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THE ROLE OF FOOD IN LIMITING BIRD NUMBERS

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1. INTRODUCTION

No-one can seriously doubt that food-supply could place an ultimate check on the population growth of any bird. Controversy has centred on, firstly, how often (if ever) particular populations reach this food limit (as opposed to being held below it by other factors), and secondly on the role of social behaviour in the limiting process. In this paper I shall review some of the arguments previously used as evidence for food limiting bird numbers. I shall illustrate each type of evidence with examples, but shall not attempt a comprehensive review; nor shall I be concerned with the influence of food on breeding rates, unless this bears directly on the subsequent breeding population.

Food can be considered limiting if it prevents a population from increasing. Food can seldom account wholly for a given population level, however, because neither mortality nor recruitment is dependent on food-supply alone. Some individuals may die from other causes during and beyond the period when other individuals are starving. In addition, territorial or other social behaviour may be involved in the limitation, resulting in the effects of food-shortage falling more heavily on certain individuals than on others. Thus, in the following account, when food is described as limiting, it is likely to be only one of several limiting factors acting on the population, and food may be essential to explain a given population level, but only in conjuction with other factors.

In this paper, I shall follow most authors and use the term "food-shortage" broadly, for food which is inadequate in quantity, quality, or availability. Food shortage may cause starvation (a deterioration in body condition to the point of death), or have more subtle effects on reproduction or spacing behaviour (Watson & Moss 1972, Newton 1977).

2. THE NATURE OF THE EVIDENCE

2.1. SOME GENERAL POINTS

Virtually all studies of population regulation in birds have been concerned with the dynamics of local populations. Yet almost all species have geographical ranges larger than an ecologist's study plot, and individual birds continually move in and out, on local or longer journeys. Hence, in most studies, the best we can hope to show is that food limits bird density at a particular place and time. It is therefore necessary to define the area carefully, for while density may be limited in this area, some individuals may move out to find food elsewhere, so that the total numbers are unaffected. The displaced individuals may or may not return at a later date. It is important to specify the time period, because more than one "bottleneck" may occur in that period, and only the last may be crucial in setting the eventual population level. For example, the numbers of birds might be limited in winter quarters by food-supply, but on reaching their breeding areas, there might still be more birds left than could occupy the available places, so that surplus individuals were excluded and died. In this case,

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food-supply reduced the numbers surviving the winter, but had no influence on the subsequent breeding density. We would have been justified in concluding that food limited winter numbers, but not that it limited breeding numbers. In most cases, we are concerned with what limits numbers or density at the start of breeding, because this is the stage each year when the population is usually at its lowest. It is also the time when individuals can most readily be counted.

Moreover, limitation by food-supply may occur only in certain years, and so be missed in a short study. Some European birds are cut back so markedly by food becoming unavailable in hard winters that they can then experience several years of increase before they next decline (for Heron *Ardea cinerea*, see Lack 1954, 1966).

Food may limit numbers in a density dependent or a largely density-independent manner. Density-dependent regulation implies competition for food, as a result of which, for a given food level, the percentage of birds that starve is greater when the population is high than when it is low. In density-independent limitation, competition for food is unimportant, and the proportion of birds that starve bears no consistent relationship to the population size. Probably few situations occur in which there is no competitive (density-dependent) element in feeding, though this may often be slight or hard to discern.

Food may limit numbers in an indirect way, and not necessarily cause deaths from starvation. Imagine that birds took territories of a size determined by the food-supply, and occupied an area to the full, so that surplus birds were excluded and died. In this case, food limited the density in the breeding habit, and the surplus could have died from various causes, not necessarily including starvation. Food shortage may also reduce a population through reducing the rate of breeding and recruitment, again not necessarily entailing the starvation of full grown birds. This type of effect may be hard to detect because of the lag between the food-shortage and population decline.

If changes in numbers are sometimes related to food, and social behaviour is involved, it is not of course safe to assume that food is the cause of all changes in numbers, nor that all social behaviour is involved in regulating numbers in relation to food. Some kinds of territorial behaviour are centred on nest-sites or mates, and may have little to do with food. Hence, for this paper, I shall accept that some (but not all) kinds of social behaviour are involved in limiting numbers in relation to food, but will not discuss this aspect in detail, as it forms the subject of other papers in this symposium (Patterson, Davies, Drent).

Undisputable proof that food-shortage limits bird numbers is unattainable, and in practice we are concerned with the quality of evidence. In what follows, I have graded different types of evidence in ascending order of reliability and usefulness from indirect evidence, not amenable to experimental testing (2.2); through circumstantial evidence, leading to testable hypotheses (2.3); to circumstantial evidence, later checked by experiment (2.4).

2.2. INDIRECT EVIDENCE, NOT AMENABLE TO EXPERIMENTAL TESTING

2.2.1. Correlation between body-size and breeding density

Schoener (1968) reviewed the data available for birds which feed in territories and concluded that territory size was strongly correlated with body-weight, the larger species defending bigger areas. He also found that species which ate animal food had larger feeding territories than omnivores of similar weight, and that omnivores had larger territories than herbivores (though few herbivorous species held feeding territories). The most likely explanation of the first trend was that small species required less food (and hence smaller areas) than large ones; and of the second trend that carnivores had larger territories because their food was sparser than that of omnivores or herbivores. Schoener (1968) commented that "if food resources were not a limiting factor, but were in indefinite or superabundant supply, then none of the highly regular variations in territory size should be observed".

The relationship between body weight and territory is evident within particular groups, such as raptors (Fig. 1). The overall trend in this group for large species to breed at lower density, in larger ranges than small species, presumably

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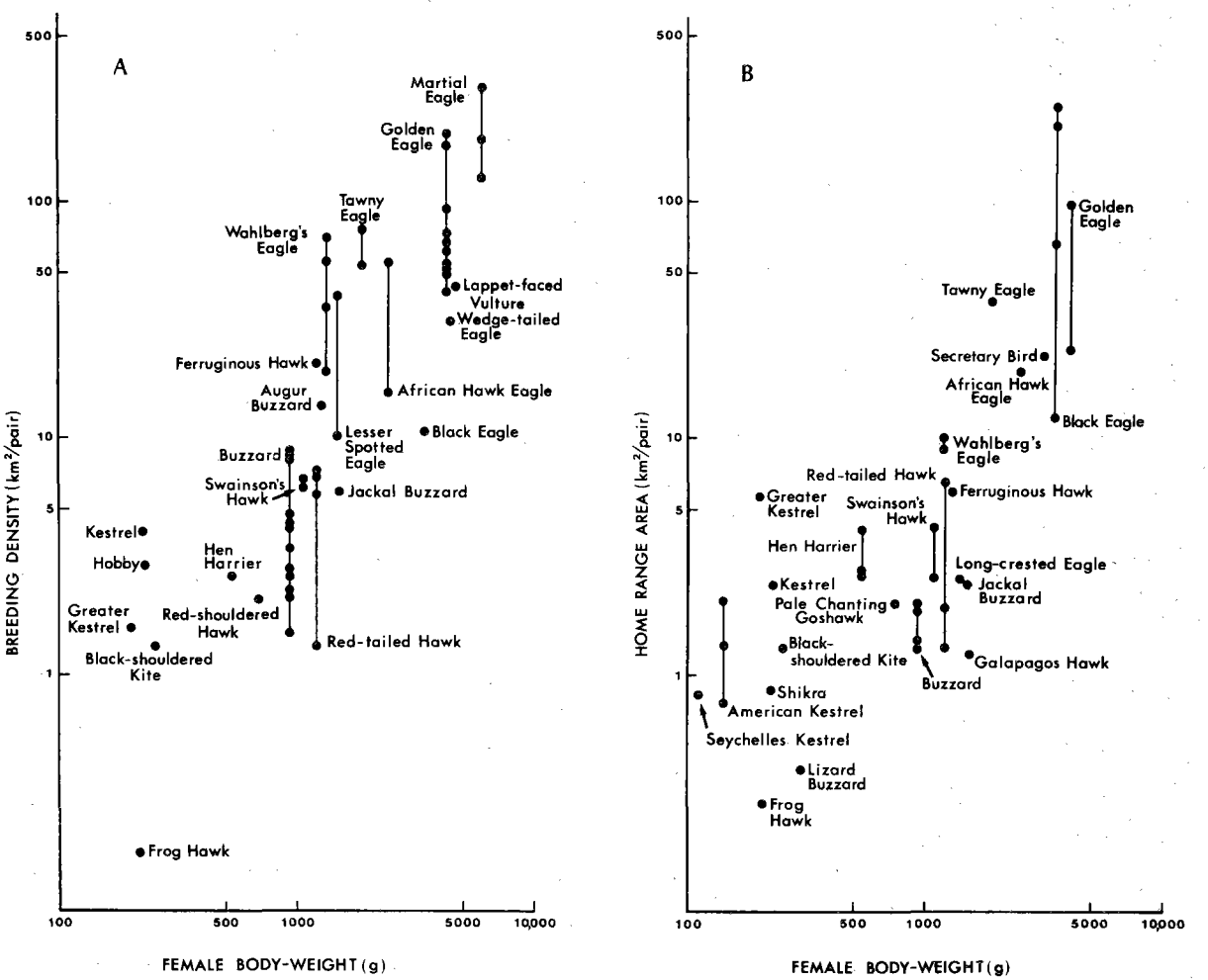


Fig. 1. Breeding density (A) and mean range size (B) in relation to body-weight in raptors. The information was mostly collected near the start of the breeding season, and the home ranges were mean values for the populations studied. Different studies on the same species are joined by lines. The populations concerned were not limited by shortage of nest-sites, and individual pairs foraged in more or less exclusive ranges. The overall trend was for large raptors to breed at lower density, in larger home ranges, than small ones. This was associated with larger raptors eating larger, sparser and slower-breeding prey than small ones. For any one population, breeding density was lower than expected from home range sizes, because study areas generally included some unused habitat. From Newton 1979.

holds because larger raptors usually eat larger prey species, and large prey species live and breed less abundantly than do small ones. So in each case, the range size of the raptor may be adjusted to the food-supply (Newton 1979).

Such correlations between body weight and breeding density have so far been based on only a small part of the bird kingdom, and generally exclude gregarious birds. They are consistent with the idea of food limiting territory (or home range) size and density; but they do not prove the idea because of the alternative explanation, that larger birds take larger territories for some other (unknown) reason, unrelated to food.

2.2.2. Principle of competitive exclusion

Lack (1954) used another line of indirect evidence that birds in general were limited by food, namely that each species living in the same region depends primarily on different foods. This reduces competition between species and, if food were not limiting, one would not expect this dif-

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ferentiation to have evolved. However, the argument rests largely on speculation about past events, and furthermore species may differ in food choice for some other reason — for example, simply because they are different species, with different morphology. The findings are thus consistent with food limiting bird numbers, but the explanation is not particularly helpful, because it cannot be tested, nor applied to specific cases.

2.3. CIRCUMSTANTIAL EVIDENCE, LEADING TO TESTABLE HYPOTHESES

2.3.1. Correlations between bird numbers and food-supply

Correlations within species between bird-numbers and food-supply provide another kind of circumstantial evidence for food limiting bird numbers, and fall into three main types: (a) area differences in food correlated with area differences in bird numbers; (b) annual differences in food correlated with annual differences in bird numbers; and (c) long-term changes in food correlated with long-term changes in bird numbers.

Differences between areas. In many studies, food was not measured directly, and the correlation was between bird numbers and some supposed index of food, such as soil productivity. Data of this type were collected for forest birds in Finland, where there are three main forest-forming trees, birch *Betula*, spruce *Picea* and pine *Pinus* (Palmgren 1930, Von Haartman 1971). On similar soil, song-birds were most numerous in birch, less numerous in spruce, and scarcest in pine, while in mixed spruce/birch woods they were most numerous of all. Most of the birds concerned were insectivores, and their densities were paralleled by similar variations in insect populations. Furthermore, for any one tree species, song-birds were more numerous in forests on good soil than in forests on poor soil (Fig. 2). This could also be linked with food-supply, for several aspects of productivity were better on good ground, such as growth and fruiting of trees, insects on the foliage, and earthworms in the soil below. Many of the birds concerned were summer visitors to Finland, and of those that stayed the winter, many then lived outside the woods. Hence, the differences in bird numbers must have been due, not to birds surviving better in some woods than in others, but to their settling in spring in greater numbers in some woods than in others. Similar trends were noted in song-birds elsewhere in Europe, whether or not they wintered locally (*e.g.* Moss 1979).

Correlations between bird-density and soil fertility have been noted within other species, comparing densities in different areas. Among game birds, Red Grouse *Lagopus l. scoticus* were more numerous on land overlying basic than acidic rock, associated with greater nitrogen and phos-

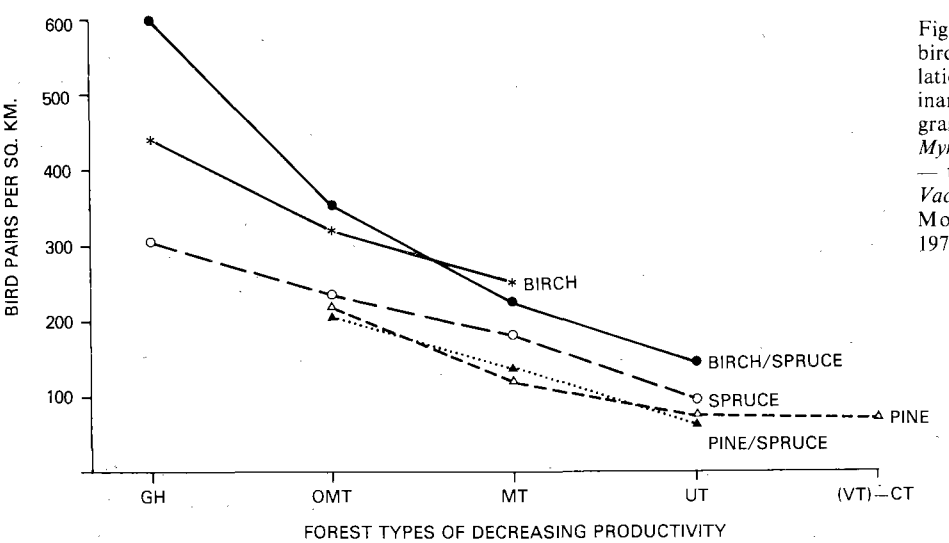


Fig. 2. Densities of breeding birds in Finnish forests in relation to forest type and dominant tree-species. GH — grass-herb; OMT — *Oxalis-Myrtillus*; MT — *Myrtillus*; UT — tobe filled in proof; VT — *Vaccinium*; CT — *Calluna*. Modified from Von Haartman 1971.

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phorus content in the food plant *Calluna vulgaris* on basic rock (Miller *et al.* 1966, Moss 1969). Among raptors, Sparrowhawk *Accipiter nisus* densities in 12 parts of Britain were strongly correlated with soil productivity and altitude, and in at least three areas where counts were made, with

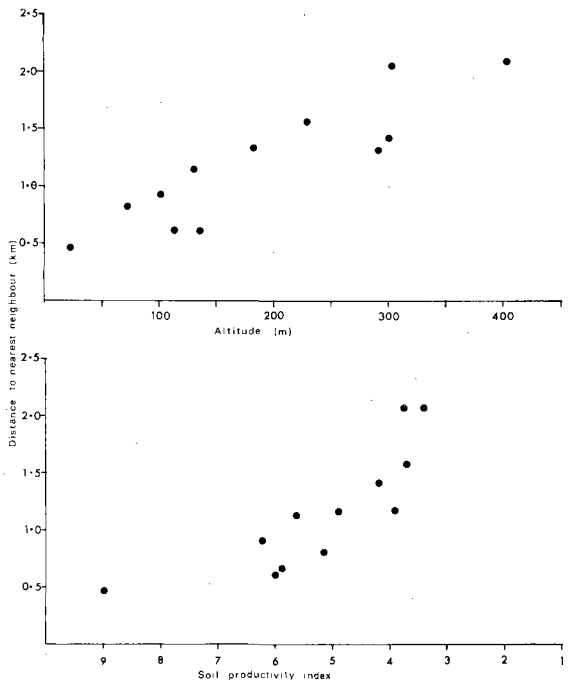


Fig. 3. Mean nearest-neighbour distances of Sparrowhawk nesting territories in continuous nesting habitat shown in relation to altitude above sea-level and land-productivity in twelve different areas. Nearest-neighbour distances widen with rise in altitude (linear relationship) or fall in land productivity (probably curvilinear relationship). From Newton *et al.* 1977.

the abundance of small bird prey (Fig. 3). Similar relationships were found for Peregrines *Falco peregrinus*, which spaced themselves at 2.6 to 10.3 km apart in different regions of Britain, according to soil productivity and associated prey densities (though prey were not measured directly) (Ratcliffe 1969). Higher Peregrine densities than any in Britain were found on the Queen Charlotte Islands, off western Canada, where the mean distance between about 20 pairs was 1.6 km, in this case linked with massive concentrations of seabirds (Beebe 1960). This population later dropped to about six pairs, following a decline in prey (Nelson & Myers 1975).

Similar relationships held in water birds, comparing nutrient-rich (eutrophic) lakes with nutrient-poor (oligotrophic and dystrophic) ones.

Table 1. Densities of birds and other animals in different types of lakes in Finland. From Von Haartman 1971

	Lake types of decreasing productivity		
	Eutrophic	Mesotrophic	Oligotrophic and dystrophic
Bottom fauna (individuals/m²)	2,000—10,000	?	0—1,000
Fish production (kg/ha)	ca 10	2—3	2—3
Birds* (pairs/km²)	11—130	21—27	1—39

Note* Including Anatidae, Podicipedidae, Gaviidae, Rallidae, and *Sterna hirundo*.

Table 1 illustrates this point, again based on Finnish studies, collated by Von Haartman (1971). The greater production of eutrophic lakes was reflected by greater densities of invertebrate and fish life, and in turn of birds. Other factors were involved, however, for the vegetation was better developed in and around eutrophic lakes and offered more nest sites; also bird densities varied partly with the lake depth and with the length of shore in relation to water surface. In this case, as for the woodland birds discussed above, the pattern results from where the birds settle to breed, not from their survival outside the breeding season, as the lakes in question support no bird-life in winter, when they are frozen.

Direct correlations between bird numbers and food supplies have been documented for various groups, including sea birds and waders (Jesperson 1929, Goss-Custard *et al.* 1977a). This occurred even at the level of the individual and its territory. In the Ovenbird *Seiurus aurocapillus*, the sizes of 13 territories were inversely correlated with the density of invertebrate prey in the leaf litter of those territories (Stenger 1958). Similarly, in the Golden-winged Sunbird *Nectarinia reichenowi*, the size of territories varied more than ten-fold; but at any one time each territory contained enough food to supply the owner's needs, and over a period of time territories were expanded as their food-contents declined (Gill &

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Wolf 1975). In cases such as these, with each bird (or pair) holding a territory of a size dependent on food, the density of birds over a wider area can become related to food over a wide area.

Such correlations between bird numbers and food are consistent with the idea of food limiting numbers, but again they do not prove it, because of the alternative possibilities, that birds are limited in each area by some unknown factor which varies in parallel with food, or that birds already limited by some other factor, then distribute themselves according to food. It is also possible that numbers are limited in the good food areas, but not in the poor ones. I am thinking here of the so-called "buffer effect", in which birds are supposed to occupy sub-optimal habitats only if compelled to do so by the birds already present at high density in the favoured habitats known to be richer in food (for various tits, see Kluyver & Tinbergen 1953; Chaffinch *Fringilla coelebs*, see Glas 1960; various waders, see Goss-Custard 1977). In the Great Tit *Parus major*, Krebs (1971) found experimental support for the idea, by removing territorial birds from woodland (the optimal habitat for breeding) and finding that they were replaced by individuals from nearby hedges (the suboptimal habitat for breeding). Hence, in the best habitats numbers may be proximally limited by territorial or other social behaviour (in relation to food), whereas in the poorer habitats, the numbers depend largely on overspill from the first; they may vary more from year to year than in the best habitat, yet seldom (if ever) reach the point at which territorial behaviour would limit density, as opposed to merely spacing the birds out.

An example of a study which indicated that density was regulated in both high and low density areas was that of Holmes (1970) on Dunlin in Alaska. In an area of low and unpredictable food-supplies, Dunlin held larger territories (and were at lower density) than in another area where food was measurably more abundant and dependable (1 pair per 6.7 ha and 1 pair per 1 ha respectively). In the low density area, the removal of individuals from territories was followed by their continual and swift replacement from the local non-breeding stock. These replacement birds then bred. Removals were not done on the high density area, but non-breeders of breeding age were seen to be present, and often fought with owners over nesting territories. Holmes concluded that Dunlin held territories related to the food-supply, that territorial behaviour limited breeding density in both areas, but at a lower level where food was scarce than where food was plentiful. Similar data supported by removal experiments were provided for Red Grouse (Jenkins *et al.* 1967). Evidence of this type is probably the best we can expect for the notion that food limits bird densities at different levels in different areas.

These examples will suffice to illustrate the general trend within species, for birds to breed more densely in areas where their food is more abundant. The evidence falls into three categories: (i) a correlation between bird numbers and some index of food, such as soil productivity, (ii) a correlation between bird density and food direct, (iii) a correlation between density and food, together with evidence to imply that numbers were limited in the high density area alone or in both high and low density areas. In all these cases, it is not possible to eliminate the possibility that some unknown limiting factor (besides social behaviour) varied in parallel with food, and caused the density differences.

Differences between years. In some birds, breeding density varies in the same area from year to year, in parallel with fluctuations in food. Some of the most striking examples are provided by predatory birds which depend on cyclic prey. Two main cycles are recognised: (a) an approximately 4-year cycle of small rodents on the northern tundras and temperate grasslands; and (b) an approximately 10-year cycle of Snowshoe Hares *Lepus americanus* in the boreal forests of North America (Elton 1942, Lack 1954, Keith 1963). Certain grouse species are also involved, but whereas in some regions they parallel the 4-year rodent cycle, with peaks usually in the same years, in others they parallel the 10-year hare cycle. The populations of these various prey animals do not reach a peak simultaneously over their whole range, but the peak may be synchronised over tens or many thousands of square kilometres. For these prey species, the role of food in their cycles is controversial, but there is

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little doubt about the predators, all of which tend to breed more densely and more prolifically in years when prey are plentiful than when they are scarce (Table 2).

The data on some of the predators are not as good as they might be, for it is not always certain whether the observer recorded fluctuations in the total population, in the numbers of settled pairs, or in the numbers of breeding pairs. In some migrant species, birds may arrive each spring, but leave soon afterwards if they are not going to breed, so the observer may miss them if he is not there at the start. Nonetheless, three classes of response of predatory birds to annual prey numbers can be recognised, comparing species (Newton 1979). Those birds which are subject to the most marked prey cycles show big local fluctuations in densities and breeding rates (*e.g.* Goshawks *Accipiter gentilis* in boreal regions); those subject to less marked prey cycles show fairly stable densities, but big fluctuations in breeding rates (*e.g.* Buzzards *B. buteo* and Tawny Owls *Strix aluco* in temperate regions), while those with stable prey populations show stable densities and fairly stable breeding rates (e.g. Peregrines in temperate regions). Much depends on how varied the diet is, and whether alternative prey are available when favoured prey are scarce. The more varied the diet, the less the chance of all food-species being scarce at the same time.

Table 2. Annual variations in the breeding populations of predatory birds with greatly fluctuating food sources

A. Species that eat rodents (approximately 4-year cycles)	
Rough-legged Buzzard *Buteo lagopus*	*(1) 0—9 pairs during 9 years, North Norway (Hagen 1969). (2) 51, 46 and 61 nests during 3 years, Colville River, Alaska (White & Cade 1971). (3) 10—82 pairs during 5 years, Seward Peninsula, Alaska (Swartz *et al.* 1974).
Hen Harrier *Circus cyaneus*	(1) 10—24 females in 33 km² during 22 years, Orkney, Scotland (Balfour, in Hamerstrom, 1969). *(2) 13—25 females in 160 km² during 5 years, Wisconsin (Hamerstrom 1969)**. *(3) 0—9 pairs in 6 years between 1938 and 1946 (Hagen 1969).
European Kestrel *Falco tinnunculus*	*(1) 35—109 clutches in 4 years; 109 clutches at vole density index 24; 97 at index 13, 35 at index 9, 50 at index 4, Netherlands (Cavé 1968). *(2) Approximately 20-fold fluctuation in index of number of broods ringed in Britain over 42 years, with peaks every 4—5 years (Snow 1968). *(3) 1—14 pairs during 5 years, North Norway (Hagen 1969). *(4) 1—16 nests during 12 years, Swabian Alps (Rockenbauch 1968). *(5) 26, 28 and 38 pairs during 3 years, south Scotland (Village 1969).
Black-shouldered Kite *Elanus caeruleus*	*(1) Increase from 1 to 8 nests in one year, associated with rodent plague, South Africa (Malherbe 1963).
Pomarine Skua *Stercorarius pomarina*	*(1) 0, 4 and 18 pairs/mile² during 3 years, Barrow, Alaska (Pitelka *et al.* 1955).
Short-eared Owl *Asio flammeus*	(1) 0—4, in places 7, pairs/mile² during 3 years, Barrow, Alaska (Pitelka *et al.* 1955).
B. Species that eat gallinaceous birds or hares (4-year or 10-year cycles)	
Ferruginous Hawk *Buteo regalis*	*(1) 5—16 pairs during 8 years in one area, 1—8 pairs during 3 years in another area, Utah (Woffinden & Murphy 1977).
Goshawk *Accipiter gentilis*	(1) 0—4 nests in 100 km² during 13 years; 2—9 nests in 200 km² during 7 eyars, in two areas of Sweden (Höglund 1964). *(2) 1—9 nests in 372 km² during 4 years, Alaska (McGowan 1975).
Gyr Falcon *Falco rusticolus*	*(1) 13—49 pairs during 5 years, Seward Peninsula, Alaska (Swartz *et al.* 1974). *(2) 19—31 occupied cliffs and 12—29 successful nests during 4 years, Alaska (Platt 1977).

* Prey population also assessed and related to raptor numbers.
** Excluding one year when population dropped from DDT poisoning.

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Raptors that have fairly stable food-supplies show some of the most extreme stability in breeding population recorded in birds (Newton 1979). Even the same species may fluctuate in one region, but not in another, depending on whether the prey are cyclic or stable.

In some of the cyclical species mentioned, not only the numbers, but also the territory sizes varied from year to year according to food. This was noted in Pomarine Skuas *Stercorarius pomarinus*, Snowy Owls *Nyctia scandiaca* and Short-eared Owls *Asio flammeus* between years (Pitelka *et al.* 1955), and in the last species within a year, as prey declined (Lockie 1955). It is an open question whether numbers were limited by territorial behaviour at different levels at different times, however, for removal experiments were not done.

Other birds which fluctuate greatly in numbers from year to year are the northern finches that depend on trees, whose seed-crops vary from year to year (Table 3). Like some raptors and owls, these finches are classed as irruptive, because their southward migrations are most pronounced in years of widespread crop failure. In the marked fluctuations of their breeding populations, they contrast with some other seed-eaters, which feed from many kinds of herbaceous plants and have more stable food-supplies from year to year (Newton 1972).

Some of the earliest data were collected by Reinikainen (1937) in mid Finland. He travelled the same route by ski each Sunday in March for eleven years, counted the Crossbills *Loxia curvirostra* met on his journeys and estimated the cone crops of spruce and pine. The number of breeding Crossbills seen each year was strongly correlated with the size of the spruce crop (though not with the pine crop), the highest number of birds being twenty times the lowest, with an increase of this order occurring from one year to the next (Fig. 4). Similar relationships between numbers and food have been found for Siskins *Carduelis spinus* and other seed-eaters elsewhere (Haapanen 1966, Newton 1972).

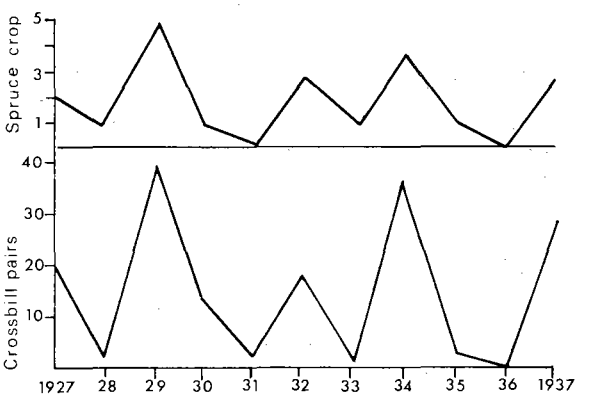


Fig. 4. Relation between the population density of the Crossbill *Loxia curvirostra* and the cone crop of spruce *Picea abies*. Crossbills in number of pairs per 120 km²; spruce crop classified in five categories. From Reinikainen 1937.

In the seed-eaters, as in some of the vole-eaters, the increases in local populations between years are often too great to be accounted for by good survival from the previous year, and must be due partly to immigration. In the seed-eaters, moreover, ringing recoveries have shown that the same individuals have summered or wintered in

Table 3. Finches which feed on fluctuating tree-seed crops. From Newton 1972

	Main food* in spring and summer	Main food* in autumn and winter
Siskin *Carduelis spinus*	spruce and pine	birch and alder
Mealy Redpoll *Carduelis f. flammea*	spruce and dwarf birch (*B. nana*)	birches (*B. verrucosa* and *B. pubescens*)
Lesser Redpoll *Carduelis f. cabaret*	herbaceous plants	birch (*B. alba*) and alder
Northern Bullfinch *Pyrrhula p. pyrrhula*	various plants	rowan and others
Pine Grosbeak *Pinicola enucleator*	various plants	rowan and others
Brambling *Fringilla montifringilla*	insects	beech

* Unless otherwise stated, seeds are implied.

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widely separate localities in different years. Thus, the evidence that food limits the density of these birds applies only on a local basis, with some individuals moving from one area to another in different years. In theory, local year-to-year fluctuations could result from continual re-distribution of a total population, limited by some other factor, yet each year settling according to food. When crop failure is widespread, however, food-shortage might provide a check on total population size, but this idea is necessarily an extrapolation from local events.

In all these species, the local correlations between numbers and food are sometimes impressive, with changes in numbers keeping strict parallel with changes in food. They are still correlations, however, with no controls, and are thus open to the possibility that some other unknown factor fluctuated in parallel with food, and caused the changes.

Long-term changes. Long-term or sudden changes in bird populations from one level to another can often be linked with long-term or sudden changes in food. The periodic crashes in the numbers of the South American guano birds have been documented since the last century, because the birds and the fish they eat are commercial assets (Idyll 1973). Three seabird species breed in huge numbers off Peru in the rich cold waters of the Humbolt current. In the poor warm waters beyond, other seabirds occur in the low numbers which are typical of tropical seas. In certain years, the warm waters come further south than usual, and envelope the Peruvian guano islands. Then the abundant plankton disappears, as does the anchovy *Engraulis ringens* which supports the seabirds, and millions of birds are found dead from starvation. Declines from 27 million to 6 million birds occurred between 1957 and 1958; after which numbers increased steadily to 17 million in 1965, when the current again shifted, causing another decline in fish, and another crash in bird numbers to 4.3 million. There was no evidence of unusual disease or predation at the time of the crashes, but in recent years human overfishing may have slowed the recovery. A smaller concentration of guano-producing seabirds, with similar conditions of cold water rich in plankton, and with similar periodic disasters due to shifts in currents, occurs off South West Africa (Lack 1954). Many other examples of long-term or sudden changes in bird populations and their food can be found in ornithological journals, though mostly at the anecdotal level.

Such studies suggest that food limited numbers at different levels in different periods, and that sudden declines in numbers were caused by sudden declines in food; in some cases (as in the seabirds), other factors, such as disease and predation, were taken into account, and excluded as being important. At best, these events fall into the category of natural experiments, but they lack controls, and one cannot exclude the possibility that some unknown limiting factor changed at the same time. Thus, in British seabirds, the increase since the last century could well be due to food (which for some species is known to have increased), but it is hard to eliminate another frequent explanation, that such birds have been recovering from human persecution in the past.

2.3.2. Measurements on the birds themselves

At least five types of data on the birds themselves have been used as evidence that food limits bird numbers: (a) deaths from starvation; (b) low weights and poor body condition; (c) low daily food intakes and feeding rates; (d) large proportion of available time spent feeding; (e) fighting over food. Each type of evidence by itself is no more than suggestive, and must be combined with other information to make a case. There are also pitfalls in the use and interpretation of such data, as discussed below.

Deaths from starvation. Proximate causes of mortality have been studied in birds, often on the erroneous assumption that they alone would indicate what limits numbers. The presence of starving individuals has been cited as evidence for population limitation by food-shortage (Lack 1954), and their frequency through the year has been used to indicate the times when food was scarcest (Goss-Custard *et al.* 1977).

Most direct information on mortality causes in birds comes from autopsies of birds found dead (*e.g.* Jennings 1961), or from the recoveries of ringed birds, in which the cause of death was given (*e.g.* Glue 1971). In most such data, star-

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vation was so infrequent that it was not even listed separately, and where it was, it was held responsible for only a minority of recorded deaths. For example, only 3 per cent of 231 Bald Eagle *Haliaaetus leucocephalus* deaths in the United States were attributed to starvation, and only 3.6 per cent of 1051 Mute Swan *Cygnus olor* deaths in Britain (Reichel *et al.* 1969 *et seq.*, Ogilvie 1967). In fact, most evidence for starvation in temperate zone birds has come during hard winters, chiefly among song-birds, waterfowl and waders (Ash 1957, Dobinson & Richards 1964, Trautman *et al.* 1939, Ogilvie 1967). With such data, there are difficulties in finding the true incidence of starvation, in deciding whether it is an ultimate or merely a proximate cause of death, and in assessing its role in population limitation. Records of deaths are usually biassed towards mortality associated with human activity, whereas much "natural" mortality goes unobserved. Even when the manner of death is known, the underlying cause may not be obvious. Thus a bird may be excluded from a favourable area by territorial behaviour, become short of food, and succumb to disease. In this case, the ultimate cause of death is socially induced starvation, but the observer may record only the proximate cause, disease. This kind of situation led to wrong conclusions being drawn about population regulation in Red Grouse, in the Grouse Enquiry of 1911 (Moss & Watson 1970). Even if the numbers of birds which starve is equal to the number lost from the population, it does not follow that starvation caused the decline in numbers. These may be birds of low social status which form a doomed surplus destined to die anyway, whether by starvation or not. This, rather than the proximate factors which may be present at the time, may be the important process. Inadequate food can also affect density in the longer term through influencing reproduction or the type of offspring produced, and need not necessarily cause starvation of full grown birds (see Watson & Moss 1972 for Red Grouse, Newton 1977 for geese). Hence, for starvation to be shown relevant to population limitation, knowledge of its seasonal incidence must be combined with other information, on numbers, social behaviour or recruitment through the year.

Weights and body-composition. In theory, data on weights and body-composition through the year serve the same purpose as data on starvation, in indicating periods when feeding is difficult. But they can also be misleading, and need interpreting with care.

In the north temperate zone, small birds are generally heavier, with more fat and protein in their bodies, in winter (when food is scarce) than in summer (when food is plentiful) (King & Farner 1966, Newton 1972). This has been attributed to the need for greater reserves in winter to survive the long, cold nights. In the milder months, weights also fluctuate according to the stage of breeding, in females increasing before egg-laying and in both sexes declining during the nestling period (Newton 1972, Bryant 1975). Evidently factors other than available food influence weights, and some of the lowest weights occur at times of apparent plenty. Also, even the heaviest individuals may die within one or two days if food becomes scarce. So starving birds are not present for long and, if they form only a small percentage of a population at one time, they may be hard to detect in a sampling programme. Their percentage in a population may rise at particularly difficult times, as during a cold spell, but if the population is not sampled on the days concerned, they may again be missed. Hence, with small song-birds, the scarcity of underweight individuals in trapped samples does not necessarily indicate that food is plentiful or that starvation is rare.

There is more chance of detecting difficult periods for large birds because under-weight individuals survive for longer, and are therefore more liable to be sampled. Birds as large as geese can survive for weeks on reduced rations (Newton 1977), so all the birds in a population might be underweight at one time, yet recover later. Hence, the interpretation of weight data should depend on the type of bird involved, and the stage in the annual cycle; at best it can only indicate periods of food-shortage, and the individuals most affected.

Feeding rates and food intake. Sometimes such measurements indicate that birds are obtaining less food per day than they need to maintain their weight, so that if this continues for long enough

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they will starve. For example, at certain seasons, Ward (1965) found that some of the *Quelea* which he collected as they arrived at roost had begun the night with an insufficient reserve of crop food and body fat to last till morning. It seemed reasonable to conclude that such birds would have died, and that changes in the proportions of underfed birds in the total sample through the year could be used to indicate periods of food-shortage.

Measurements on feeding rate in the field have also been used to indicate periods of difficulty. As food density declines, so does the rate of intake, until a bird can no longer obtain its daily needs in the time available (Fig. 5). Not all individuals are affected similarly, for some feed less efficiently than others, either because they are inexperienced or subordinate (Orians 1969, Goss-Custard 1977). As individuals become affected over a period of time, they either starve or move away, so that numbers in that locality are reduced by food-shortage. This kind of evidence has been produced for Woodpigeons feeding on grain and clover (Murton 1968) and for various waders feeding on estuarine invertebrates (Goss-Custard 1969, 1977). At best it can indicate the proportions of birds in difficulties at different seasons in the locality concerned, and the age, sex, and social status of the individuals involved. Whether bird numbers are reduced over a wider area depends on whether the emigrants find alternative feeding places or whether they do not and starve.

Proportion of time spent feeding. Data of this type, collected through the year, have been used to define the periods when birds spend most time feeding, and thus by implication when they have greatest difficulty in meeting their food needs. It has also been argued that, if birds spend practically the whole day feeding for themselves, they must be near the food limit (Lack 1954). When breeding, many birds forage for long periods to collect food for young.

Such data have been obtained either by watching particular individuals for long periods (Gibb 1956), or by frequent scanning of feeding flocks and each time counting the proportion of birds that were feeding (Goss-Custard *et al.* 1977). Only by the first method can individual birds be compared, whereas the second method gives average values for a population, provided that feeding and non-feeding birds are equally visible. Most temperate zone species that have been studied have been found to spend more time feeding in winter than in autumn or spring. In mid-winter, this proportion rose to 90 per cent or more of the daylight hours in various tit species (Gibb 1954, 1960), and to 95 per cent or more in Woodpigeons and various waders (Murton *et al.* 1966, Goss-Custard *et al.* 1977). For Rooks *Corvus frugilegus*, however, food was scarcest in mid-summer when birds spent more than 90 per cent (equivalent to 15 hours) of the daylight feeding (Feare 1972). For all these species, the seasonal change in feeding routine paralleled seasonal changes in measured food-stocks.

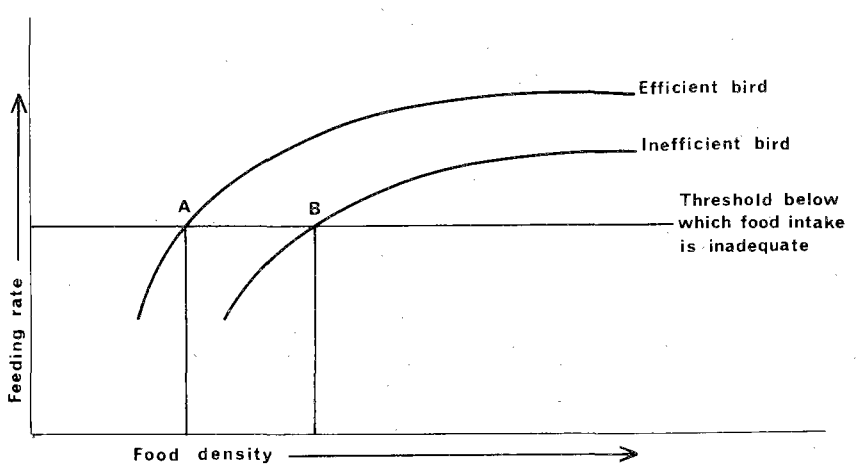


Fig. 5. Theoretical response curves showing feeding rate in relation to food density for efficient (upper curve) and inefficient (lower curve) individuals respectively. The food density below which an adequate intake cannot be maintained is given by the vertical lines from A for an efficient bird and B for an inefficient one. Modified from Murton (1968), based on data collected on Woodpigeons feeding on grain and clover.

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Such data on their own do not prove food-shortage, however, because they give no indication whether the birds succeed or fail in their attempts to get enough food. Moreover, in some kinds of birds, a tendency to feed for only a short time each day does not necessarily indicate that all is well. Certain herbivorous birds might fill their crops in a short time, but may then be unable to digest the food well enough or fast enough to maintain body-weight (*e.g.* Kenward & Sibly 1977). In some raptors, hunting periods may be hard to define, and food might be obtained in only a few minutes of intense activity, yet not frequently enough to keep the bird alive. Hence, information on feeding periods are of use in some species, but not in others, and the results will normally do no more than pinpoint the difficult periods.

Fighting over food. Birds often fight over food items or feeding places, and measurements of fighting through the year have been used to indicate difficult periods. In some cases, the study was broadened to include other kinds of interactions which lower feeding rates, such as birds avoiding or paying more attention to one another. Several studies showed that birds interacted over food more in winter than in spring or autumn, or more as their density rose (Gibb 1954, 1960, Goss-Custard 1977). In some cases the harmful effects fell more heavily on the young or subordinate individuals, as shown for Juncos *Junco hyemalis* by Fretwell (1969).

There are several problems with this type of information. For one thing, fighting may be more related to the distribution or type of food than to its total amount. In Rooks, Patterson (1970) found that much more fighting occurred during snow periods, when birds were concentrated (*i.e.* close together) in limited places, than in summer, when food was scarcer but more scattered and when most mortality occurred. Fighting may have regulated density in particular places, but had no bearing on limiting total numbers if alternative places were available, or if different individuals fed at different times. Likewise, the incidence of food robbing may be more related to the size of food-morsels than to other factors. Food robbing was rare when tits took small items that could be swallowed quickly, but increased greatly when they took large items, which had to be manipulated before being swallowed, thus giving more opportunity for food robbing to occur (Gibb 1954, 1960). In various seed-eaters, aggression did not increase, but decreased, when food became scarce, because feeding took priority (Pulliam *et al.* 1974). Caraco (1977) obtained the same result by supplementing the natural food of wintering Yellow-eyed Juncos *J. phaeonotus* — time spent feeding decreased, while time spent fighting increased. Hence, again there are difficulties with this kind of information, and each case should be assessed carefully.

It has also been argued that the very occurrence of fighting for food can be taken as evidence that food is limiting, for there would otherwise be no point in the birds wasting time and energy (Lack 1954). This argument is probably invalid, however, for it would be advantageous for an individual to fight whenever it could obtain food more easily that way than by seeking it elsewhere (providing there was no strong counter selection).

In conclusion, all these various measures on the birds themselves have often proved useful in indicating the times of year when feeding was difficult, and in certain cases the proportions and types of birds that were worst affected. All four kinds of information are more useful for certain species than for others, and in any case must be interpreted with caution. To assess any possible impact of food-shortage on the population, other data — for example, on seasonal changes in numbers — are also needed. Existing results would also have been more valuable if they had been obtained after predicting them from some previous independent data suggesting food-shortage, rather than being collected along with a variety of observations all made at the same time, and interpreted retrospectively.

2.3.3. Measurements on the food-supply

Many northern birds have a more or less fixed amount of food to last them through the winter, with little or no replenishment of stocks until the spring. This applies, for example, to seed-eaters and to many insectivores. For some species, it has proved possible to measure the standing crop

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of food, and the extent to which it is depleted through the winter. If the birds remove a "considerable proportion", the argument goes, they are more likely to be up against a food limit than if they remove only a small proportion.

In several species, for which such measurements were made, food-stocks were depleted by more than 50 per cent during winter, and in other species, by more than 90 per cent (Lack 1954, 1966). Other studies showed that the food of certain birds largely disappeared over winter, though no estimate was obtained of the proportion eaten by the birds themselves. For Bullfinches *Pyrrhula pyrrhula* in an English wood, practically all the seeds disappeared in years of poor seed production, but only a small proportion in years of good production (Newton 1972), and the same was true for various sparrows in Arizona (Pulliam & Parker 1979). If these seed-eaters were food limited, therefore, this was likely only in the poor years.

Results from winter studies often contrast strikingly with those on other species from summer, when prey are more abundant and reproducing. In most data in the literature, birds took less than 10 per cent of potential food in the breeding season, but occasionally up to 37 per cent (see Lack 1954, 1966 for examples). Many summer data were collected during insect plagues, however, when it was not surprising that insectivorous birds took a negligible proportion.

Measurements on food stocks, like those on the birds themselves, can usually do no more than define the periods when food is scarcest. There are also problems in measuring certain kinds of food accurately, and with the interpretation of existing data. In some cases the total stock of food was estimated, but no indication was given of what proportion was available to the birds — a proportion which may have varied with environmental conditions. Second, while for some birds all known foods were assessed, in others only favoured or particular foods were assessed. It was always possible that, when favoured (or known) foods were finished, the birds could turn to alternatives, perhaps previously unknown to the observer. Third, it was not usually known how much food the birds had to remove before they got into difficulties, and even if they removed nearly all their food, they might still have survived. Alternatively, only a small reduction in food density may have been enough to reduce the birds foraging efficiency below the level necessary for survival.

This is especially so for herbivores, such as tetraonids, which often appear surrounded by food, but feed selectively on the most nutritious items (Watson & Moss 1979). Such birds normally remove a tiny fraction of the food available (about 2 per cent in Red Grouse, Savory 1978) if food is defined as the total quantity of leaves, shoots, buds and fruits present. However, preferred plants often show obvious overgrazing, while other plants nearby remain untouched (*e.g.* Seiskari 1962). If it can be assumed that only these preferred plants provide food adequate for survival, then overgrazing of these could be important. This raises the related point that plants might respond to heavy grazing by reducing their nutrient content or by increasing the chemicals that make the plant unpalatable or indigestible, thus reducing the "real" food-supply even further (Schultz 1964, Haukioja & Hakala 1975). Moreover, for some herbivores, the efficient exploitation of a particular food requires changes in behaviour, gut anatomy and gut flora. Woodpigeons take 10—15 days to acclimatise to a diet of brassica leaves, so are unable to cope with a quick change in diet without loss of body condition (Kenward & Sibly 1978). Sudden changes in diet occur mainly after snowfalls, when previous foods become unavailable.

While the proportion of food removed usually gives no indication of whether food is limiting, this statistic may sometimes be useful in showing how close are the birds to the food-limit. If it is found, for instance, that birds already remove more than 90 per cent of their food, and that no apparent alternatives are available, then a big increase in bird numbers is clearly not possible. In many cases, however, the proportion of food removed may be less than 20 per cent, in which case other information is needed in order to predict whether further increase in numbers would be possible. It would also be important to determine whether the decline in food was due to the birds themselves, or to something else (other animals or weather). If it was due to the birds

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then larger numbers would lower food density further, increase competition, and cause more losses. If it was due to something else extra birds might be accommodated without worsening the situation.

In conclusion, measurements on the food-supply can normally do no more than measurements on the birds themselves, and indicate likely periods of difficulty. Again, they are more use on some species than on others, and special care is needed with species that feed selectively on vegetation. Before they can give a clue on the effects of food on numbers, periodic counts of birds are also needed — for example: (a) if within one year a conspicuous drop in food-stocks coincided with a conspicuous drop in numbers or a low point in the population cycle (for *Quelea*, see Ward 1965), or (b) if annual variations in winter food-stocks correlated with annual variations in losses of birds (for Coal Tit *Parus ater*, see Gibb 1960). Such evidence would be still correlative, however, and could not be taken as conclusive.

2.4. CIRCUMSTANTIAL EVIDENCE, FOLLOWED BY EXPERIMENT

Most of the evidence so far given above for particular species is of two types: (a) a correlation in space or time between changes in bird numbers and changes in food-supplies; or (b) a coincidence in one area between a period of population decline and a period of apparent food scarcity, as defined by measurements on the birds themselves or on their food (Table 4). Such events may occur because change in food is (a) a sufficient condition to account for population change, (b) a necessary condition to account for population change, (c) a non-causal factor associated with the important causal factor, or (d) a completely spurious association, not in any way linked directly or indirectly with change in

Table 4. Evidence for population limitation by food-shortage in various bird-species that have been studied in detail

Rook *Corvus frugilegus* in northeast Scotland, (Feare 1972, Feare *et al.* 1974).	Population at lowest density, and spread over largest area, in mid-summer. At this time food-stocks were minimal, because of a reduction in the numbers of fields in which birds could feed, an absence of grain, and the disappearance of large invertebrates (earthworms and tipulid larvae) from the soil surface. Associated with high mortality (especially of juveniles) and low weights, and with lower feeding rates (150 cals/day) and longer feeding periods (90 per cent of daylight, or 15 hours) than at any other season. Another potential food-shortage occurred during periods of deep snow in winter, when birds competed for space at localised feeding sites; however, the birds then spent only 30 per cent (3 hours) of the active day feeding, and obtained 240 cals per day.
Red-billed Dioch *Quelea quelea* in Nigeria, (Ward 1965).	Period of sudden population decline (due partly to emigration) coincided each year with temporary shortage of food, when grass seeds germinated at the onset of the rains. Starved and underfed birds were most prevalent then.
Coal Tit *Parus ater* in southeast England, (Gibb 1960).	Over five years, a close correlation was found between winter bird density and winter foodstocks (invertebrates on foliage): survival from October to March varied greatly from year to year in relation to measured food-stocks. During this period, the birds ate around 50 per cent of several main prey species, and in mid-winter spent more than 90 per cent of the day feeding.
Wood-pigeon *Columba palumbus* in southeast England, (Murton *et al.* 1964, 1966).	Period of population decline in winter coincided with depletion of grain, then clover stocks. The lowest bird densities, low weights, low feeding rates, and most starving birds occurred in late winter, when clover stocks were minimal. Temporary food-shortages occurred during periods of deep snow, when the birds were concentrated on localised brassica sites.
Red Grouse *Lagopus l. scoticus* in northeast Scotland. (Jenkins *et al.* 1967, Lance 1978, Miller *et al.* 1966, 1970, Moss 1969, Watson & Moss 1972).	Greater mean breeding densities and success on moors overlying base-rich rock than on moors on base-poor rock, corresponding with greater nutrient content of heather on base-rich areas. Within areas, an inverse correlation between the territory-size of individuals and the nitrogen content (taken to reflect nutritive value) of the heather in each territory. Also, an increase in breeding density, following the experimental fertilising or burning of areas of heather (the food-plant), when compared with densities on nearby control areas.

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numbers. One way to disentangle such relationships in seeking causal evidence is by experimental alteration of the food-supply, and monitoring the response of the population against an appropriate control.

In Red Grouse, burning or fertilising areas of heather (the food-plant), promoted an increase in breeding density one year later over the previous level, as well as over that in control areas nearby (Miller *et al.* 1970). This occurred when the experiment was started in years with low or moderate densities, but in a later trial, fertilising an area failed to halt a big decline (Watson & Moss 1979).

Another experiment involved the provision of food (sunflower seeds) to tits in winter to find whether it increased the numbers breeding in the wood next spring. By comparison with control areas, the numbers of Blue Tits *Parus caeruleus* breeding were increased after this treatment, but the numbers of Great Tits were not (Krebs 1971). This may have been because Blue Tits were limited in breeding density by the winter food-supply, while Great Tits were limited by some other factor. Other experiments, involving the provision of extra food to Great Tits, were described by Von Haartman (1973) and Van Balen (this symposium), both of whom concluded that, in their situations, food did increase survival and subsequent breeding density.

In another experiment, extra food (hen's eggs and chicks) was put out for Carrion Crows *Corvus corone* throughout winter and spring, to find whether territories would shrink and extra pairs would settle (Yom-Tov 1974). This did not happen, although the food was taken, and nest-sites were present in excess. So this experiment went against the idea that food regulated breeding density in Crows in a direct and simple way. However, it may have been unreasonable to expect a sudden increase in a bird such as this, in which individuals are long-lived and territories normally remain stable for years, despite some fluctuation in natural foods (Charles 1972). The result might have been different if food was provided over a longer period (and not just in one winter and spring), or if the existing birds had been removed to enable different ones to settle (though this could have introduced other complications).

Because of cost or practical difficulties, this kind of experiment can be done only on certain birds. It is surprising, however, that the reverse experiment of reducing the food (for example by use of insecticides or herbicides) seems not to have been tried. Such experiments provide as good evidence for food limiting numbers as we are likely to get, but even when a positive result is obtained, there is still the possibility that some unknown limiting factor changed in parallel with food, and caused the change in numbers. They are an improvement over observing natural changes, however, because in experiments it is the observer who brings about the change. Such experiments need careful fore-thought, however, including a knowledge of the bird's annual cycle of numbers and behaviour, so that the change in food can be made at an appropriate time. And where extra food is provided directly, care must be taken to ensure that the food provided is not unsuitable or nutritionally inadequate. Finally, even if a clear-cut result is obtained, allowing the conclusion that change in food changed numbers, it is not of course safe to assume that all changes in nature are due to changes in food. Food may be sufficient for some changes, but not necessary to explain them all.

3. BIRDS NOT LIMITED BY FOOD

This last section mentions some populations which seem to be limited by factors other than food. Like food, nest-sites can be considered as a resource, and are thus in contrast to disease and predation which may hold numbers below the level at which they are limited by any resource, as may various human factors, such as pesticides. Numbers are sometimes said to be limited by snow or other bad weather, but this usually acts through reducing the availability of food, and is thus not an independent factor in population limitation.

Nest-sites. The evidence that the breeding density of certain species is in some areas limited by shortage of nest-sites is of two types: (i) breeding pairs are scarce or absent in areas where nest-sites are scarce or absent, but which seem suitable in other respects (non-breeders

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may live there); and (ii) the provision of artificial nest-sites is sometimes followed by an increase in the number of breeding pairs. The species concerned mostly use special sites (such as tree-holes), and include Pied Flycatchers *Ficedula hypoleuca* Sternberg 1972), tits (this symposium), Kestrels *Falco tinnunculus* (Cavé 1968), and Wood Duck *Aix sponsa* (McLaughlin & Grice 1952). In some cases, it could be argued, nest-sites limited breeding numbers but not total numbers, but in practice the non-breeders could never increase indefinitely independently of the breeders. Some species not only increased in density, but also spread over thousands of square kilometres following the provision of nest-sites (*e.g.* Mississippi Kite *Ictinia misisipiensis* and other raptors which spread in western American grassland following tree planting, Parker 1974, Newton 1979). In all these cases, the food was present beforehand, but lack of nest-sites precluded breeding. Other aspects of habitat structure, involving cover or roosting sites, can also be considered as resources, occasionally limiting bird density (*e.g.* Nighthawk *Chlordeiles minor* home range sizes correlated with the number of flat roofs, used for nesting and display areas, Armstrong 1965).

Disease. Although knowledge of bird diseases has increased greatly in recent years, I have found no case in the recent literature in which endemic disease was held responsible for limiting numbers. However, occasional outbreaks caused heavy mortality in certain species, and introduced diseases may have eliminated some species of island birds and restricted the range of others (Warner 1968).

Predation. This has been repeatedly suggested as limiting the numbers of some gallinaceous birds, a view accepted by Lack (1966). It was found to be the main cause of winter loss in Red Grouse and Ruffed Grouse *Bonasa umbellus* and was often numerically important, especially in years of decline (Jenkins *et al.* 1963, Bump *et al.* 1947, Eng & Gullion 1962). However, it was apparently only the proximate rather than the ultimate cause of decline. Thus in Red Grouse predation was mainly on surplus birds excluded from territories, while in Ruffed Grouse the removal of predators had no obvious effect on the grouse population, comparing experimental with control areas (Bump *et al.* 1947). For these species, therefore, predation has not been conclusively shown to limit breeding densities.

There is less doubt about the influence of recent human predation on waterfowl numbers in some areas. Many North American populations increased or decreased from year to year in response to planned changes in shooting pressure (e.g. Hine & Schoenfield 1968). If populations were limited by some other factor, such as food, one would not expect them to respond so faithfully to change in shooting (though nothing is known of what limited their numbers beforehand). Persecution by man has been held responsible for the demise of several bird species, and in parts of Europe still seems to limit the numbers and distribution of some birds of prey (Newton 1979). On the other hand, human predation failed to reduce the breeding densities of Woodpigeons and other pest-species, while food-shortage apparently did so (Murton 1968).

Pesticides and pollutants. The use of organochlorine pesticides (such as DDT) has in recent years reduced the populations of some species below what their habitat would support (Ratcliffe 1970, Newton 1979). The bird-feeding raptors declined most (apparently because of greater food-chain concentration), and the Peregrine *Falco peregrinus* disappeared as a breeding bird from much of its range, including the eastern United States (Fyfe *et al.* 1976). Other species which suffered marked declines were the bird eating accipiters, such as the Sparrowhawk *Accipiter nisus* and Sharp-shinned Hawk *A. striatus*, and fish-eaters, such as the Osprey *Pandion haliaetus*. The declines were due mainly to reduced breeding rates, but in some populations also to increased mortality of full grown birds (Newton 1979). After restrictions in the use of these chemicals came into effect, the populations of these various raptors began to recover, but for two or three decades, they were apparently well below the level that the food-supply would have permitted.

4. DISCUSSION

When Lack (1954) proposed that the numbers of most birds were limited by food-shortage, his main lines of evidence were indirect, and not par-

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ticularly convincing. Most were mentioned above. One other argument was that, since there was little evidence that disease or predation were important in checking numbers, food-shortage must do the job. This is logical, but precisely what Darwin warned against in his advice "never to trust in science to the principle of exclusion" (Chitty 1967). Since Lack wrote, there has been an enormous increase in the available information, and some progress in understanding. In my view, the most important advance stems from a clarification of the value and relevance of different types of evidence, and the use of experiments to test the role of food.

The weakness of circumstantial evidence alone is that it remains open to explanations other than the one being offered. The proper testing of any hypothesis consists of trying to falsify it by experiment. To show that change in food (the cause) is both necessary and sufficient for change in population (the effect), we must have evidence of failure to find the cause without its effect, or the effect without its cause. If study shows that change in food is not necessary for change in population, we may be able to eliminate food from the relevant variables, or we may conclude that it is one of several factors that are sufficient to produce a change in population, without being necessary (indispensable). The conclusions permissible from experiments involving a change in food-supply are given in Table 5. The conclusions in boxes (1) and (4) of this table are tentative, because it remains possible that the next experiment could show the opposite outcome, but the conclusions in boxes (2) and (3) can be regarded as valid, so long as statistical and other methodological criteria are met.

A second advance of recent years has been a fuller appreciation of the role of social behaviour in population control, and of the need to focus on the ultimate, rather than on the proximate, causes of death. Whenever behaviour was studied, it was shown to be involved in the limiting process, through territorialism or other dominance hierarchies, which caused food-shortage to fall more heavily on the subordinate (often young) members of a population. In various tits and Red Grouse, territorial behaviour caused a sudden drop in density in the favoured habitat supposedly before food became scarce, and it seemed that the excluded individuals died in other habitats during the ensuing months (Jenkins *et al.* 1963, Kluyver 1970). In these species, territory sizes and population densities varied between areas, at least partly according to food. In flocking species, such as Woodpigeons and Rooks, the reduction in numbers occurred more gradually, while food-supplies were declining, or were at their seasonal low (Murton *et al.* 1966, Feare *et al.* 1974). Thus in any species, evidence on the role of food in population limitation requires information, not only on food-supplies, but also on numbers and social behaviour through the year.

A third advance has come from the growing realisation of the importance of quality, as opposed to mere quantity, of food. Wide variation in the nutritive value of vegetable foods is now well accepted, but some variation in animal foods would also be expected from the known differ-

Table 5. Conclusions permissible from experiments involving a change in food supply

Experiment	Response	
	Population increases	Population stays the same or decreases
Food increased	1 food is a sufficient or necessary explanation	2 (a) increased food is not sufficient to prevent a decline (b) reduced food is not necessary to cause a decline
Food decreased	3 (a) increased food is not necessary to allow an increase (b) reduced food is not sufficient to prevent an increase	4 food is a sufficient or necessary explanation

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ences in the body composition of prey organisms and the tendency that some prey have to produce harmful or distasteful chemicals. Thus, some progress in future studies could come from more careful definition of food and from further concentration on the more relevant aspects of it.

As might be expected food is by no means a universal factor limiting the breeding density or the total numbers of birds. Some species have been shown to be limited in certain areas by shortage of nest-sites, or to have been exterminated or restricted in range by some new disease, or by human persecution and pesticide use. Moreover, a given species may be limited by different factors in different areas, seasons or years.

Some fields of ecology have benefitted in recent years from mathematical modelling of one sort or another, but this has only just begun in the field under review. Most modelling of bird populations has so far been concerned with demography, trends and processes in populations, rather than with underlying mechanisms. The incorportation of food data into multi-factorial population models, in the way done for some insects, could provide the next step forward in understanding the interactions between bird populations and their food supply.

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6. SUMMARY

1. Food-shortage can be considerd limiting if it prevents a population from increasing. However, social behaviour and other mortality agents may also be involved in the limiting process. In any study, it is important to define the time period, because populations may be limited by different factors at different seasons, or in different years. It is also important to define the area, for food may limit local densities, but not total numbers if birds excluded from one area find food in another.

2. In seasonal environments, food is likely to be limiting only at certain times of year. It may limit numbers in a density-dependent or a density-independent manner, and need not necessarily entail any direct deaths from starvation. This is especially so (a) when social behaviour regulates local density in relation to food, and excluded birds succumb to other mortality, such as from disease or predation; or (b) when food-shortage lowers the breeding and recruitment rates, and thus the population density, without causing deaths of full-grown birds.

3. Indisputable proof that food limits a population is unattainable, and so we have to decide what will constitute acceptable evidence. Existing evidence might be graded as follows, in order of soundness:

(a) Circumstantial evidence, followed by experiment, in which a deliberate change in food-supply promotes a corresponding change in numbers, compared with trends in a control area, where food is not manipulated.

(b) Circumstantial evidence alone, useful for framing hypotheses which are open to experimental testing; of two main types: (i) where a drop in numbers coincides with one or more of the following: starvation, low weights, low feeding rates, long feeding periods, increased fighting, or depletion of food-stocks; (ii) correlations between bird numbers and food-supplies in different areas, or in different years in the same area.

(c) Indirect evidence, not open to experimental testing, such as the correlation between body weight and territory size among birds in general, or the existence of diet differences between species.

4. Data on mortality, weights, feeding rates, feeding periods, fighting and food-stocks are sometimes helpful in indicating likely periods of food-shortage, but on their own they provide no evidence on population limitation, and may be misleading.

5. Whenever social behaviour has been studied, it has been shown or suspected to be important in regulating density in relation to food, through territorialism or dominance hierarchies, both of which may result in mortality falling most heavily on the subordinate (often young) members of a population.

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