parasites and pathogens (=disease agents), or competitors.

Predators

One of the most thorough studies of predation on a bird population concerns the effects of Hen Harriers *Circus cyaneus* and Peregrines on Red Grouse *Lagopus lagopus* (Redpath & Thirgood 1997; Thirgood *et al.* 2000). The study extended to several widely scattered moors, but was based primarily at Langholm, in southern Scotland, where for several decades grouse had fluctuated in regular cyclic pattern with peaks in numbers every six years or so (the troughs possibly due to the parasitic disease, strongylosis). During a six-year period, Hen Harriers and Peregrines were allowed to breed freely, although other predators, such as crows and foxes, were controlled as usual. During this time, harrier numbers increased from two to 20 breeding females, and Peregrines from three to six pairs. Over the same period, grouse breeding numbers remained at relatively low level. They produced insufficient young each year to support shooting, with productivity declining during the study, and failed to increase to a peak expected in 1996 or 1997. In comparison, on two other moors, where predator control continued as usual and where grouse had previously fluctuated in parallel with those at Langholm, a marked peak occurred in 1997. The implication was that raptor predation, at the levels sustained, held the Langholm grouse at low level, lower than they would have achieved in some years in the absence of raptors. Measurements of predation rates revealed that these two predators could fully account for the depressed grouse numbers, and that no other factor was likely to be involved. At such low grouse densities, there was no outbreak of strongylosis.

A simple mathematical model of the grouse population at Langholm, combining the estimated reduction in breeding productivity with the observed pattern of winter losses, predicted that over two years, in the absence of breeding raptors, grouse breeding numbers would have increased by 1.3 times and post-breeding numbers by 2.5 times, enough to reach the expected peak in 1996 or 1997, and provide a sufficient surplus for driven shooting.

Overall, taking the observational evidence from many studies, it seems that predators can have the following four types of impact on bird populations, depending on circumstances:

1. No obvious reduction in breeding density. This is apparent in many species which suffer considerable predation, but are demonstrably limited by other factors, such as food or nest sites, as discussed above. It is also apparent in some large bird species, which nowadays suffer virtually no predation as adults, and often have a large non-breeding surplus of mature adults unable to get nesting territories (such as Mute Swan *Cygnus olor* and Common Raven *Corvus corax*).
2. Hold breeding density at some level below that at which resources would otherwise permit (as in the Red Grouse discussed above and also in Grey Partridge *Perdix perdix*; Potts 1980).
3. Cause marked fluctuations in breeding density, either irregular or regular (cyclic), as suggested for some northern gallinaceous birds exposed to periodic heavy predation (including Willow Ptarmigan *Lagopus lagopus* in northern Europe and Ruffed Grouse *Bonasa umbellus* in North America, Lack 1954; Keith 1963).
4. Cause decline to extinction, as in some birds on oceanic islands exposed for the first time to mammalian predators, such as rats and cats, introduced accidentally or deliberately by people (Atkinson 1985).

Predator-removal experiments have not been concerned with distinguishing these different types of effects, only in testing whether an effect was apparent, in other words in distinguishing (1) from the rest. Most of the 30 experiments described in the ecological literature concerned ground-nesting gamebirds and ducks. The parameters that were measured most commonly included: (1) nest success (proportion of nests from which young hatched); (2) post-breeding numbers (or ratio of large young to adults); and (3) subsequent breeding numbers. In 27 studies in which nest success was measured, 23 showed an increase in success under predator removal; in 17 studies in which post-breeding numbers were measured, 12 showed an increase; and of 17 studies in which breeding numbers were measured, ten showed an increase. Improved nest success was not always followed by increased post-breeding numbers, and even less often by increased breeding numbers. Overall, it seems that in more than half the studies in table 1 that measured breeding density, this density was limited by predation, although all the species concerned experienced heavy predation at some stage of their lives.

How general are these experimental findings on predation likely to be? Because almost all the species studied nested on the ground, they may have been more vulnerable to predation (especially from mammals) than other birds which nest in safer sites. The predators were all generalists which fed on other prey, such as voles or rabbits, and turned to birds when birds were readily available. In all experiments, the effects of predator removal were short-lived, and when the control stopped, the experimental areas were soon recolonised by predators, and predation returned to its former level. The maximum breeding densities achieved under predator control were about twice as high as in areas where predators were left. This is about the same level of difference as achieved in food provision experiments.

Parasites and pathogens

Ecologists often separate parasites into two kinds: macroparasites which are mostly big enough to see with the naked eye, and include parasitic worms, ticks, fleas and others; and microparasites which are invisible to the naked eye, and include pathogenic bacteria, protozoa and viruses. Ticks, fleas and others live externally on the body surface of their hosts, while all the others live within the body of their hosts. A feature of microparasites is that they mutate frequently, and often appear as different strains, some of which may be relatively harmless and others disabling or lethal. Different bird species, like other kinds of animals, differ in their vulnerability to particular microparasites, so that some host species are unharmed and can act as reservoirs of infection for other species which can die. A topical example of a microparasite with a strain which is fatal to at least some bird species is the H5N1 strain of the avian influenza virus.

In general, parasites can have the same effects on host populations as predators on their prey, leading to either (1) no obvious reduction in breeding density; (2) an equilibrium level lower than resources would permit; (3) marked fluctuations in abundance; or (4) decline to extinction. Sometimes a new disease, or disease vector, has been introduced to a new area, with devastating effects on the local avifauna. The best documented examples have involved Hawaiian birds, following the introduction of mosquitoes able to transmit avian malaria and pox (Warner 1968; van Riper *et al.* 1986). Hawaiian birds had not previously been exposed to these diseases, so had no natural immunity. In such cases, the disease organism may completely eliminate its new host (as probably happened with some native species on Hawaii), or it may eliminate the most vulnerable individuals, leaving more resilient ones and allowing a measure of resistance to evolve.

Nearer to home, experimental studies attempted to find the effects of strongylosis (caused by the strongyle worm parasite *Trichostrongylus tenuis*) on Red Grouse. Removal of this parasite from individual grouse, using an anthelmintic drug, led to increases in both the breeding success and survival of individual grouse compared with untreated ones (Hudson 1986; Hudson *et al.* 1992). Treatment of about one-fifth of grouse prevented a cyclic decline in grouse bags on five occasions on four different moors compared with trends on control moors where grouse were untreated (Hudson *et al.* 1998). The conclusion was that treatment of this particular parasite at the level practiced could prevent the periodic crashes in grouse bags previously attributed to this parasite. Parasites had thus apparently limited the densities of grouse, at least in the crash years. Further work on four other moors confirmed that parasitism could reduce productivity (and hence the post-breeding population), and also spring densities. However, spring populations declined over the years on both experimental and control areas, suggesting that some other factor was also involved in causing cyclic fluctuations (Redpath *et al.* 2006). During all these studies, predators were controlled.

Turning to a different kind of parasite outside the categories mentioned above, some studies in North America have examined the effects of the removal of Brown-headed Cowbirds *Molothus ater* on some of their host species. This cowbird lays its eggs in the nests of various insectivorous passerines, greatly reducing their **productivity**. It has increased and spread in recent decades, affecting a greater proportion of potential hosts, and even new host-species, not previously exposed to its effects. Experimental cowbird removal led to improved nest success in six different host species, and to increased subsequent breeding density in three of them (table 1). It is probably only a matter of time before experiments reveal the effects of other parasites on bird breeding numbers.

Competitors

Most bird species share part of their food with other species of birds and other animals, and some share the same kinds of nest sites. Species which eat the same kinds of foods as one another can therefore be regarded as competitors, if food is limiting, and so can species which require the same types of nest site, if nest sites are limiting. Competition may involve ‘resource depletion’, where individuals of one species reduce the amount available to another species (e.g. where Great Tits eat beech mast that would otherwise be available to other tits). Or it may involve ‘interference’, where individuals of one species, by aggressive or other means, reduce access to a resource by individuals of another species (as when a Mistle Thrush *Turdus viscivorus* aggressively defends a fruiting tree against Blackbirds *T. merula*). In any pair of competing species, it is rare for both to suffer equally from resource shortage, and in any situation the effects are usually ‘asymmetric’, falling more heavily on one species than on the other.

In a relatively stable avifauna, the effects of competition on populations are practically impossible to demonstrate without an experiment in which one competing species is removed, and the response of the other is monitored. In 11 out of 12 such experiments known to me, the removal (or reduction) of one species led to an increase in another (table 1). Most such experiments involved nest sites. For example, in six forest plots in Sweden, almost all nest boxes were occupied every year by one or other of three species. The numbers of all three fluctuated from year to year, but increases in the numbers of Great and Blue Tits *Cyanistes caeruleus* were accompanied by decreases in the numbers of Collared Flycatchers *Ficedula albicollis*, and vice versa (Gustafsson 1988). The implications were that the boxes were not limiting for the earlier nesting tits, but that the later arriving

flycatchers were relegated to whatever boxes were still unoccupied. The numbers of flycatchers in the plots thus depended on the numbers of tits. As an experiment, the numbers of tits in two plots were reduced in two successive years. This led to a large increase in the numbers of flycatchers, compared with those in a control plot. In a further experiment in a Norwegian forest, Slagsvold (1979) blocked the entrances of all nest boxes except those already occupied by Great Tits. In consequence, later arriving Pied Flycatchers *F. hypoleuca*, which were abundant in previous years, were completely prevented from breeding there. Males fought unsuccessfully with Great Tits for possession of boxes, while females left the area. These experiments revealed how competition for nest sites could limit the breeding density of flycatchers, and how annual fluctuations in the numbers of **breeding** flycatchers varied inversely with the numbers of tits. Other experiments have revealed competition for nest sites in other bird species, and yet others have revealed competition for food (Newton 1998).

Review of experiments

The findings from 109 relevant experiments published in the scientific literature are summarised in table 1. As discussed above, some involved the provision of extra winter food or nest sites, while others involved the removal of predators, parasites or competitors. These experiments varied in design and quality but, taken together, they provide confirmation that all the main potential limiting factors, whether resources or natural enemies, do indeed limit the local breeding densities of one bird species or another. They also reveal that particular species may be limited by different factors in different areas or in different years. In the Great Tit, for example, winter food proved limiting in some areas, but nest sites in other areas.

While some experiments lasted up to ten years, most lasted only 1–3 years (the usual duration of a student grant). In many studies breeding numbers were still increasing when the experiment stopped, so it was not possible to see the full impact of the treatment on breeding density. Nevertheless, most experiments resulted in at least a doubling of breeding density compared with the previous situation in the study area or with the concurrent situation in a control area. However, nestbox studies resulted in much bigger effects, sometimes giving up to twenty-fold increases in the densities of target species. In some experiments, the provision of nest sites attracted species into the study area that were previously absent there. Hence, for many species that require special nest sites, the shortage of such sites emerged as an especially potent factor in limiting distribution and abundance.

Another point needs to be kept in mind when assessing the experimental findings. For each species, experiments were done on the factors that previous observational evidence had suggested was limiting. If it looked like food was important, food was provided. If it seemed that predation was important, predators were removed. While this is a perfectly legitimate procedure, it means that, as a group, existing experiments may be biased towards giving positive results. If species for the different experiments had been selected at random from the local avifauna (in practice not possible), rather than on the basis of prior knowledge, the number of positive results may well have been less than the 78% recorded overall.

Interactions between limiting factors

So far, I have assumed that a population, at any one time and place, may be limited by one factor only – resources or natural enemies. In reality, no single factor is likely to account wholly for a given population level. During a period of food shortage, for example, some

individuals may starve, while other non-starving individuals may die from other causes. In such cases, the limiting factor can be considered as that which, once alleviated, will permit the biggest increase in numbers.

There is another kind of interaction, however, which has only recently begun to receive serious attention, namely the influence of one limiting factor on the action of another. For example, food-shortage might predispose predation, in that hungry birds become less wary, and allow a much closer approach by humans and other predators. This presumably makes them more likely to be captured than in situations with plentiful food. Likewise, the mere presence of predators might deter birds from feeding in certain places, and thereby in effect reduce their food supply. Similarly, predators might deter many birds from nesting in any but the safest sites, thereby limiting the range of nest sites available to them. Such examples emphasise that bird numbers cannot always be considered as limited by single factors, but by combinations of factors (for other examples see Newton 1998). Two factors acting together may sometimes increase the overall losses in a population (as when predators enhance the effects of food shortage, as mentioned above), or they may reduce the overall losses (as when predators capture individuals already close to death from parasitic disease rather than healthy individuals, and thereby prevent the disease from spreading more widely).

Consider some further examples in more detail. The restriction of some colonial birds to patches of nesting habitat can lead to depletion of food supplies near the colonies, while food remains abundant farther away. Indeed, it has been argued that some seabird populations, restricted to the vicinity of the colonies, may be regulated by localised competition for food in the breeding season, which in turn limits the production of young (Ashmole 1963). Regulation is thus achieved not by numbers of nesting places alone, and not by food supply alone, but by a combination of the two, with local concentrations of nest sites leading to local concentrations of birds, leading in turn to localised food shortage. Although individuals might survive by feeding farther afield, where food is more plentiful, they could not reproduce there, through lack of nest sites. Pelagic birds, nesting on remote oceanic islands, provide the most extreme examples.

To take another example, food shortage can enhance predation on nestling birds in two recognised ways: first, by causing hungry chicks to call more, thereby attracting the attention of predators; and, second, by causing parents to spend more time foraging and less time guarding their chicks. This latter effect has been noted in such diverse species as gulls, crows and raptors. Moreover, when supplementary food was placed near the nests of Carrion Crows *Corvus corone* and Magpies *Pica pica*, more young were raised, not because the young were better fed, but because they suffered less predation (Yom-Tov 1974; Hogstedt 1981). The extra food enabled the parents to spend more time near the nest, better able to protect their chicks against raids by other crows. Other interactive effects were shown in adult tits, where experimental food provision led to improved overwinter survival, through reducing both starvation and predation. The extra food enabled birds to spend more time than otherwise in safer sites, and on vigilance behaviour (Jansson *et al.* 1981). In such cases, then, food-supply and predation interact to influence nest success or survival.

Apart from causing direct mortality, predators can accentuate food shortage in their prey when their repeated attacks discourage prey from feeding in places where they are at high risk, such as far from cover, or by disturbing them so often that they have too little time to

feed effectively. The same may result from continual human disturbance, which can keep birds out of some areas altogether (effectively reducing their food supply) or prevent them from obtaining sufficient food in the time available (for an example see Gill *et al.* 1996). When exposed to people or predators, birds not only avoid certain areas, they also spend more time on the alert or in hiding, leaving less time for feeding (Krebs 1980).

Once one begins to consider the interaction of not just one factor but three or more, the number of possible situations is almost limitless, but we can perhaps generally expect that one or two factors will predominate in their effects on bird numbers. In the various experiments discussed above, only a single factor was manipulated, and none was concerned with the interactive effects of two or more limiting factors acting together. Experiments on interactions between limiting factors are likely to prove expensive, but they could provide a fruitful field for future research, providing further insight into how bird numbers are limited.

Demographic parameters

From the foregoing, it is clear that we can understand what limits populations, and manage them accordingly, without any knowledge of births, deaths or movements. Providing that inputs (births + immigrants) balance losses (deaths + emigrants), population level can be sustained on a wide range of reproductive or survival rates. Only when one or both of these rates fall so that losses exceed inputs, do numbers decline. Study of demographic rates is particularly useful in indicating where the problem lies in a declining population. If, in a population that swings from stability to decline, mortality remains constant, while reproductive rate declines, the problem lies in the breeding areas, but if reproductive rate stays constant while mortality rises, the problem could lie in either breeding or wintering areas, wherever the extra deaths occur. The situation of constant survival was true for Northern Lapwings *Vanellus vanellus* in Britain, as they switched over the years from stable to declining numbers, giving a strong indication that reproductive rates had declined, and that the problem lay in breeding areas (Peach *et al.* 1994). In contrast, the situation of stable reproductive rate but reduced survival was the case in a European Golden Plover *Pluvialis apricaria* population, suggesting that the problem lay in the wintering areas (Parr 1992).

This type of study has become particularly important when examining the decline of migratory bird populations, where it is not immediately obvious whether the problem lies in breeding or wintering areas. Until this question can be answered, it is not clear where conservation measures could most usefully be applied. Among 53 populations of migratory birds for which sufficient data were available, some 22 seemed (from their long-term trends or year-to-year fluctuations) to be limited primarily in their wintering areas, 29 primarily in their breeding areas, while two (**White Stork *Ciconia ciconia* and Great Skua *Stercorarius skua***) were demonstrably affected by changes in both breeding and wintering areas (Newton 2004). In the latter **two**, the long-term trend was apparently driven by events in one of these areas, and the year-to-year fluctuations about the trend by events in the other area.

Territorial and other social behaviour

Fifty years ago, much confusion centred on the role of territorial and other aggressive behaviour in limiting bird and other animal populations. Through their territorial behaviour, birds space themselves through suitable habitat. Clearly, this spacing could provide a possible mechanism through which density could be limited, but an alternative possibility

is that local birds – whatever their numbers – simply divide the available habitat between them. If there are few birds, they have large territories; if there are many, they have small territories. The issue was resolved **from the nineteen-sixties** by the discovery (or appreciation) of surplus non-territorial birds and by experimental studies demonstrating the role of territorial behaviour in density limitation.

So-called ‘removal experiments’ played a crucial role in resolving the role of territorial behaviour in density limitation. The procedure was to wait until birds had settled on their territories in spring and density had stabilised, and then remove some of the territorial individuals. If these birds were replaced in the same spring by other individuals, so that overall density was maintained, it could be concluded that territorial behaviour limited local density. If, in addition, it could be established that the replacement birds had been drawn from a non-territorial sector, rather than from other territories, this would further show that territorial behaviour contributed to the existence of a non-territorial, non-breeding sector. In this case, territorial behaviour, as well as limiting breeding density, also prevented some birds from reproducing, and thus limited the breeding output of the population as a whole.

At least 60 removal experiments have now been conducted, involving 43 different bird species from passerines to auks (table 2). In about 80% of these experiments, removed birds of one or both sexes were replaced rapidly. In many of the experiments, the replacements were ringed, and known to derive from a non-territorial contingent, **an early experiment on Red Grouse being particularly influential (Watson & Jenkins 1968)**. The limitation of breeding density by territorial behaviour thus appeared to be widespread among birds. This does not mean that the densities of all territorial bird populations are limited in this way everywhere every year. For various reasons, many populations might not achieve densities at which their territorial behaviour would become limiting.

If territorial behaviour limits densities, how can we relate this to other findings that food or nest sites are crucial? In many bird species, territories vary in size in relation to local food supplies. Two examples from North America are given in fig. 5. In both species, territory size declined with increasing food density and, in the hummingbird, territory size changed from week-to-week, or even day-to-day, according to changes in their nectar food supply, as flowers opened or died. The same relationship held true for Eurasian Sparrowhawks *Accipiter nisus* in different parts of Britain, in which territory sizes were not measured directly, but as distances separating the nests of neighbouring pairs in continuous nesting habitat (fig. 6). Comparing different regions, mean nearest-neighbour distances increased as local prey densities declined, with neighbouring pairs adjusting their spacing to the local food supply (Newton *et al.* 1986). So here we have a simple behavioural mechanism through which changes in food supply are translated into changes in bird densities. The food supply can be regarded as the ultimate factor influencing breeding density, and territorial behaviour the proximate mechanism through which this influence is achieved. This is not to imply that food supply is the only factor that can influence territorial behaviour. In some situations, birds may also adjust their spacing to reduce the risk of predation or parasitic infection, although as yet, to my knowledge, such indications have not been properly tested.

The manner in which territorial behaviour might limit bird densities is depicted in the model shown in fig. 7. As birds arrive in their breeding areas in spring, their numbers rise steadily. The first birds to arrive get territories, because space is plentiful. But later arrivals

have increasing difficulty in squeezing in, and after a certain point, territories can be compressed no further, and territory densities stabilise. Any additional birds that arrive after this time must either replace existing territory holders, accumulate locally as a non-territorial surplus, or move elsewhere. This mechanism could thus provide powerful density dependent control of territorial density and, if only territorial birds are able to breed, it also provides density dependent control over reproduction. This could perhaps be one of the strongest and most widespread regulatory mechanisms operating in many bird populations.

However, territorial behaviour is not the only proximate mechanism that can regulate bird densities. Any kind of dominance behaviour, including fighting, supplanting and avoidance behaviour, frequently seen in flocking birds, can do the same. This is because, in any competitive situation, some individuals get more (or better) resources than others, and through such interactions, densities become adjusted to local resource levels, and birds which cannot meet their needs must leave or die. Good examples of social interactions (involving interference and depletion of food supplies) acting in this way in flocking species were provided by Murton (1968) in wintering Wood Pigeons *Columba palumbus* and by Goss-Custard *et al.* (1982, 1984) in wintering Oystercatchers *Haematopus ostralegus*. In these ways, territorial and other dominance behaviour, evolved for the benefit of individuals, has emerged as a major proximate mechanism through which bird numbers can be adjusted to resource levels. Typically, the effects of such competition and interaction fall most heavily on young subordinate birds, whose food intakes decline in consequence. These are the individuals that must leave or die, and not surprisingly their mortality rates are often greater than those of adults. Whether such social interactions occur with respect to food supplies, nest sites, mating opportunities or predator avoidance, it nearly always resolves to defence of a single resource – space. Compared with the situation 50 years ago, this represents a major advance in understanding, because it explains the spacing and dominance behaviour of birds in terms of individual fitness, and reveals its consequences in density regulation. Before that, spacing behaviour was sometimes considered as a regulating mechanism in its own right, which acted in isolation from resource levels or other external factors.

Density dependence

It has long been appreciated that bird populations normally fluctuate between much narrower limits than are theoretically possible, and hence that densities must be regulated in some way (Lack 1954). This requires the operation of density-dependent regulating factors which allow numbers to increase when they are low and cause numbers to decrease when they are high. Potential regulating factors include competition for food or other resources, predation, and parasitism by infectious disease agents, all of which could affect a greater proportion of individuals as their numbers rise, lowering the average *per capita* survival or reproductive rates within the population. Movements can also affect local numbers if the ratio of immigration to emigration falls in response to rising population density. Such factors contrast with density-independent factors, such as extreme weather or other catastrophic events, which can remove many individuals from a population regardless of their numbers (as in the effects of hard winters on the population levels of Wrens *Troglodytes troglodytes*, Dartford Warblers *Sylvia undata* and others). Initially, the argument for the importance of density dependence in regulating bird populations was based almost entirely on logic, as this was the only way in which their relative year-to-year stability could be explained (Lack 1954). It was an act of faith, for no good field evidence was available for birds. In addition, there was a counter view, championed by Andrewartha & Birch (1954), who claimed that weather and other density-independent factors were of

over-riding importance in limiting animal numbers. Clearly, both factors could affect bird populations and, gradually, effort shifted to assessing the relative importance of density-dependent and density-independent factors in influencing the year-to-year changes in bird numbers.

It was many years before any substantial body of evidence on density dependence accumulated for bird populations. There were two major problems. First, the numbers of birds were of course influenced by both density-dependent and density-independent controlling factors. So in any run of data, such as annual counts or breeding rates of birds, it was hard to separate the density-dependent signal from density-independent noise. One needed long runs of data collected over many years, and sophisticated statistical methodology, neither of which were available to earlier researchers, such as David Lack in the 1940s and 1950s. Secondly, food supplies (and other resources which affect the carrying capacity of habitats) vary greatly in abundance from year to year, so measurements of density were being made against a continuing changing baseline. This problem could have been overcome if density had been measured, not as numbers per unit of area, but as numbers per unit of food (or whatever other resource the birds were competing for). But then, as now, few observers measured resources as well as bird numbers and performance, so density was almost always measured on the basis of area (for a recent exception see Lindström *et al.* 2005).

Despite these problems, evidence for density dependence in bird populations is now available for a wide range of species (Newton 1998). Fig. 3 shows three examples to illustrate different points. In the Sparrowhawk, breeding density remained fairly stable from year to year, with nest numbers over a 26-year period fluctuating no more than 15% on either side of the mean level. Stability in breeding density was achieved by density-dependent recruitment of new breeders, with the numbers added each year approximately matching the numbers of established breeders lost from the population since the previous year (fig. 3a). This situation arose because the number of territories in this 200 km² area was more or less fixed, which kept an approximately constant ceiling on breeding density (Newton 1991). A similar mechanism is also apparent in species whose breeding densities fluctuate much more from year to year than those of the Sparrowhawk, except that the ceiling is much more flexible.

The second example illustrates spatial density dependence. At the start of winter (October), the densities of Red Grouse varied greatly on different areas of moorland in southern Scotland (Redpath & Thirgood 1997). Over-winter losses of grouse (between October and April) were greatest in those areas that had the highest October densities (fig. 3b). These losses were caused primarily by predation, but the fact that the two areas with the lowest October densities gained birds during the winter indicated that movements were also involved. Nevertheless, differential over-winter loss led to spatial stabilisation in the densities of grouse by the following breeding season.

The third example shows the effects of competition for a resource in limited supply. In the area concerned, the numbers of Wood Duck *Aix sponsa* pairs in some years exceeded the number of available nestboxes. In consequence, different pairs interfered with one another, which led to density-dependent reduction in breeding success (Jones & Leopold 1967). As in many competitive situations, however, the relationship between productivity and density was not linear, but curvilinear. This illustrates another difficulty in measuring density dependence: over part of the density range in fig. 3c the density dependence is readily

apparent, but over another part it is not. In other words, the chance of detecting density dependence could depend greatly on the range of densities experienced during the study.

For several decades, then, one priority was to collect evidence for density dependence in bird populations. But as such evidence accumulated, the emphasis shifted to determining the shape of the relationship (whether linear or curvilinear) for use in population models. It has also shifted towards assessing the relative importance of density-dependent, as opposed to density-independent, processes in influencing year to year population changes. It may be added that not all forms of density dependence are stabilising. Inverse density dependence or delayed density dependence can lead to fluctuations in density, but these aspects are outside the scope of this review (for examples see Newton 1998).

Concluding remarks

Over the last 100 years, we have developed a considerable understanding of the various factors that limit bird numbers, whether food supplies and nest sites, or predators, parasites and competitors. Experiments have confirmed the role of all these various factors in one species or another. They have also thrown light on the role of territorial and other dominance behaviour as a proximate behavioural mechanism in adjusting densities to the resources available. Territorial and other aggressive behaviour not only influence the numbers of birds that can survive or live in a given area, but also which particular individuals can do so, with dominants gaining advantage over subordinates.

The findings from research, and especially from experiments, are not always as expected. For example, many people have difficulty in understanding why a species that is subject to year-round predation is not limited by predation. The answer is that some other factor provides much more stringent limitation. Day after day, we can watch tits being taken by Sparrowhawks in our gardens, but this predation has been found to have little or no effect on the subsequent breeding densities of tits (Newton & Perrins 1997). This is because, as experiments have confirmed, tits are limited at even lower level by the winter food supply or by nest-site shortages. The implication is that, if tits were not eaten by Sparrowhawks or other predators, a similar number would have to die from food shortage, adding to the other uneaten tits that die in this way. Moreover, when breeding begins, there are still more tits than nest sites in some areas, so that a spring surplus of tits cannot reproduce. Despite the recovery of Sparrowhawk populations over the past 30 years, Great Tit and Blue Tit breeding numbers have continued to rise, as BTO monitoring has revealed. If this steady rise in tit populations has resulted from increased feeding of garden birds, it would be thoroughly in line with the experimental findings reported above, that winter food has a big influence on the population levels of these species.

Another lesson from the above observations is that different mortality causes are not necessarily additive in their effects on populations. They may be compensatory. If a number of birds are not killed by predators or disease agents, they (or a similar number) are soon destined to die from food shortage or from some other cause. Those species of birds that have a fixed stock of food to last them through the winter (such as those that live on plant seeds) present even more intriguing possibilities. In such species, if predation or disease removes a proportion of individuals before the start of winter, food stocks may last longer, resulting in a greater number surviving the winter than would have occurred in the absence of predation. Similarly, imagine that predators selectively removed diseased individuals from a prey population because they were easier to catch. Predators might thereby prevent an infection from spreading more widely, enabling the prey population to

remain at higher level than in their absence. Although these possibilities have emerged from field studies, they are not proven, but clearly the combined action of different limiting factors could result in various and sometimes unexpected effects on population levels.

Consideration of predation highlights the different attitudes shown by conservationists and game managers, the latter seeking to reduce predation in order to increase the game bag. Both conservationist and hunter are concerned with the long-term maintenance of breeding stock, which can usually be achieved without the control of predators. However, the game manager is also concerned with the production of as large a post-breeding surplus as possible. By control of predators that eat the eggs and chicks (as well as the adults), he contrives to increase the production of young by gamebirds and hence the potential harvest. For conservation purposes alone, in contrast, predation on eggs and young is irrelevant, providing that it does not set future breeding numbers into indefinite decline. It is no paradox that predators might reduce the size of the seasonal post-breeding peak population, but have little or no effect on breeding numbers at the seasonal low. Considering the high rates of predation on the eggs and chicks of many birds, predation may often be the major factor limiting their post-breeding numbers. Yet during the course of the ensuring winter, other factors such as food shortage take over to limit the number of breeders at even lower level than could be achieved by predators alone. And as stressed at the outset, in conservation terms, it is the breeding populations that count.

So what are the main developments in research that have got us where we are now? First, there is the obvious point that, during the past 100 years, from little more than game bag records, we have accumulated an enormous amount of information, an effort to which both amateurs and professionals have contributed. Within Britain, **an appreciable** component of this process has been the collection and management of nationwide data by the BTO, and the increasing analysis and publication of these data in recent decades. On a wider scale, information has come from an ever expanding range of bird species, and from an ever expanding range of habitats and geographical areas. Second, **in the last 50 years**, ideas have been increasingly tested experimentally in field conditions. This has been especially important in elucidating the role of territorial behaviour as a proximate mechanism in regulating bird densities, and the role of resources and natural enemies as ultimate limiting factors. Third, there have been technological advances, particularly in the development of statistical methodology, and in computing power, both of which have given us the means to assess and weigh evidence much more reliably than in the past, and to handle larger volumes of data. **The use of statistical tests in population papers became more or less routine from the 1960s on, and the use of computers from the 1980s on, as they became more widely available.** Perhaps the most heartening development of all, however, is that this accumulated knowledge is now being put to good use in conservation, in assessing the causes of bird declines and defining the external limiting factors, so that appropriate management can be put in place. This means that restricted conservation funding can be used more effectively than in the past, when conservation actions, often based on little more than 'gut feeling', were inevitably much more 'hit and miss'.

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Prof. Ian Newton, Centre for Ecology and Hydrology, Monks Wood, Abbots Ripton, Huntingdon, Cambridgeshire PE28 2LS. Email: ine@ceh.ac.uk

26 Look at the birds of the air; they do not sow or reap or store away in barns, and yet show more ourselves has also double? Do Not Worry. 25 "Therefore I tell you, do not worry about your life, what you will eat or drink; or about your body, what you will wear. Is not life more than food, and the body more than clothes?" The reason for our increase in population most probably stems from a higher life expectancy due to our increased understanding in medical science. More people in a given place means a higher demand in food to keep them fed. Boom. Please upload a file larger than 100x100 pixels. We are experiencing some problems, please try again. You can only upload files of type PNG, JPG, or JPEG.