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POPULATION PROCESSES IN SOME BRITISH SEED-EATING BIRDS

by

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CHAPTER 1

REPORT OVERVIEW

The British populations of several species of seed-eating birds that feed on agricultural land have decreased during the last three decades. It has been suggested that this has been the result of changing agricultural practices, leading to reduced food supplies. Plausible explanations have been put forward as to why some species have declined while others have not. It is possible that the provision of supplementary food in gardens could be of benefit to those whose populations have suffered. This report aims to examine three areas relevant to that question by the analysis of the unique nationwide data banks held by BTO.

Chapter 2 reviews population changes in British seed-eating birds, their use of gardens, and the way in which the latter has changed. It reviews the explanations that have been put forward for the changes in numbers, or lack of them, species by species. Although the declines of some species can plausibly be explained in terms of changing agricultural practices, there is no evidence that more farmland species have declined than woodland species. However, species that commonly use gardens are less likely to have declined than those that have not.

Chapter 2 identifies six species for further consideration in the report. These species were chosen because they inhabit agricultural land and because we have enough information available from which to draw meaningful conclusions.

In Chapter 3 we consider the reproductive performance of these six species and how it has changed during the last three decades. Although the timing of breeding has changed in some of the species, this has not been associated with long-term changes in clutch size, even though clutch size is known to vary according to the date of laying within any one year. Changes in the number of nests lost before the young have fledged, a major determinant of the annual reproductive output, have been greater than those in clutch size. Greater losses in Linnets and Reed Buntings have occurred during the period when their populations have declined, while lower losses in Chaffinches, Greenfinches and Yellowhammers have occurred while their populations have been more or less stable. This suggests a causal link but, in contrast, Corn Buntings have declined but their nest losses have not increased. It is possible that nest losses could be influenced by food availability, so this further possible link fits in with the idea that the population declines have resulted from reduced food supplies.

Mortality of fledged birds is more difficult to study than is the production of those fledged birds. Ringing recoveries provide some evidence. We discuss the seasonal patterns of ringing recoveries in Chapter 4 and conclude that, although this evidence may be biased, it suggests that spring and even early summer may be a time of stress for seed-eaters. This is not surprising, since seed stocks are probably lowest in spring, before new seeds have been produced that will replenish the stocks after germination, rotting, and consumption have taken their toll.

Taken together, the evidence supports the view that some seed-eating birds have declined because agricultural changes have reduced their food supplies, that these birds may suffer food shortages in spring, and that this may cause some of them to breed less successfully. The provision of supplementary food in gardens could help some of these species by allowing them to enter the breeding season in good condition. For those individuals breeding in or near gardens, supplementary feeding could help even during the breeding season itself.

In Chapter 3, the analyses took regional and altitudinal differences into account. By carrying out more detailed analyses, relating changes in breeding success to the precise changes in agricultural practices in particular regions, it would be possible to reach much firmer conclusions. It would also be valuable to extend both the breeding and recoveries analyses to a much wider range of species, including insectivores, to produce more powerful comparative evidence.

An important consideration for further work in this area would be to bring together BTO data sets more comprehensively, to carry out detailed studies of the population dynamics of the various species using key factor analysis and to build proper population models. These would allow a deeper understanding of the reasons for population changes and of the potential impact of supplementary feeding.

It is intended that a modified version of Chapter 3 shall be published in the scientific literature. The finding in Chapter 2, that fewer seed-eaters that commonly use gardens have declined than those that do not, will be reported in BTO News and in the new Garden Bird Enquiry newsletter. The findings of Chapter 4 are too tentative to be published in the scientific literature but will be given prominence in BTO News and the Garden Birds Enquiry newsletter. Press releases will be made at the time of publication, which will be in early spring for the findings of Chapter 4.

CHAPTER 2

POPULATION TRENDS OF SOME BRITISH SEED-EATING BIRDS IN GARDENS AND THE WIDER COUNTRYSIDE

INTRODUCTION

Some species of seed-eating birds have declined in numbers in Britain. This has been attributed to changing food supplies resulting from changes in agricultural practices. Not all seedeaters, not even all those found on agricultural land, have declined but the differences can be related to differences in their feeding ecology (O'Connor & Shrubb 1986a). It is also important to consider the non-farmland habitats in which these species occur, use of which may be important in determining how their populations fare (O'Connor 1985, 1987). Some of them commonly occur in gardens, sometimes more commonly now than in the past, and it is tempting to believe that the provision of food by householders may be important for populations of these species. The main purpose of this chapter is to consider the changes in the national populations of these species and in their occurrence in gardens against the background of their habitat and feeding ecology, in order that the potential role of garden bird feeding in their population dynamics can be assessed. We have restricted our attention to the sparrows, finches and buntings (*Ploceidae, Fringillidae,* and *Emberizidae*), the typical small seed-eating birds of Europe. It should not be forgotten, however, that most of them take foods other than seeds. Furthermore, there are birds of other families for which seeds are an important component of the diet: the Skylark is a prime example and is yet another species for which agricultural changes provide an explanation of declining numbers (Marchant *et al.* 1990).

A secondary aim of the chapter is to provide a background for the other chapters of this report. These consider a subset of the species (the choice of which is explained in this chapter) and describe two aspects of their population biology for which data are available. The first is reproductive performance, particularly in terms of long-term changes that might explain long-term population trends. The second is the seasonal pattern of mortality, as reflected in recoveries of ringed birds, which may indicate what times of year are particularly stressful and whether food shortage at some times may be important.

DATA SOURCES

The two main sources of data are both BTO surveys. Each is based on the work of volunteers and are geographically biased (though to approximately the same extent) towards south-east Britain, where there are most volunteers, though we attempt to minimise this bias.

Population trends are based on the Common Birds Census (CBC), in which volunteers visit study plots on 10 occasions each spring and map the distribution of birds. From these maps, trained analysts assess the number of occupied territories of each species. There is some turnover of plots from year to year but most plots are surveyed for several years and comparison of numbers of territories on plots surveyed in two successive years provides an index of population change between years. By setting the population level at an arbitrary value of 100 in one year and by chaining together successive indices of proportional change, one can obtain an index of population levels for a period of years.

Most censuses are in farmland or woodland; only these habitats are considered here for most species, though data from other sites have been used where necessary. There have been 150 - 350 plots in total each year, with a total area of 5-12,000 ha. In habitat terms, the farmland plots are representative of farmland in the south-eastern quarter of Britain (Fuller *et al*. 1985) but, because observers choose their own plots, they may not be truly representative in ornithological terms, though the observers are asked to survey representative areas. The scheme and the effects of such possible biases are described more fully elsewhere (Marchant *et al*. 1990). These biases are unlikely to affect the broad conclusions discussed here.

For the Reed Bunting, census data are also available from the Waterways Bird Survey (WBS). This is similar to the CBC but covers linear waterways and their margins.

The Garden Bird Feeding Survey (GBFS) involves observers recording the peak number of birds of each species seen feeding in their gardens each week from October to March inclusive. To assess changing levels of usage, a mean peak count is calculated for each garden for each winter and the unweighted mean of these means used as a peak count index (PCI) for that winter. There are 200 participants each year, about one-third with rural gardens and two-thirds with suburban or urban gardens. Urban gardens are few and are included with suburban for analytical purposes. It is likely that the gardens are not a fully representative sample of all gardens, since GBFS participants are particularly enthusiastic bird-gardeners. The GBFS and its results have been described more fully in previous BTO Reports (Thompson 1987, 1988).

The report by Thompson (1988) covered CBC data up to 1986 and GBFS data up to 1986/87. The CBC graphs presented here include two further years' data but we have not incorporated further GBFS data: the gain in information would have been too slight in relation to the work involved. We have included CBC results for two species which were not included in the 1988 report and for seven species not considered in that report because they occur in gardens too infrequently for trends in their occurrence to be determined.

To provide an assessment of abundance, Table 1 shows estimates of breeding populations and wintering populations from other BTO surveys. The former are for Great Britain only, the latter for both Britain and Ireland. The table also shows the percentage of GBFS gardens in which each species occurs. This table and Figs. 1-14, which illustrate CBC and PCI trends for each species, should be used as the background for the individual species accounts that follow. Scientific names of all the species are shown in the table.

HOUSE SPARROW

This species is probably among the five commonest breeding in Britain and the ten commonest present in winter.

Its distribution is closely associated with man and it usually nests on or close to buildings, often semi-colonially. This makes it a difficult species to census using routine methods. As a result, information about its population trends is unexpectedly poor. Though Summers-Smith (1988) suggested that numbers have been stable (within 10%) during the period 1959-84, the CBC, which is the only systematic evidence covering much of the country, suggests a downward trend during the early 1980s (Fig. 1a),

Grain is an important component of the House Sparrow's diet (Hammer 1948, Keil 1970, Grun 1975) and it is possible that earlier burning and ploughing of stubbles (associated with increased acreages of winter, rather than spring, cereals (O'Connor & Shrubb 1986a)) may be responsible for any decline that there has been. However, this explanation does not fit with the apparently greater decline of House Sparrows in suburban gardens than in rural gardens.

House Sparrows occur in most British gardens and are rivalled in average abundance, as garden feeders, only by Starlings (Glue 1982, Thompson 1987). There is some evidence of a decline in the House Sparrow PCI for suburban gardens but not for rural gardens

(Fig. 1b), the difference in trend (measured by slopes of linear regressions) being statistically significant (P<0.01), though the decline in suburban gardens is very uneven. It is possible that the increasing Do-it-Yourself activities of householders has reduced the number of potential nest sites on houses. However, it is as difficult to come to clear conclusions about trends in the species' use of gardens as it is to come to clear conclusions about trends in its overall population levels.

House Sparrows are very sedentary, even during the non-breeding season (Lack 1988), so those occurring in gardens must belong to local breeding populations - in contrast to many other birds, which may move long distances outside the breeding season.

Because the population data for this species are so poor and the breeding data are not currently available in computerised form, we do not consider it further in this report.

TREE SPARROW

Numbers of Tree Sparrows in Britain are much less than 10% those of House Sparrows and they occur in only about 10% of gardens (Thompson 1987). The national breeding population has declined since the mid 1970s but the numbers feeding in gardens do not seem to have changed consistently, though they have fluctuated widely (Fig. 2). It is possible that the recent national decline has been the result of a decline in the abundance of arable weeds, the species being one of those that feeds extensively on arable land (Marchant *et al.* 1990). However, long-term data, derived from various BTO schemes, suggest that the species was even scarcer prior to the mid 1950s, after which its numbers increased rapidly for about 10 years (Summers-Smith 1988, 1989).

The reasons for these long-term changes are obscure but may include massive immigration from continental Europe (Summers-Smith 1989). Such immigration, for which there is good evidence, contrasts with the species' normally highly sedentary disposition: like House Sparrows, Tree Sparrows do not normally move far, so those feeding in gardens probably come from fairly local breeding populations. Tree Sparrows visit relatively few gardens and then mainly in cold winters (Thompson 1988).

The ecological differences between Tree and House Sparrows extend to diet: the former takes smaller seeds (fewer cereal grains and more weed seeds) and more animal food (Hammer 1948, Keil 1970, Grun 1975).

Because the Tree Sparrow occurs in only 11% of gardens, because it produces relatively few ringing recoveries, and because the breeding data have not been computerised, it is not considered further in this report.

CHAFFINCH

This is an extremely numerous and widespread species in Britain (Sharrock 1976, Lack 1986). It is probably the commonest British breeding bird and in the winter, with numbers swollen by continental immigrants, it is even commoner. Though primarily breeding in woodland, it is also common on farmland and in gardens, especially in winter. It takes a variety of seeds, including agricultural grain, but primarily smaller seeds of weed species (Newton 1972).

Chaffinch numbers, thought to have been reduced in the late 1950s through poisoning by organochlorine seed-dressings (Newton 1972), have increased steadily since the early 1960s, equally in woodland and farmland (Fig. 3a).

O'Connor & Shrubb (1983) suggested that Chaffinches have sustained themselves in farmland despite decreases in the availability of the weed seeds that are their major food source (Newton 1972) because they feed their young largely on insects. They also remarked that the species is one that resorts to stockyards to feed in winter, which may help to sustain populations. However, it may be that Chaffinch populations on farmland are simply sustained by immigration from woodlands, which are the species' main habitat.

Even though it was already occurring in 97% of GBFS gardens in the 1970s (Table 1), the Chaffinch has continued to increase in numbers in both suburban and rural gardens (Fig. 3b). Indeed, while the approximate doubling in the PCI in suburban gardens during 1970-86 is consistent with the rate of increase of the breeding population suggested by the CBC, the PCI for rural gardens has increased substantially more rapidly. (The difference between the slopes of the regressions for the two types of gardens is highly significant: $P<0.001$).

This greatly increased PCI may indicate a change in habits but it is not obvious why it should have been so much greater in rural gardens. Another possibility is that the number of winter immigrants has increased even more rapidly than that of breeding birds and that such immigrants make proportionately more use of rural than of suburban gardens.

BRAMBLING

The Brambling breeds in the northern forests of Scandinavia and Russia, nesting only irregularly and in small numbers in Britain (Batten *et al.* 1990). In winter it arrives from the continent in hugely varying numbers, from 50,000 to 2 million, depending on the availability of food in northern Europe (Lack 1986, 1988). In invasion years some gardens may attract Bramblings, often in association with Chaffinch flocks (Fig. 4). Their occurrence in gardens is pronounced only in years when the production of beech-mast (the species' major winter food) is poor (Thompson 1988), for otherwise they tend to stay in woodlands unless the weather is especially cold. Gardens that themselves provide beech-mast may be particularly favoured, but Bramblings certainly take seeds provided by householders and such supplementary feeding could be important in winters in which beech-mast is scarce. There has been no long-term trend in the PCIs (Fig. 4).

Since it scarcely breeds in Britain, since we have few ringing recovery data, and since it is so irregular in gardens, the Brambling is not considered further in this report.

SERIN

Serins occur in 32% of gardens in Spain and Iberia (Thompson & Greenwood 1991) and do occur in gardens in their few English localities. But they are extremely rare in Britain and hence clearly irrelevant to this report.

GREENFINCH

The Greenfinch ranks in Britain's 20 commonest birds in both summer and winter. Many visit gardens in winter and commonly breed in gardens and similar habitats, as well as on woodland fringes and clearings. Greenfinches also breed in farmland and, though they are not among the commoner farmland birds (Newton 1972), many of them use farmland for feeding in winter. The species feeds on a great variety of seeds, including cereal grains on farmland and peanuts in gardens (Newton 1972). The national population increased during the 1960s but has been fairly stable since then (Fig. 5a). It has been suggested (O'Connor & Shrubb 1986a,b, Marchant *et al.* 1990), however, that this stability may mask changes in the Greenfinch's ecological circumstances that result from agricultural changes: it may have benefitted from increased cereal acreage (clutch sizes are 14% larger in cereal-growing regions than where non-cereal crops predominate) and, perhaps even more, from increased production of oil-seed rape, which Greenfinches use in mid-summer, before cereal grains are available; on the other hand, cleaner harvesting, earlier ploughing, and the virtual cessation of winter stockyard threshing may have made life more difficult in winter.

Long-term trends in Greenfinch PCIs have been different in suburban and rural gardens (Fig. 5b, $P<0.001$). There is some evidence of a decline in suburban gardens in the early 1970s but numbers have been fairly stable since then. But in rural gardens they have tended to increase. This contrast between suburban and rural gardens may be a result of gardens generally being such a suitable habitat for Greenfinches that they are essentially full up, with rural gardens getting more only when birds are forced off farmland when food supplies become inaccessible through frost and snow (Newton 1972) or when farmland food runs out. Lack (1988) has pointed out that numbers of Greenfinches in the wider countryside tend to decline during cold spells even though the evidence suggests that they do not leave the country. It is thus possible that they are simply moving out of farmland into gardens during such bad weather, which would affect rural gardens more than suburban, just because they are closer to farmland. However, GBFS data show no obvious association between the occurrence of Greenfinches in gardens in each winter and the mean temperature of that winter (Thompson 1988), which seems contrary to Newton's suggestion that gardens are, at least in part, a hard-weather refuge for Greenfinches. On the other hand, if the birds were moving rapidly to and fro between the countryside and rural gardens in their search for food, this might not have much effect on the peak counts. Whatever the exact relationship between feeding in farmland and gardens, the sustained increase in occurrence of Greenfinches in rural gardens could well be a result of winter food for Greenfinches now being less abundant in farmland than previously.

Greenfinches have long exploited peanuts and other supplementary seed supplies in gardens (Newton 1972) and can commonly be seen feeding from hanging feeders, though, like House Sparrows, not best adapted to such behaviour. The spread of the Greenfinches' habit of feeding on the fruits of *Daphne mezereum* (Pettersson 1956, 1961) has been taken as a classic example of a new foraging habit developing in association with man, comparable to the opening of milk-bottles by tits (Fisher & Hinde 1949, Hinde & Fisher 1952) and other birds (Prŷs-Jones & Mead 1991), though there is some doubt about both the recency and the rate of spread of the habit (Snow & Snow 1988).

GOLDFINCH

The Goldfinch is substantially less common than the Chaffinch and Greenfinch in Britain and it is much less frequent in gardens. It has a similar habitat to that of the Greenfinch, though only locally breeding in gardens. Its diet is quite different from that of the Greenfinch, however, comprising primarily the small seeds of Compositae and of trees such as alder and birch (Newton

1972). Many Goldfinches move southwards in winter, even emigrating to continental Europe, especially in colder weather (Newton 1972, Lack 1988).

This species is believed to have done well during the agricultural depression of the first 40 years of this century, its population growth fuelled by increasing abundance of agricultural weeds (O'Connor & Shrubb 1986a). Goldfinch populations seem to have increased gradually through the 1960s and early 1970s but later to have declined somewhat, though the particularly marked drop in the CBC index for non-agricultural habitats may be rather unreliable, since Goldfinches occur on so few non-farmland plots (Fig. 6). That this species has fared better than the Linnet (see below) has been ascribed to its eating more tree seeds and seeds of Compositae, the latter surviving better in waste patches than do the more strictly arable weeds on which the Linnet specialises (O'Connor & Shrubb 1986a, b). The fact that it sometimes exploits conifer seeds (Shaw & Livingstone 1991) is probably irrelevant; the habit is too occasional and the distribution of the new conifer forests too geographically widespread to account for the Goldfinch's comparative success nationwide.

Since the Goldfinch rarely occurs in gardens and is not particularly associated with arable farmland, it will not be considered further in this report.

SISKIN

This is not a common species in Britain but its numbers have increased dramatically with the spread of conifer afforestation (Fig. 7a). It is a conifer woodland specialist, feeding on conifer seeds (see Shaw & Livingstone 1991 for a recent discussion), though moving onto seeds of plants growing in open ground when conifer supplies decline, onto birches in autumn, and alders in winter (Newton 1972). Large numbers move into Britain in winter, their movements being unpredictable in scale and direction (Lack 1988), but presumably in response to variations in available food.

As its overall numbers have increased, the Siskin has occurred more in gardens (Fig. 7b). Anecdotal evidence suggests that it is particularly attracted to peanuts hung in red mesh bags and surveys show that once Siskins have discovered that a particular garden is a good food source they will quickly learn to use it and thereafter do so consistently at the same time of year in successive years, so long as supplementary feeding continues (Spencer & Gush 1973). Because Siskins are forest specialists and still not common in gardens, they will not be considered further in this report.

LINNET

The national abundance of this species is intermediate between those of its relatives, the Greenfinch and Goldfinch. It breeds on rough ground with bushes, in which it nests, and on farmland, where it uses hedges for nesting. In winter it is found in a variety of open country, including farmland. Its chief food is the seeds of herbaceous plants that commonly comprise the weeds of cultivation (Newton 1972). It occurs in just a few percent of GBFS gardens.

O'Connor & Shrubb (1986a,b) have argued that the fortunes of the Linnet have been largely driven by those of arable weeds, linking its particular susceptibility to declining weed populations to the fact that the adults feed their nestlings as well as themselves on weed seeds, in contrast to many other finches, which feed invertebrates to the young. They argue that Linnet numbers increased during the agricultural depression of the first 40 years of the century, as crops became weedier, but that over the last 30 years Linnets have declined considerably (Fig. 8), in parallel with increased use of selective herbicides in cereal crops and a consequent decline in the supply of weed seeds. In cereal growing areas, Linnets seem to lose more of their chicks through starvation than do the Goldfinches which, as noted above, feed on seeds of plants whose abundance has probably diminished less (O'Connor & Shrubb 1986a). Especially in colder weather, Linnets move south and to the coast in winter (Lack 1988). Unlike Greenfinches, for example, they take refuge neither in stockyards nor gardens.

TWITE

Some farms in the Pennines and on the northern and western fringes of Britain have Twites as visitors but these birds mostly inhabit moorlands in summer and coastal areas in winter. They are very rare in gardens. We know nothing of any changes in their population levels. They are thus not relevant to this report.

REDPOLL

This species is less common than the Linnet in Britain but much more common than the Twite, to both of which it is closely related. It is a woodland species, associated through much of its range with northern birch and conifer forests, but breeding in scrubbier habitats than this in Britain, even in hedgerows and in young conifer plantations (Newton 1972). Like Linnets, Redpolls are infrequent in gardens. Birch seeds are an important food source; arable weeds are eaten but are very much less significant than for Linnets (Newton 1972).

The changing fortunes of the Redpoll in Britain (Fig. 9) are difficult to explain but, given its habitat and food preferences, are unlikely to have been influenced by agricultural changes. For this reason, and because Redpolls are so scarce in gardens, they are not considered further in this report.

CROSSBILL

This, and its close relative the Scottish Crossbill *Loxia scotica*, specialise on feeding almost exclusively on the seeds of conifers and are therefore largely confined to conifer woodlands (Nethersole-Thompson 1975). They rarely occur in gardens and even more rarely feed on supplementary food provided by householders, even in the Scottish highlands, though they are recorded not infrequently eating broken putty from windows (Nethersole-Thompson 1975) and, like Redpolls, they are attracted to gardens with water (D. Glue, pers. comm.). They are not relevant to the subject of this report.

BULLFINCH

This is a moderately common woodland species that also occurs in thick hedgerows and shrubby gardens. Bullfinches are well-known for feeding on buds (notoriously, those of fruit-trees) in spring, their main foods are the seeds and fruits of trees, shrubs, and various herbaceous plants (Newton 1972). They have declined in numbers since the mid 1970s, especially in farmland (Fig. 10a). The clearance of scrub and hedgerows may be one reason for this but Newton (1986) has suggested that it might be a result of increased numbers of Sparrowhawks *Accipiter nisus*. Because numbers in gardens are so low, the PCI values are subject to considerable error. Nonetheless, numbers in Rural gardens have declined in parallel with national figures (Fig. 10a). Those Bullfinches that do occur in gardens are probably local birds, as this is a sedentary species (Lack 1988). This species is not considered further, as it is not closely associated either with arable farming or with gardens.

HAWFINCH

The Hawfinch is scarcer than the Bullfinch both nationally and in gardens but, like that species, associated with damage in orchards: it is the only British bird capable of cracking cherry stones and commonly feeds on fallen cherries, apples and pears, and on buds and blossom earlier in the season. Its chief foods are the large fruits of woodland trees (Newton 1972). It may nest and feed in mature gardens but rarely takes supplementary foods (though Hawfinches sometimes demonstrate a fondness for peas in the pod). Its national population has been fairly constant (Fig. 11). By virtue of their woodland habitat and scarcity, Hawfinches are clearly not relevant to the subject of this report.

LAPLAND BUNTING

This is a very rare breeder on the tundra of the Scottish hills and a rare winter visitor to the British east coast. It is not relevant to this report.

SNOW BUNTING

This is a rare breeder on the high tops of Scotland and an uncommon winter visitor both to coastal areas and to the Scottish hills. It is not relevant to this report.

YELLOWHAMMER

This is the commonest British bunting. It is a bird of open country with some shrubs, and even of woodland, and thus flourishes on farmland. It feeds on a variety of seeds, fruits, and invertebrates (Sharrock 1976) but the large seeds of cereals and other Gramineae form the bulk of its diet, with invertebrates mainly being taken in summer (Prŷs-Jones 1977). It has been suggested that it has sustained its numbers in Britain (Fig. 12) only because increased cereal acreages have compensated for the reduction in stubble grains resulting from cleaner harvests and earlier ploughing (Marchant *et al.* 1990). Indeed, it has been suggested that Yellowhammers move into gardens in winter because of food shortages in fields (O'Connor & Shrubb 1986a). If so, such movements must involve only a small proportion of the population, for the species is found in few gardens. Unpublished BTO data show substantial declines in Irish Yellowhammer populations, centred on areas in which the proportion of tilled land is lowest, which fits in with this species flourishing where cereal grains are available.

CIRL BUNTING

Though this is a farmland species it is rare in Britain and therefore not relevant to this report.

REED BUNTING

Normally a bird of waterside habitats, this species spread into drier habitats during the 1950s (Kent 1964, Bell 1969), but this was a temporary change, probably as a result of overspill at high national population levels (Marchant *et al.* 1990). On farmland, weedy areas in crops are particularly important for nesting and Reed Bunting numbers (and their nesting success in wheat-growing areas) declined at the same time as cereals became less weedy (O'Connor & Shrubb 1986a; see Fig. 13a). Detailed studies of their diet show that Reed Buntings take many more small grass seeds and seeds of other weeds (and less cereal grains) than do Yellowhammers; they also take more animal food, especially in winter and spring (Prŷs-Jones 1977). It is striking, as Dr R P Prŷs-Jones has pointed out to us, that in both the House Sparrow/ Tree Sparrow and Yellowhammer/Reed Bunting species pairs it is the species that takes more cereal grains that has fared better and the species that takes more weed seeds and invertebrates that has fared worst; the former species may have benefitted from increased cereal acreages but the latter suffered from these crops being cleaner. There is good evidence that the ability of populations of these species to tolerate harsh winter climates is dependent on their access to food resources, which may be much influenced by human activity, especially cereal production (Prŷs-Jones 1984).

Reed Buntings now visit suburban gardens in much greater numbers than 20 years ago, though in rural gardens the increase has not been significant relative to the short-term fluctuations that have occurred (Fig. 13b: the difference between suburban and rural regressions is significant, P<0.001). In gardens, Reed Buntings will feed from hanging food containers but prefer to take food from the ground (JJDG pers. obs.). In contrast to the changes in garden abundance, after a recovery from the effects of hard winters in the early 1960s, the national population of this species has declined from the early 1970s onwards. The bird is largely a ground-feeder in the winter and seems susceptible to the effects of hard weather, which reduces the accessibility of food on the ground (Prŷs-Jones 1984). It is possible that part of the recent decline is a result of hard winters in the late 1970s and early 1980s, which may also account for the species' increased use of gardens in winter. Personal observations suggest that individual birds are faithful to particular gardens in winter and that small flocks may occur in some gardens but not in others that are nearby and in which food and water are provided just as abundantly. Such conservatism could lead to a species being slow to exploit a new feeding habitat, such as gardens with abundant supplementary food, but to a rapid increase in exploitation once the new habitat had been discovered. Thus the cold winters, by encouraging Reed Buntings to explore beyond their normal bounds, may have initiated a change in habits that has persisted.

CORN BUNTING

This is not a common bird and has become even less common in recent years (Fig. 14). Furthermore, it rarely occurs in gardens. Its ecology is not well understood but there is no doubting that it is very much associated with arable farming. Its fortunes ebb and flow with the acreage of barley (O'Connor & Shrubb 1986a), though the exact reasons for this are unclear. Because of its association with arable farming it is included in the further chapters of this report.

DISCUSSION

The fortunes of seed-eating birds have varied markedly, even if one considers only those that inhabit farmland. Some have declined, while others have maintained more stable populations or increased. The interpretations that can be placed on these different patterns, in terms of changes in agricultural practice, are more or less convincing but all depend merely on broad correlations. We note, furthermore, that some woodland species have also declined. More detailed investigations of the ecology of individual species would throw further light on these problems but would have the disadvantage that they could not be retrospective, which reduces their potential value in explaining what has happened in the past. Another way of approaching the matter, which we take up in Chapter 3, is to use information from BTO surveys other than those discussed already to illuminate population processes in these species. These suffer from being extremely broad in their approach, not having been designed specifically with these species or these particular problems in mind. But they have the advantage of having been gathered over a long time, covering the period during which the population data were gathered.

The accounts above have also shown that the seed-eaters vary considerably both in the use they make of gardens and how this level of use has changed. It is possible that supplementary food in gardens is important for some of them. Note that species that commonly use gardens tend to have increased or kept their populations level (Chaffinch, Brambling, Greenfinch and Siskin - but not Reed Bunting and possibly not House Sparrow), whereas those that do not use gardens much tend to have declined (Tree Sparrow, Goldfinch, Redpoll, Bullfinch and Corn Bunting - but not Yellowhammer). However, while it is almost certain that the provision of supplementary food is greatest in winter, it is not clear whether this is the period when the birds are most stressed. This is another area on which BTO data can shed some light (Chapter 4).

To summarise, the species chosen for further study in this report are as follows.

Chaffinch and Greenfinch: very common and fairly common species respectively, both having fairly stable populations; increasingly common in gardens.

Yellowhammer: fairly common with fairly stable population, but scarce in gardens.

Linnet: fairly common but declining; scarce in gardens.

Reed Bunting: less common and declining, but increasing in some gardens.

Corn Bunting: scarce, declining, rare in gardens.

SUMMARY

This chapter is mainly based on the results of two BTO surveys, which have indexed population levels and usage of gardens by birds in Britain since 1962 and 1970 respectively. It reviews the changing fortunes of all British sparrows, finches, and buntings. Population changes (or lack of them) can be explained, for the predominantly farmland species, by their individual ecologies in relation to changing agricultural practices, though further studies are needed to investigate such explanations more deeply.

REFERENCES

Batten, L.A., Bibby, C.J., Clement, P., Elliott, G.D. & Porter, R.F. 1990. *Red Data Birds in Britain.* T. & A.D. Poyser, London.

Bell, B. 1969. Some thoughts on the apparent ecological expansion of the Reed Bunting. *British Birds* 62: 209-218.

Fisher, J. & Hinde, R.A. 1949. The opening of milk bottles by birds. *British Birds* 42: 347-357.

Fuller, R.J., Marchant, J.H. & Morgan, R.A. 1985. How representative of agricultural practice in Britain are Common Bird Census farmland plots. *Bird Study* 32: 56-70.

Glue, D. 1982. *The Garden Bird Book.* Macmillan, London.

Grun, G. 1975. Die Ernährung der Sperling *Passer domesticus* (L.) und *Passer montanus* (L.) unter Verschiedenen Unweltbedingungen. *Int. Stud. Spar. 8:* 24-103.

Hammer, M. 1948. Investigations on the feeding habits of the House Sparrow (*Passer domesticus*) and the Tree Sparrow (*Passer montanus*). *Dan. Rev. Game Biol. 1(2):* 1-59.

Hinde, R.A. & Fisher, J. 1952. Further observations on the opening of milk bottles by birds. *British Birds* 44: 393-396.

Keil, W. 1970. Untersuchungen zur Ernährung von Haus- und Feldsperling - *Passer domesticus* und *Passer montanus* in einem Getreideanbaugebiet in Winterhalbjahr. *Luscinia 41:* 76-87.

Kent, A.K. 1964. The breeding habitats of the Reed Bunting and Yellowhammer in Nottinghamshire. *Bird Study* 11: 123-127.

Lack, P.C. 1986. *The Atlas of Wintering Birds in Britain and Ireland.* T. & A.D. Poyser, Calton.

Lack, P.C. 1988. The Winter Atlas in Britain and Ireland; a review of the methods, and the movements of the finches, buntings and sparrows. *Sitta* 2: 3-20.

Marchant, J.H., Hudson, R., Carter, S.P. & Whittington, P. 1990. *Population Trends in British Breeding Birds.* British Trust for Ornithology, Tring.

Nethersole-Thompson, D. 1975. *Pine Crossbills.* T. & A.D. Poyser, Berkhamsted.

Newton, I. 1972. *Finches.* Collins, London.

Newton, I. 1986. *The Sparrowhawk.* T. & A.D. Poyser, Calton.

O'Connor, R.J. 1986. Dynamical aspects of avian habitat use. In *Modelling Habitat Relationships in Terrestrial Vertebrates*. Eds. J. Verner, M.L. Morrison & C.J. Ralph, pp. 235-240. University of Wisconsin Press, Madison.

O'Connor, R.J. 1987. Organisation of avian assemblages - the influence of intraspecific habitat dynamics. In *Organisation of Communities Past and Present*. Eds. J.H.R. Gee & P.S. Giller, pp. 163-183. Blackwell Scientific Publications, Oxford.

O'Connor, R.J. & Shrubb, M. 1983. Some effects of agricultural development on British bird populations. *Proc. Symp. Birds & Man, Johannesburg 1983*: 131-152.

O'Connor, R.J. & Shrubb, M. 1986a. *Farming and Birds*. Cambridge University Press: Cambridge.

O'Connor, R.J. & Shrubb, M. 1986b. Recent changes in bird populations in relation to farming practices in England and Wales. *Journal of the Royal Agricultural Society of England* 147: 132-141.

Pettersson, M. 1956. Diffusion of a new habit among Greenfinches. *Nature* 177: 709-710.

Pettersson, M. 1961. The nature and spread of *Daphne*-eating in the Greenfinch, and the spread of some other habits. *Animal Behaviour* 9: 114.

Prŷs-Jones, R.P. 1977. Aspects of Reed Bunting ecology, with comparisons with the Yellowhammer. D.Phil. Thesis, University of Oxford.

Prŷs-Jones, R.P. 1984. Migration patterns of the Reed Bunting *Emberiza schoeniclus schoeniclus*, and the dependence of wintering distribution on environmental conditions. *Le Gerfaut* 74: 15-37.

Prŷs-Jones, R. & Mead, C. 1991. Birds, milk, and *Campylobacter*. *The Lancet* 337: 975.

Sharrock, J.T.R. 1976. *The Atlas of Breeding Birds in Britain and Ireland*. British Trust for Ornithology, Tring.

Shaw, G. & Livingstone, J. 1991. Goldfinches and other birds eating sitka Spruce seed. *BTO News 174*, 8-9.

Snow, B. & Snow, D. 1988. *Birds and Berries*. T. & A.D. Poyser, Calton.

Spencer. R. & Gush, G.H. 1973. Siskins feeding in gardens. *British Birds 66: 91-99*.

Summers-Smith, J.D. 1988. *The Sparrows*. T. & A.D. Poyser, Calton.

Summers-Smith, J.D. 1989. A history of the status of the Tree Sparrow *Passer montanus* in the British Isles. *Bird Study* 36: 23-31.

Thompson, P.S. 1987. The seasonal use of gardens by birds with special reference to supplementary feeding. Unpublished BTO Research Report No. 27.

Thompson, P.S. 1988. Long-term trends in the use of gardens by birds. Unpublished BTO Research Report No. 32.

Thompson, P.S. & Greenwood, J.J.D. 1991. Birds in European Gardens in the Winter and Spring of 1988-89. Unpublished BTO Research Report No. 53.

Table 1 British populations and frequency of occurrence in gardens of Ploceidae, Fringillidae, and Emberizidae.

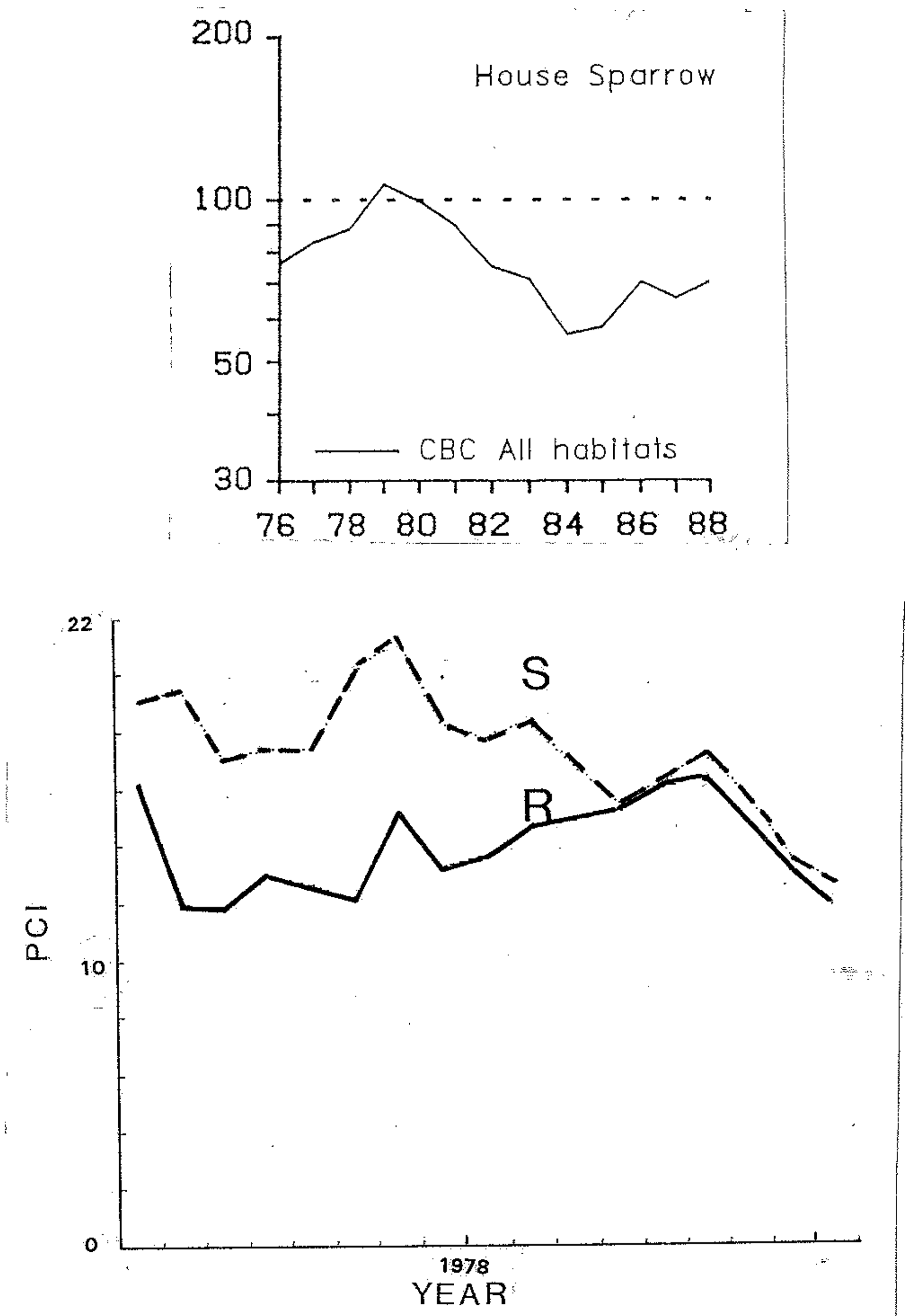
	Breeding Population (pairs)	Wintering Population (birds)	Percentage Garden Occurrence
House Sparrow *Passer domesticus*	4-4½ million	10-15 million	97
Tree Sparrow *Passer montanus*	260 thousand	800 thousand	11
Chaffinch *Fringilla coelebs*	5 million	30 million	92
Brambling *Fringilla montifringilla*	1-3	50-2000 thousand	10
Serin *Serinus serinus*	1-5	0	+
Greenfinch *Carduelis chloris*	800 thousand	5-6 million	91
Goldfinch *Carduelis carduelis*	250-300 thousand	100 thousand	3
Siskin *Carduelis spinus*	14-28 thousand	150 thousand	7
Linnet *Carduelis cannabina*	600-700 thousand	3 million	2
Twite *Carduelis flavirostris*	17-34 thousand	100-150 thousand	+
Redpoll *Carduelis flammea*	140-150 thousand	350-850 thousand	3
Crossbill *Loxia curvirostra*	½-5 thousand	1-15 thousand	+
Bullfinch *Pyrrhula pyrrhula*	300-350 thousand	1-1½ million	21
Hawfinch *Coccothraustes coccothraustes*	5-10 thousand	20 thousand	+
Lapland Bunting *Calcarius lapponicus*	0-15	200-1000	+
Snow Bunting *Plectrophenax nivalis*	5-15	10-15 thousand	+
Yellowhammer *Emberiza citrinella*	1½ million	3½ million	6
Cirl Bunting *Emberiza cirlus*	60	500	+
Reed Bunting *Emberiza schoeniclus*	400 thousand	1.2 million	14
Corn Bunting *Miliaria calandra*	30 thousand	100-150 thousand	+

Sources of data:

1. Breeding populations (for Great Britain): Marchant *et al.* (1990).

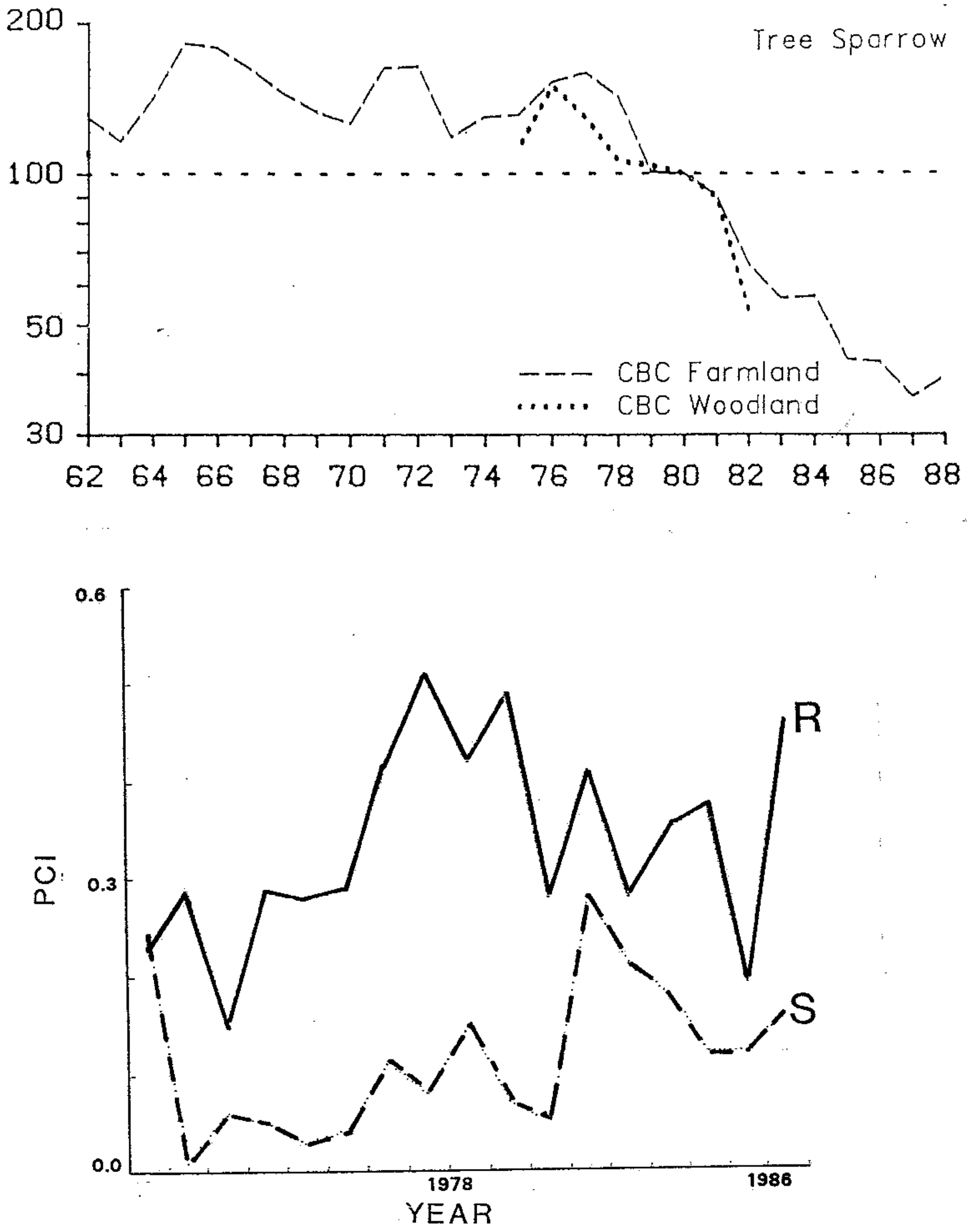
2. Winter populations (Great Britain and Ireland): Lack (1986).

3. Percentage garden occurrence, i.e. percentage of GBFS gardens in which the species occurred in the 1970s (Glue 1982); + indicates that species has been recorded in GBFS gardens but at a frequency of less than 1% and possibly through mistaken identity (BTO unpublished records).



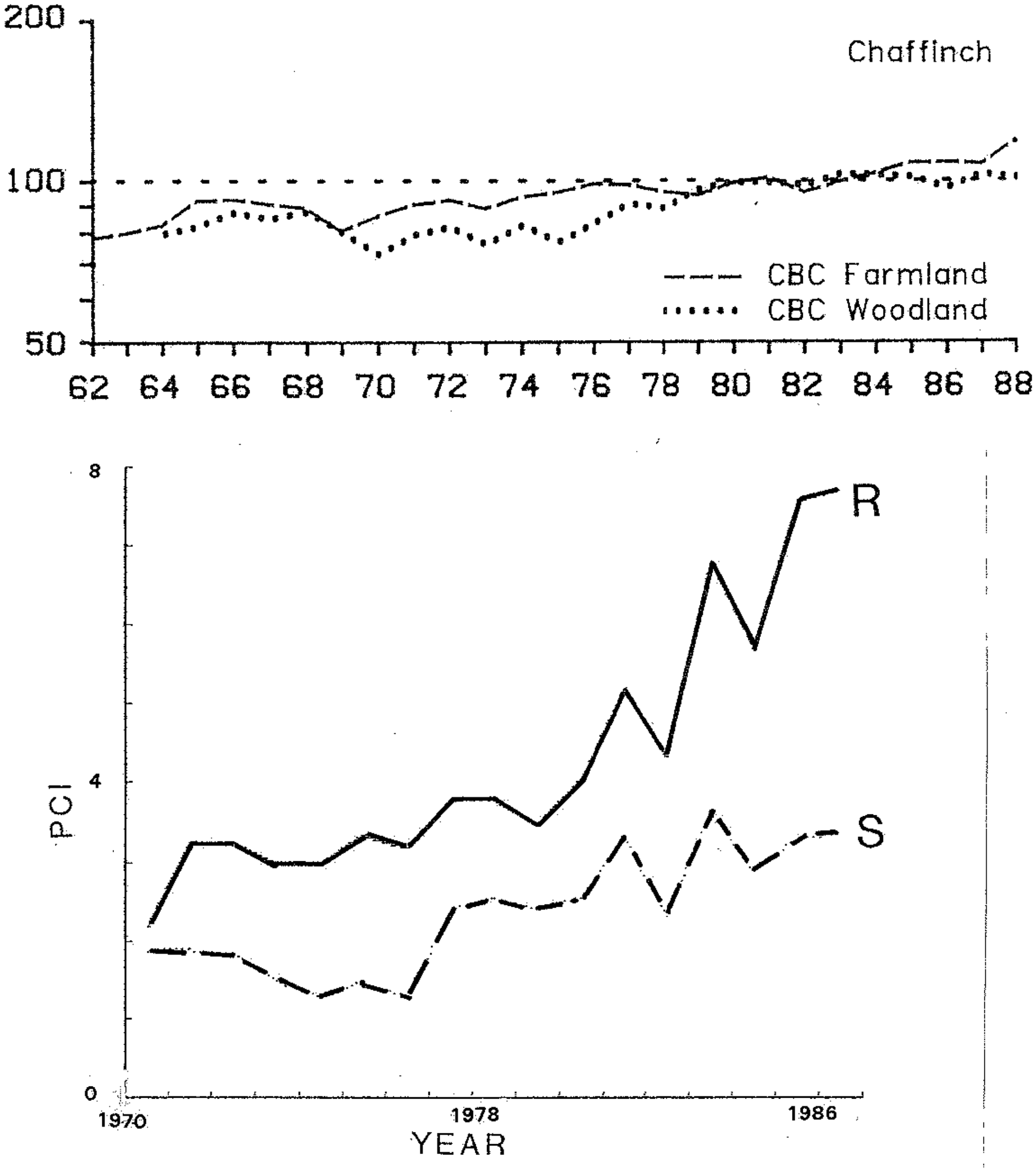
Rural: b = 0.073, t = 0.92, n.s.
Suburban: b = -0.318, t = -4.20, P < 0.01

Figure 1 Indices for House Sparrow of
(A) national population levels and
(B) use of gardens



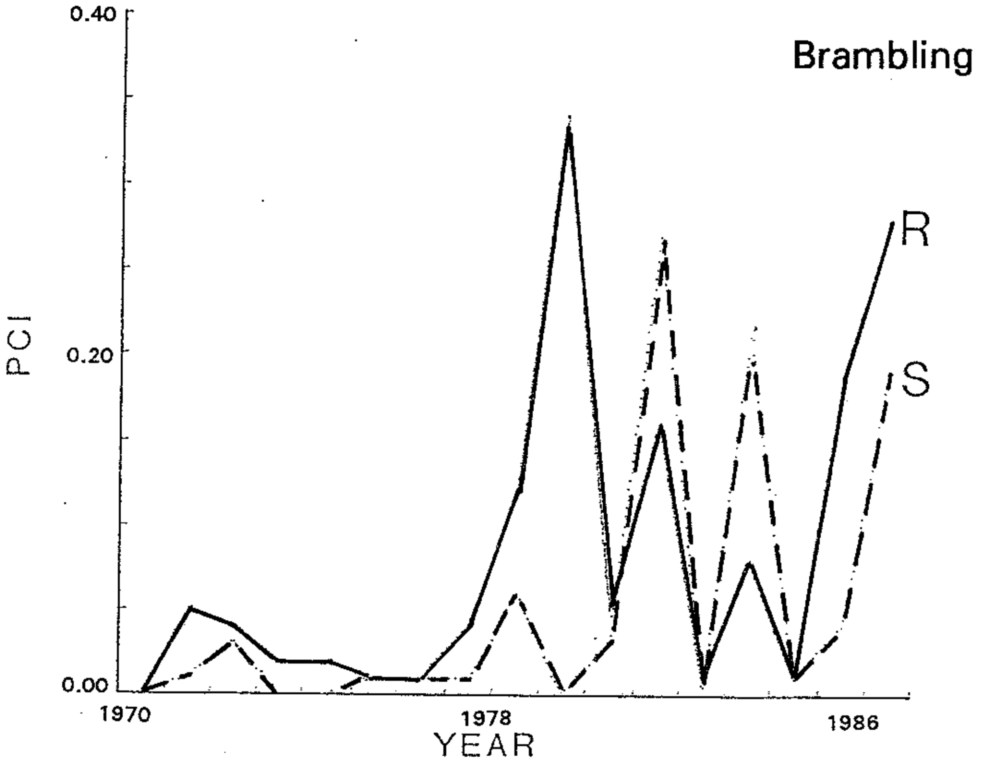
Rural: b = 0.007, t = 1.38, n.s.
Suburban: b = 0.006, t = 1.63, n.s.

Figure 2 Indices for Tree Sparrow of
(A) national population levels and
(B) use of gardens



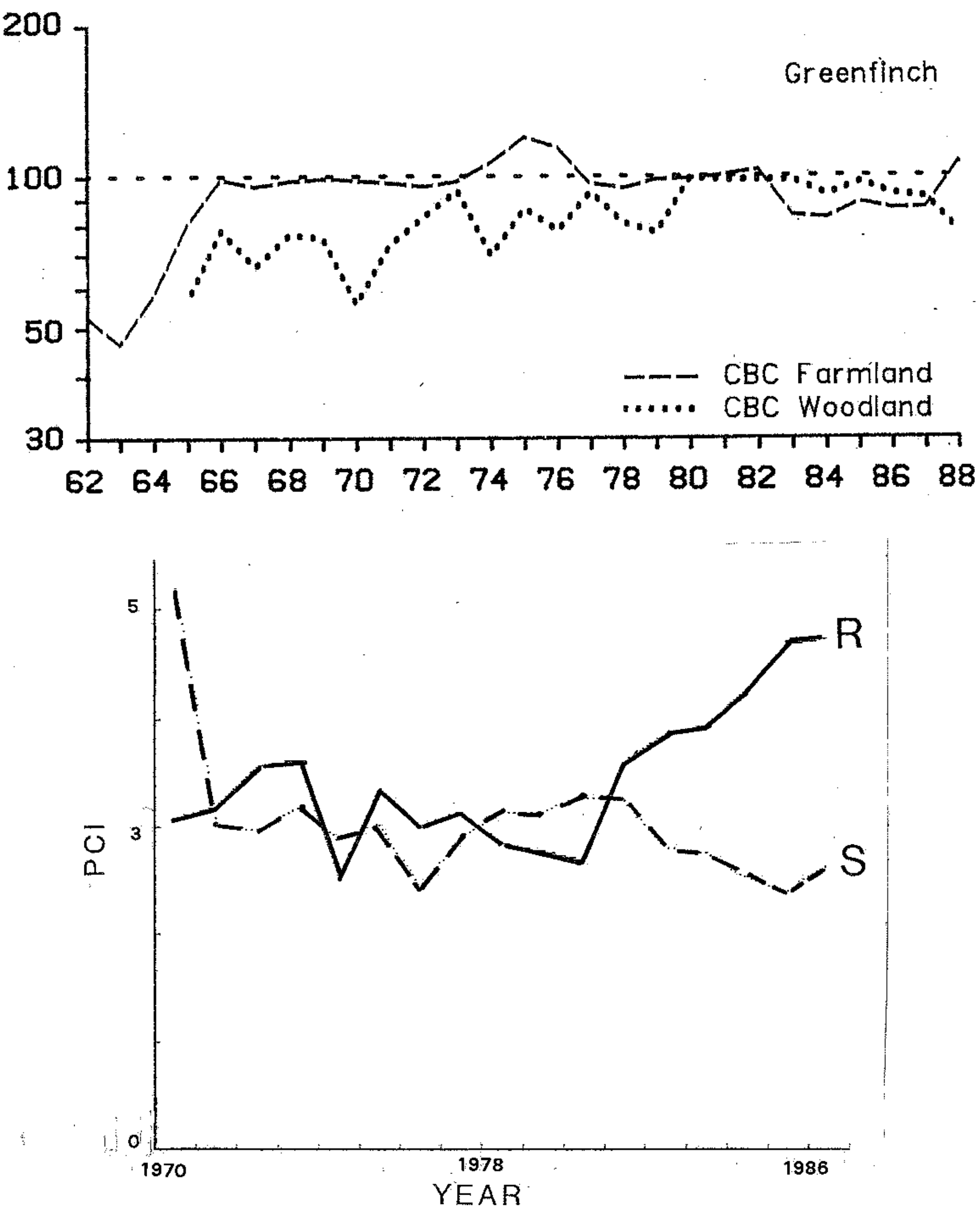
Rural: b = 0.296, t = 7.64, P < 0.01
Suburban: b = 0.124, t = 5.66, P < 0.01

Figure 3 Indices for Chaffinch of
(A) national population levels and
(B) use of gardens



Rural: b = 0.010, t = 2.25, P < 0.05
Suburban: b = 0.008, t = 2.27, P < 0.05

Figure 4 Indices for Brambling of use of gardens



Rural: b = 0.085, t = 3.30, P < 0.01
Suburban: b = -0.067, t = -2.52, P < 0.05

Figure 5 Indices for Greenfinch of
(A) national population levels and
(B) use of gardens

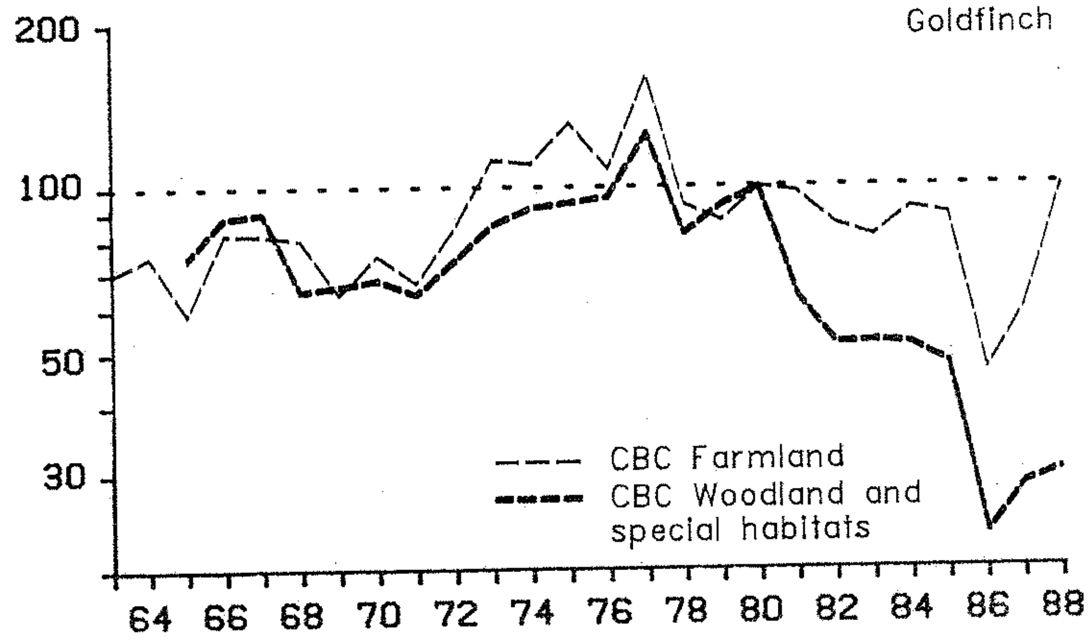
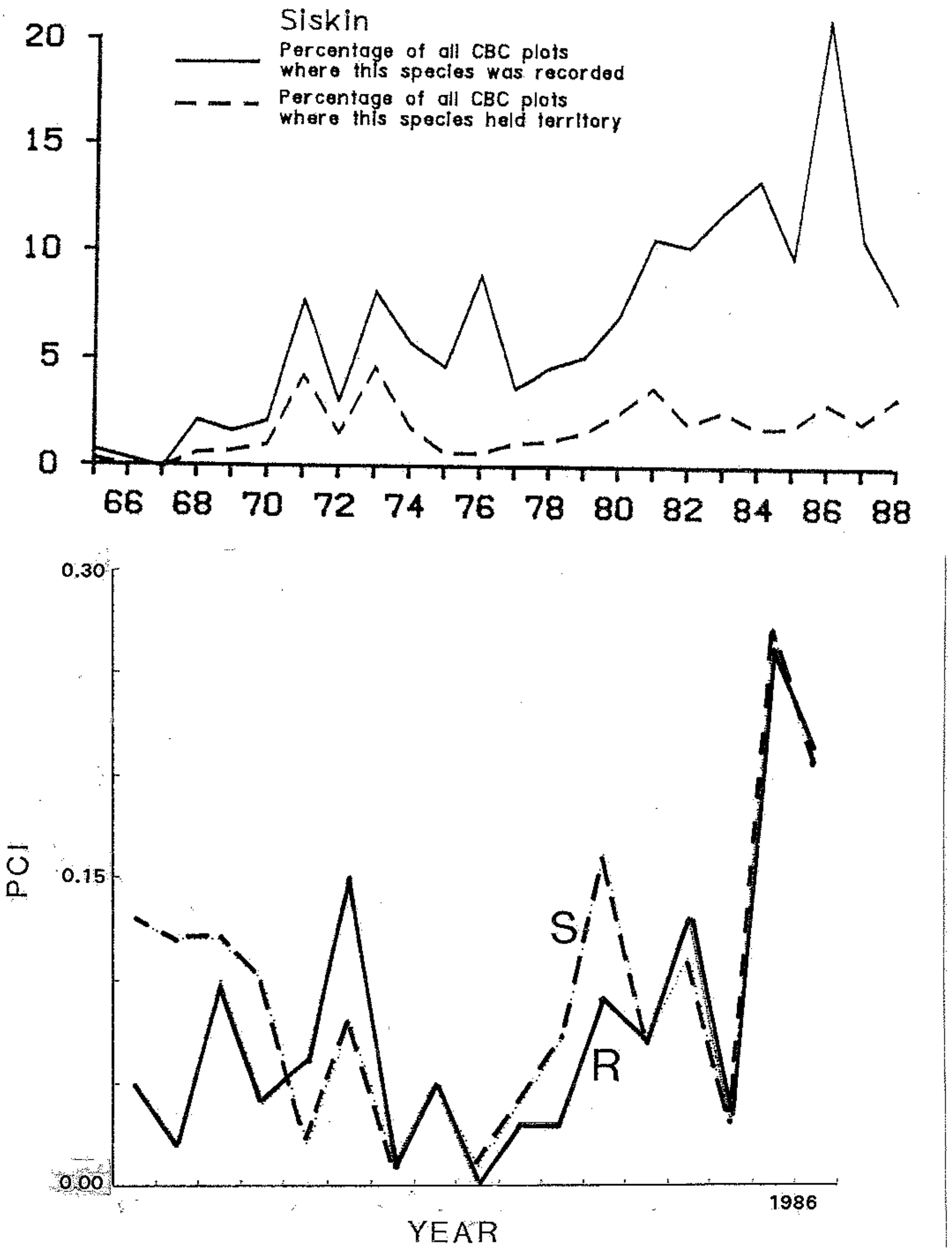


Figure 6 Indices for Goldfinch of national population levels



Rural: b = 0.007, t = 2.19, P < 0.05,
Suburban: b = 0.004, 5 = 1.19, n.s.

Figure 7 Indices for Siskin of
(A) national population levels and
(B) use of gardens

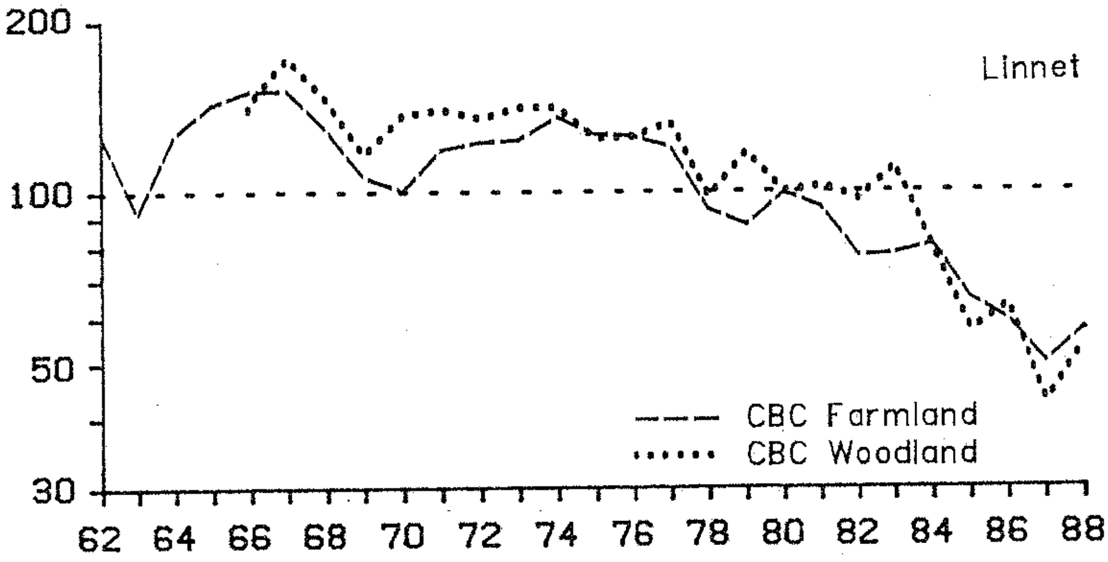


Figure 8 Indices for Linnet of national population levels

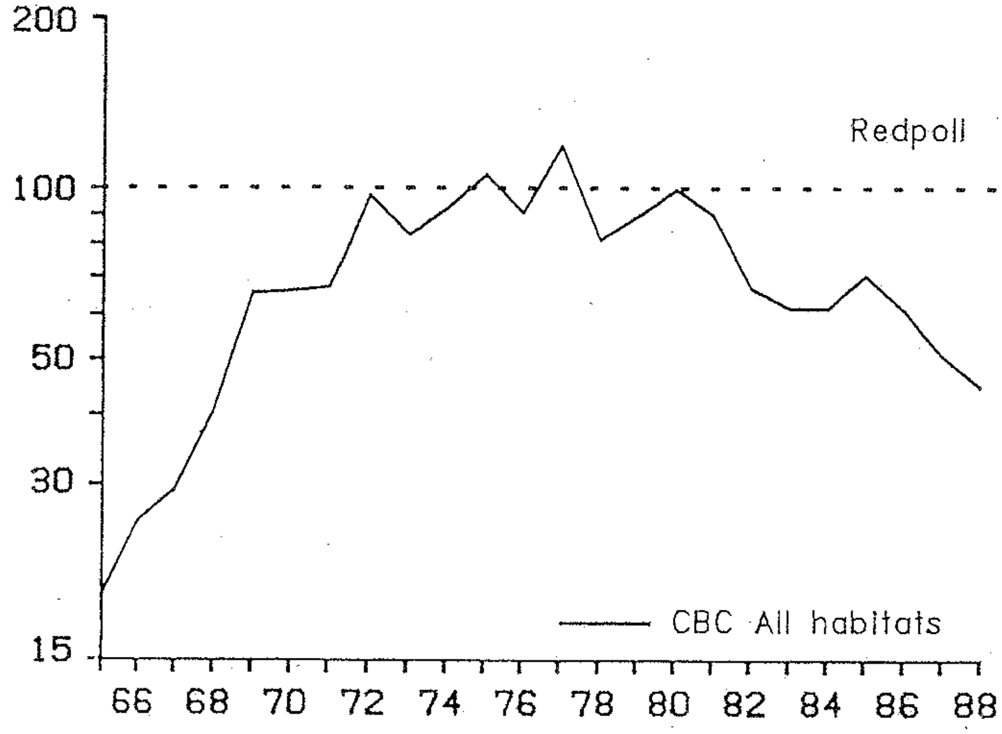
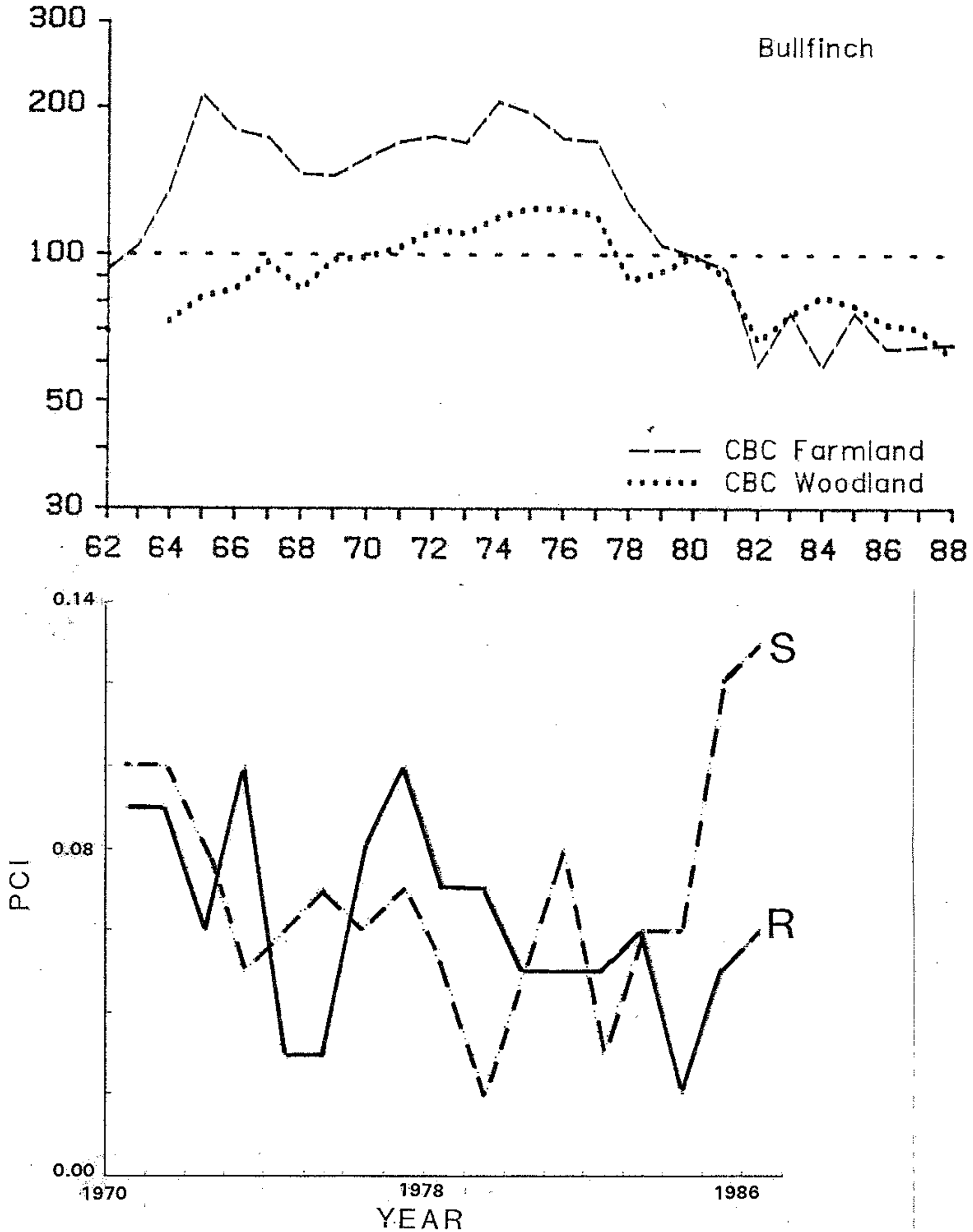


Figure 9 Indices for Redpoll of national population levels



Rural: b = -0.002, t = -2.04, $P < 0.05$
Suburban: b = 0.000, t = 0.24, n.s.

Figure 10 Indices for Bullfinch of (A) national population levels and (B) use of gardens

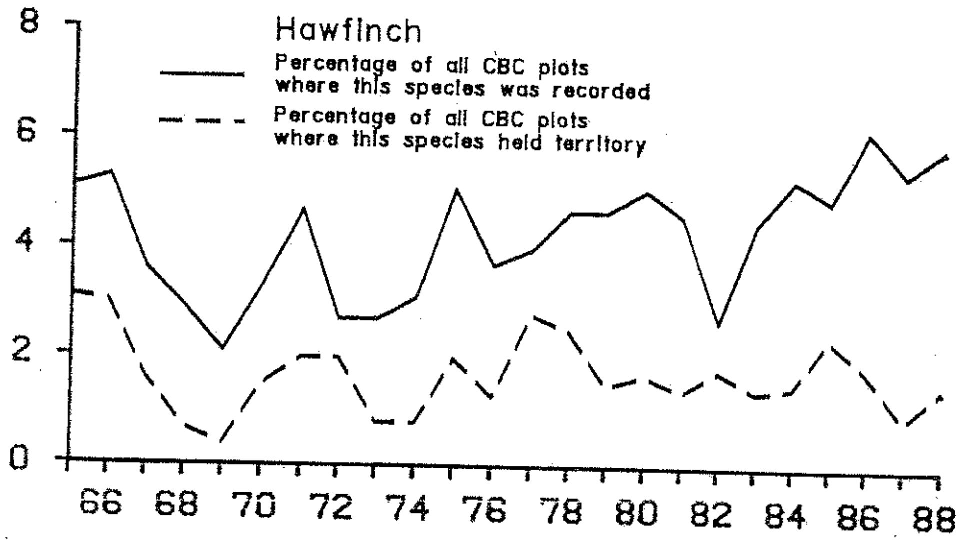


Figure 11		Indices for Hawfinch of national population levels

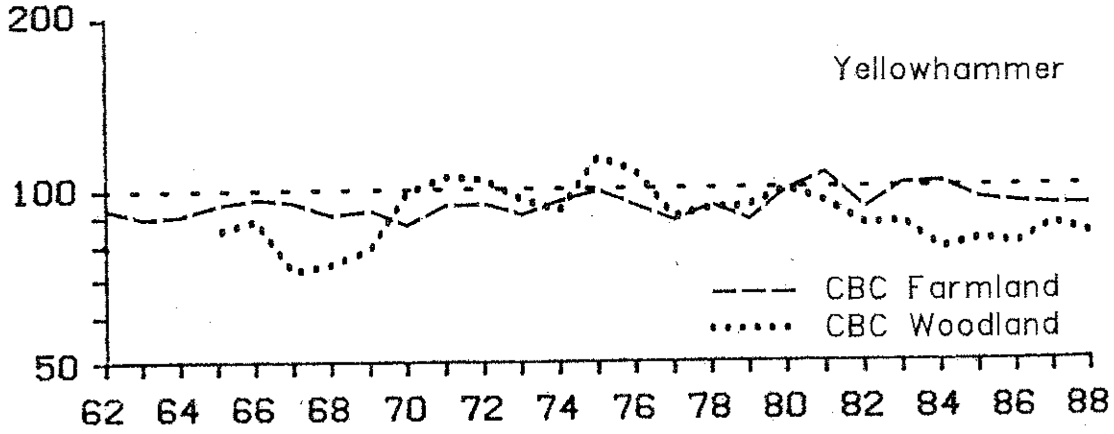
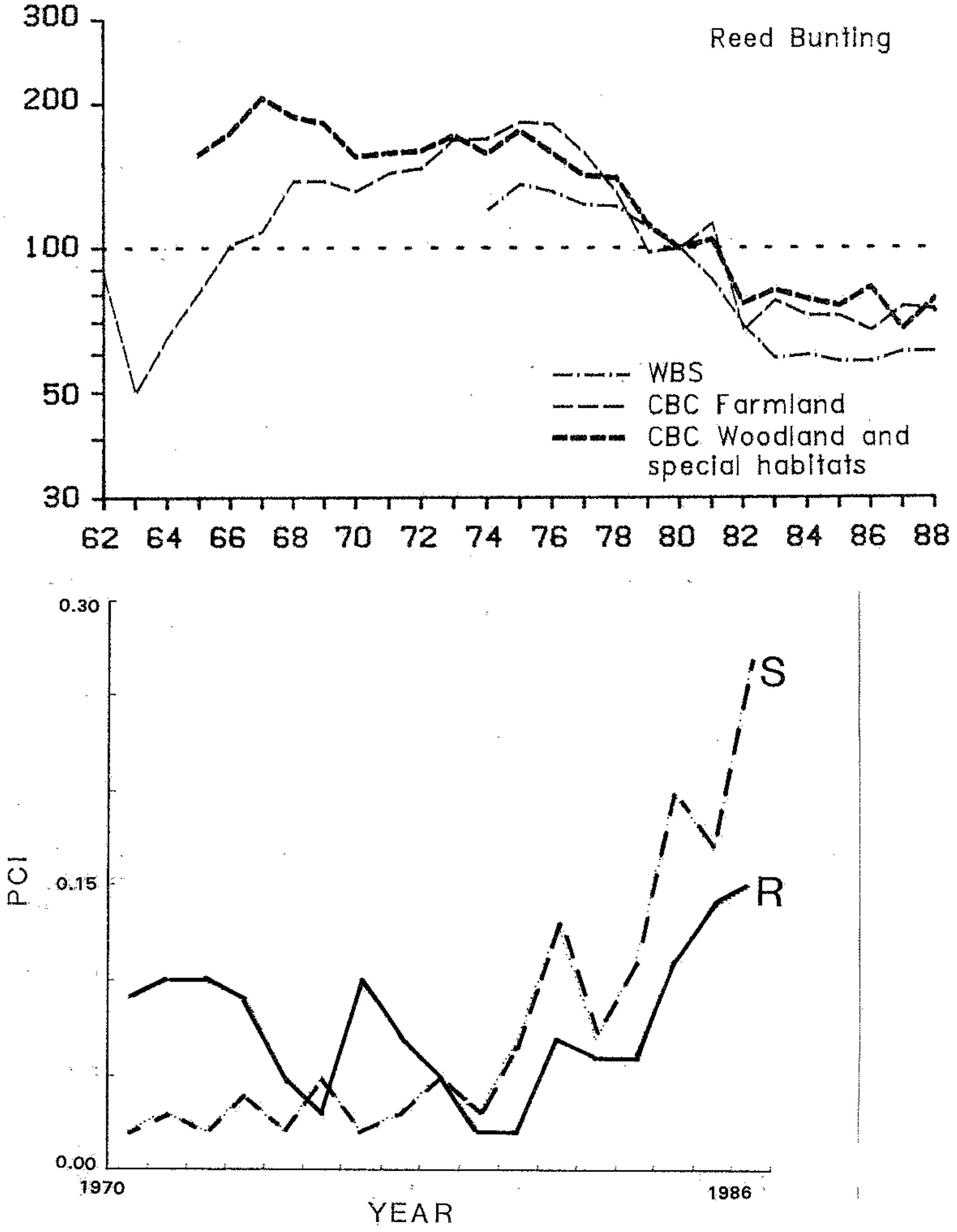


Figure 12 Indices for Yellowhammer of national population levels



Rural: b = 0.001, t = 0.80, n.s.
Suburban: b = 0.012, t = 5.73, P < 0.01

Figure 13 Indices for Reed Bunting of
(A) national population levels and
(B) use of gardens

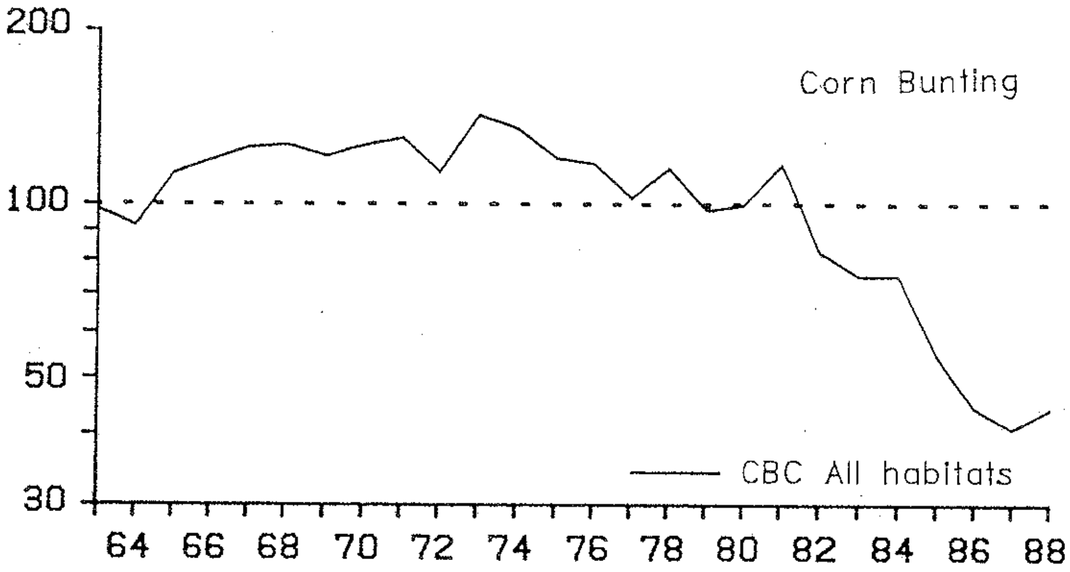


Figure 14 Indices for Corn Bunting of national population levels

CHAPTER 3

REPRODUCTIVE PERFORMANCE IN SOME SEED-EATING BIRDS

INTRODUCTION

Chapter 2 has established how the populations of some, but not all, seed-eating birds in Britain have declined and how these declines (or lack of declines) have been explained in terms of the effects of changing agricultural practices on the birds' food supplies. It also showed how some, but again not all, of these birds use gardens extensively for feeding, though to an extent that has sometimes changed over the years. In that chapter, six species were picked out for further study. They comprise the following:

Chaffinch *Fringilla coelebs* and Greenfinch *Carduelis chloris*: very common and fairly common species respectively, both having fairly stable populations; increasingly common in gardens.

Linnet *Carduelis cannabina*: fairly common but declining; scarce in gardens.

Yellowhammer *Emberiza citrinella*: fairly common with fairly stable population, but scarce in gardens.

Reed Bunting *Emberiza schoeniclus*: less common and declining, but increasing in some gardens.

Corn Bunting *Miliaria calandra*: scarce, declining, rare in gardens.

The aim of this chapter is to determine how reproductive performance may have changed in these species and to assess the extent to which such changes might explain the population changes described in Chapter 2. This will be a contribution not only to understanding the population biology of these species, some of which are important members of the garden bird community in Britain, but also to clarifying how likely it is that some of these birds suffer food shortages in spring, which might be alleviated by supplementary feeding.

The data we have used were gathered by the BTO Nest Record Scheme. This is a volunteer-based scheme and there is no control over the distribution of effort, with the result that apparent changes in, for example, clutch size over the country as a whole could be the result of changes in the proportion of records coming from different regions, combined with regional differences in clutch size. We have, therefore, analysed the data on a regional basis. We have also taken altitude into account, as it seemed likely that this might also be important in determining reproductive performance.

The measures of reproductive performance that we have studied are clutch size and the proportion of nests lost. The former represents the starting point for reproductive output but the latter is of great significance in determining the number of young that reach the flying stage. In the species that we are considering, losses of whole nests are much more important in determining this number than are failures of individual eggs to hatch or deaths of individual chicks (O'Connor 1988), so we have not considered these.

The most common causes of nest losses are probably predation (of the eggs or chicks) and abandonment by the parents (O'Connor 1988). Predation of chicks is more likely when they are hungry, since they then beg more noisily (Perrins 1979). Desertion can occur because of disturbance but can also result from one of the parents dying (since, in all but the polygynous Corn Bunting, the other is unlikely to be able to rear a brood by itself) or from deteriorating weather conditions (e.g. O'Connor & Morgan 1982), which may cause birds to concentrate on keeping themselves alive until conditions improve enough for them to produce another clutch of eggs. Note that many of these causes of desertion are also more likely to occur when birds are short of food.

We are unable to get information on the number of clutches laid in each season by each pair of birds from the Nest Record Scheme. This is a major (but insurmountable) problem because the replacement of clutches that are lost to predators and the laying of true second broods could be important in determining the birds' reproductive performance.

Since it influences the number of eggs laid and is liable to vary according to weather conditions (Lack 1947, 1954; Klomp 1970; Perrins 1970), we have also studied the timing of the breeding season in the six species.

We have concentrated our attention on long-term changes in the variables that we have studied, i.e. changes on the scale of decades rather than years, because it is these that are possibly important in determining long-term changes in population levels. It should not be forgotten, however, that there can be great differences in reproductive performance between successive years, usually at least as great as the long-term trends over several decades. In our analyses such annual variation is treated as part of the 'residual error'.

METHODS

Data gathering

The BTO's Nest Record Scheme began in 1939 (Mayer-Gross 1970). Volunteer contributors complete Nest Record Cards, providing information on the species and the dates of inspection and contents at each visit to the nest.

Values of some variables, such as clutch size, can be obtained directly from the cards. Others may need to be estimated: for example, the date of laying of the first egg can be estimated from the date of hatching since we know (from intensive studies) both the length of the incubation period and how long it is from the date of laying of the first egg to the start of incubation.

Data used

We used all available data for the years 1962-89 inclusive, the years over which trends in population levels have been measured (Chapter 2). The regional divisions used were arbitrary. They are shown in Fig. 1. The Altitudinal divisions were 0 - 49m above sea level, 50 - 99m a.s.l., and higher than that (Low, Medium, High): these divide the available data into roughly equal samples. Use of 'Region' or 'Altitude' with capitals in this Chapter always refers to these divisions.

Because not all cards provide all the information required, sample sizes varied between analyses. Table 1 shows the total sample size available for the analysis of time of breeding in each species, the percentage distribution of these samples between Regions, the percentage distribution of the samples between Altitudes, and the percentage by which the total sample available for clutch size exceeded (or fell short of) that available for time of breeding. Table 2 shows the sample sizes for the Mayfield analyses of rates of nest loss (see below). The Regional and Altitudinal distribution of the samples for the analysis of size and for the Mayfield analyses was similar to that of the timing of breeding samples.

For the purposes of this paper, timing of breeding was measured by the date on which the first egg of a clutch was laid. Clutch size was defined as the total number of eggs laid in a clutch. Records were discarded if a nest had been visited only once, if laying could still have been in progress on the last recorded visit, or if observations began after the eggs had hatched. Nest losses were defined as all cases where none of the eggs laid resulted in chicks that left the nest successfully, through whatever cause (predation and desertion being the most usual causes).

Statistical methods

Time of breeding, clutch size, and rates of loss of eggs all vary considerably from year to year. Since we are interested in long-term trends, we have fitted regression lines to the series of annual data. Since it is unlikely that any trends have been uniform over the 28 years studied, we have fitted quadratic regressions in addition to linear. Differences between Regions and Altitudes in both the average for each variable (such as clutch size) and in the way in which that has varied over the years (that is, in the shape of the regression curves) have been explored using a traditional analysis of covariance approach, for which we have employed the GLM procedure of SAS (SAS 1985). This allowed us also to test whether differences between Altitudes were the same in different Regions and vice versa (that is, the Region x Altitude interaction).

Average daily rates of loss of nests for each year were estimated using the Mayfield method (Mayfield 1961, 1975; Johnson 1979). Estimates were made for each Region and for each Altitude separately. Sample sizes were frequently too small to produce reliable estimates for each Region x Altitude combination, so these were not made. The analyses of the effects of Region and of Altitude were therefore made independently, so we could not test whether the effects of Altitude were the same in all Regions. Doing Regional and Altitudinal analyses independently produced two separate tests of the trends over time. We carried out a third set of tests based on countrywide estimates of daily rates of nest loss, combining the data for all Regions and all Altitudes. The patterns revealed by these three separate analyses of temporal trends were always substantially similar though their statistical significance sometimes differed.

Further details of the statistical methods are given in the Appendix.

TIMING OF BREEDING

General

Table 3 and Fig. 2 show that Linnets and Greenfinches have similar breeding seasons, the modal Date being early to mid May, with most clutches being started within a 6-week span. The distribution of Dates of First Egg tails out later in the season, with a suggestion of a second mode in mid-June, about 6-7 weeks after the main mode. Reed Buntings differ in having more of their breeding attempts concentrated in the main mode; Yellowhammers in having more later clutches, with a clear second mode; Chaffinches in breeding a little earlier and with less variation in Dates, particularly with fewer late Dates; and Corn Buntings in breeding much later, with no late tail to the distribution.

Tables 4, 5 & 6 summarise the results of the statistical tests, both of temporal trends and of differences between Regions and Altitudes, which are discussed in the following subsections. Detailed references to the Tables are made in the Chaffinch subsection, to assist in interpreting the Tables, but are thereafter omitted, to make the text more readable. The Figures for each species show the fitted quadratic curves, to indicate the magnitude of the differences between Regions and between Altitudes, as well as the temporal trends. They should be interpreted with caution, since some differences or trends that appear to be substantial may not be statistically significant; cross-reference to the Tables is essential.

Chaffinch (Fig. 3)

There has been no overall trend during 1962-89 in the egg-laying dates of Chaffinches (Table 5: Year, Linear). There has been a tendency for eggs to be laid later during the middle years of this period (Table 5: Year, Quadratic) but the magnitude of this effect is slight (Fig. 3). These temporal changes do not differ in slope in different Regions or at different Altitudes (Table 4).

There are significant differences in the means (over all years) between both Regions and Altitudes, with some interaction:

Chaffinches nest later in Scotland than elsewhere, at all Altitudes; they nest later in Northern England than in the Southwest and Southeast, especially at higher Altitudes; and they nest later at higher Altitudes, especially in Scotland and Northern England (Tables 5 & 6, Fig. 3).

Greenfinch (Fig. 4)

There are no significant differences between Regions in mean Dates in this species but there are consistent differences between Altitudes, with Dates for nests above 100m being about 8 days later than those in lower altitude nests. Overall, there seems to have been an advance in Date of about 1 day per 5 years over the last three decades, similar in magnitude in all Regions. There is a marginally significant difference between Altitudes in the way in which Dates have changed over the years, which makes the interpretation of the overall trends less straightforward.

Linnet (Fig. 5)

There are no significant differences between Regions or Altitudes in mean Dates nor have there been any overall trends over the period in question. A marginally significant difference between Regions in the relationship between Date and Year is actually small in terms of the magnitudes of the changes involved.

Yellowhammer (Fig. 6)

During 1961-89, clutches of Yellowhammers in Northern England and Scotland were started about 10 days earlier, on average, than those in the Southwest and Southeast, but there have been no clear differences between Altitudes. (This Regional difference may result from different proportions of second clutches - see Discussion). Breeding seems to have become later as the years have gone by, though not uniformly in all Regions.

Reed Bunting (Fig. 7)

Mean Date for Reed Buntings has been substantially later in Scotland than in the Southeast and Southwest but, although there are no overall differences between Altitudes, there is a strong Altitudinal difference in Northern England, so that the mean Date in the North is similar to that in Scotland at High Altitude but to those in the Southeast and Southwest at Medium and Low Altitudes. There have been no significant trends over the years.

Corn Bunting (Fig. 8)

There is a strong interaction between Region and Altitude in this species, so that neither alone is a good predictor of Date. In addition, there have been strong, non-linear trends with time: in all areas, breeding seems to have been substantially later in the 1970s than in the 1960s and 1980s.

Further comparisons between species

There were no clear similarities between species in the patterns of timing of breeding described above. In particular, in view of similarities between the finches in Clutch Size variation (see below), we tested for such similarities in Date but found none.

CLUTCH SIZE

General

Table 7 and Fig. 9 show that Clutch Size distributions were almost identical in Greenfinches and Linnets, over half the clutches of each species being of 5 eggs. Reed Buntings had a very slightly smaller mean Clutch Size, Chaffinches even smaller (with almost as many c/4 as c/5) and Corn Buntings smaller again (with a modal Clutch Size of 4). Yellowhammers laid far fewer eggs per clutch than any other species. In each species except Corn Bunting, three Clutch Sizes accounted for well over 90% of the clutches and the distributions were skewed, with fewer clutches larger than the modal value than smaller. The Corn Bunting had a broader and less skewed frequency distribution of Clutch Sizes.

Tables 8, 9 & 10 summarise the results of the statistical tests of Clutch Size in the same way as Tables 4, 5 & 6 summarise those for Date of First Egg.

Chaffinch (Fig. 10)

In the country as a whole, Chaffinch Clutch Sizes have not shown long-term trends during 1962-89 (Table 7) but there have been differences between Altitudes in this respect (Table 8: Altitude, Linear): at Low Altitudes there has been a slight decline and at Medium Altitudes a slight increase in Clutch Size (Fig. 10). The overall absence of trends has held over all Regions (no Region effects in Table 8).

On average, there have been no clear differences between Regions or Altitudes, but this masks an interaction (Table 7), with differences between Altitudes being quite inconsistent between Regions, and conversely (Table 10).

Greenfinch (Fig. 11)

The variation in Greenfinch Clutch Size has been like that in Chaffinches: there have been no long-term trends in the country as a whole or differences between Regions; there have been significant (though slight) differences in trends between Altitudes; and the overall differences in average Clutch Size between Altitudes have not been consistent between Regions (or conversely).

Linnet (Fig. 12)

Linnet Clutch Sizes show similar patterns to those of Chaffinches and Greenfinches: there have been no long term trends in the country as a whole or differences between Regions; there have been significant (though slight) differences in trends between Altitudes; and the overall differences in average Clutch Size between Altitudes have not been consistent between Regions (or conversely).

Yellowhammer (Fig. 13)

There have been no long-term trends in Clutch Size in this species. As with the three previous species, there is a significant Altitude x Region effect: differences in Clutch Size between Altitudes have not been consistent between Regions or conversely.

Reed Bunting (Fig. 14)

There is evidence of a difference between Regions in long-term trends in Clutch Size in this species, with Scotland and Northern England having smaller clutches in the middle of the period 1962-89 but Southwest and Southeast England showing little long-term variation. The temporal changes in northern Britain have been sufficiently strong to render the testing of overall differences between regions largely meaningless, so the Region and Region x Altitude effects in Table 9 should be ignored.

Corn Bunting (Fig. 15)

Regions differ clearly in long-term trends in Corn Bunting Clutch Sizes: in Scotland there has been a huge increase, in Northern England a substantial decline, and in southern England a slight increase, all of these being individually significant at the 5% level in tests of linear regression , except for that in Northern England (for which $P = 0.065$). These substantial changes overwhelm any average differences between Regions or Altitudes.

Further comparisons between species

Among the buntings, there are no obvious similarities in the Regional, Altitudinal, or temporal differences discussed above, nor any particular similarities with any of the finches.

Among the finches, however, there are similarities: High Altitudes in Scotland have the lowest Clutch Sizes in all three, for example. The similarity was tested by taking the 12 Region x Altitude means for each species in Table 10, ranking them, and calculating Kendall's coefficient of concordance between the species. This attained the significant value of 0.63 ($X^2 = 21$, $P<0.025$). The concordance between Greenfinch and Linnet is particularly striking. A further similarity between these species is in the pattern of differences between Altitudes in temporal trends: in both species, the Clutch Size graph is slightly U-shaped at Medium Altitudes but the opposite at High and Low Altitudes (though only very slightly for Low Altitude Linnets).

RELATIONSHIP BETWEEN CLUTCH SIZE AND TIME OF BREEDING

This has been explored, for British birds generally, by H Q P Crick, D W Gibbons and M.D. Magrath (in prep.), using BTO data. In summary, Chaffinch Clutch Sizes vary little with Date of First Egg; Greenfinch, Linnet, and Yellowhammer Clutch Sizes are higher in the middle of their breeding seasons than at their beginning or end; Corn Bunting Clutch Sizes rise slightly as the season progresses but drop a little at the end of the season; while Reed Bunting Clutch Sizes rise a little at the beginning but then fall.

The 12 Region x Altitude correlations were ranked according to both mean Date of First Egg and mean Clutch Size; Spearman's coefficients for the correlations between these two rankings were calculated for each species. None was significant, suggesting that the differences between Regions and Altitudes in Clutch Size are not simply explicable in terms of differences in the timing of breeding.

RATES OF LOSS OF NESTS

Chaffinch

The mean rates of loss of Chaffinch nests during 1962-89 were similar at the egg and chick stages (Table 11). But these means hide considerable variation.

At the egg stage, rates of loss declined markedly over the period (Table 12, Fig. 16). Neither Region or Altitude significantly affected losses at this stage (Tables 12, 13, 14).

At the chick stage, there was no general change in rates of loss (Table 12, Fig. 16). But within Altitude classes there were shorter-term changes that were different at different Altitudes - higher rates during the middle years at High and Medium Altitudes, but the converse at Low Altitudes (Fig. 17). These differences were statistically significant (Table 12), though when the patterns for individual Altitude classes were tested individually, only that for High Altitude was significant (variance ratio, $F(1,25) = 6.5$; $P = 0.017$). There were no overall differences between Altitudes in rates of loss at the chick stage (Table 14). Neither mean rates (Table 13) nor temporal trends (Table 12) differed significantly between Regions.

There were also significant differences between Altitudes in the rates of nest loss measured over the whole nest period - a significant decline at High Altitude (F(1,26) = 6.45, P = 0.018, for linear trend) and non-significant increases at other Altitudes (Table 12, Fig. 17). These largely cancel out when all Altitudes are considered together (Fig. 16). Mean differences between Altitudes (Table 14) are small compared with the trends within Altitude classes. Once again, there were no Regional effects (Tables 12 & 13).

Greenfinch

Mean rates of loss of Greenfinch nests during 1962-89 were similar at egg and chick stages. Variation around these means was simpler than in the Chaffinch.

Losses at the egg stage declined in the 1960s but have since shown no general trend (although they have varied from year to year); losses at the chick stage have shown no long-term changes; and losses over the whole nest period have paralleled those at the egg stage, though with a less marked trend (Table 15, Fig. 18). Nest losses in Greenfinches have not varied significantly according to either Region or Altitude (Tables 15, 13, 14).

Linnet

Once again, the overall mean rates of loss were similar at egg and chick stage (Table 11). However, while losses at the chick stage showed no long-term trends (Table 16, Fig. 19) and were similar at all Altitudes (Tables 16 & 14), there was a marked overall increase in the rate of loss of nests at the egg stage (Fig. 19), though the patterns of change were different at different Altitudes (Table 16, Fig. 20).

Over the whole nest period, the national picture was similar to that for the egg stage (Fig. 19), though in this case there were no differences between Altitudes (Table 16).

There were no significant differences between Regions in rates of loss of Linnet nests (Tables 13 & 16).

Yellowhammer

Rates of loss of nests of Yellowhammers are the same in the egg and chick stages (Table 11) and in both stages there has been a very marked decline (Table 17, Fig. 21). At the egg stage and over the whole nest period, there are no significant differences between Altitudes in the mean rates of loss and in the steepness of this decline, but at the chick stage significant differences have occurred (Tables 17 & 14): at both Medium and Low Altitudes there have been significant declines ($P<0.005$ in each case) but at High Altitudes there has been a non-significant increase (Fig. 22). There have been no Regional differences in rates of nest loss or in the extent to which they have decreased (Tables 17 & 13).

Reed Bunting

Table 11 shows that, during 1962-89, Reed Buntings lost nests at the egg stage at less than half the rate at which they lost them at the chick stage. This difference was sustained through the whole period, the mean annual difference in rate being 0.0144 nests lost per day (s.e. 0.0021, $t = 6.7$, $P<0.0001$). Yet, though there was no overall change in egg losses during this period, there were significant variations, with smaller losses in the early 1970s than in the 1960s or 1980s (Table 18, Fig. 23). Much the same was true of losses over the whole nest period. Neither Region nor Altitude affected nest losses at the egg stage or over the whole nesting period (Tables 18, 13, 14). Losses at the chick stage have declined steadily (Table 18, Fig. 23). At first sight, Altitudes seem to have differed in the rate of decline (Table 18) but inspection of the data suggests that this is a result of occasional small sample sizes at High and Medium Altitudes, producing aberrant estimates of rate that unduly influence the apparent relationship between nest losses and Year.

Region has no effect on rates of loss at any stage in this species (Tables 18 & 13). The apparent interaction of Region with Quadratic effect of Year (Table 18) is, again, probably a result of small sample sizes from Scotland.

Corn Bunting

Sample sizes for Corn Bunting were very small, so we adopted a two-pronged approach. In one set of analyses, we did the same as for the other species, thus using a set of Mayfield estimates rendered rather unreliable by the small samples from which they were derived. In the second set, years were grouped into four 7-year blocks, to give more reliable Mayfield estimates, but rather few of them. These approaches yielded essentially the same results: no significant temporal trends or effects of Region or Altitude were apparent (Table 19). This does not, of course, mean that such trends or effects were absent, merely that they were not strong enough to be significant with such small sample sizes - the almost significant decline in losses at the chick stage, in particular, should not be dismissed. Inspection of the data, and the trend lines shown in Fig. 24, suggests that any trends or systematic differences between Regions or Altitudes were small.

Comparisons between species

Overall, Yellowhammers and, to a lesser extent, Chaffinches appear to suffer higher rates of nest loss than the other species (Table 11).

In three species, Chaffinch, Greenfinch and Yellowhammer, losses at egg stage declined during at least part of 1962-89 without subsequent recovery; this was translated into similar declines over the whole nest period in Greenfinches and Yellowhammers. But in Reed Buntings an early decline was later reversed and in Linnet there has been an increase, starting around 1975. Only in Yellowhammer and Reed Bunting have losses at the chick stage changed in the long-term, declining in both cases.

Thus the different species have shown quite different patterns in respect of changes in rates of nest loss. The Altitudinal effects on temporal patterns of loss (Figs. 17, 20, 22) have been different in the different species.

DISCUSSION

The breeding seasons revealed by the data presented here have to be interpreted with caution, since those data include not only first clutches but all subsequent clutches, including both true second (and subsequent) clutches and replacements following the loss of a clutch. To determine the time at which first clutches tend to be laid, the 5-percentile date may therefore be more useful than the mean, median or mode. Thus the relatively early mean for the Chaffinch is not reflected in an early 5-percentile and may be explained largely by the infrequency with which this species produces second clutches (Newton 1972), which is reflected in the extremely early date of the ending of this species' breeding season as shown by the 95-percentile (Table 3). The infrequency of second clutches in the Chaffinch is itself probably a result of the rapid decline in early summer of the availability of insects on which Chaffinches feed their young (Newton 1972). Though Corn Buntings often nest in scrub, they do seem to be associated with arable crops, especially barley (O'Connor & Shrubb 1986), but barley tends to be harvested earlier than other cereals, which does not fit with the late breeding of this species. Yom-Tov (in prep.) has suggested that the late breeding results from the Corn Bunting being polygynous, with the consequence that the females have to delay breeding until food is abundant enough to support them but Dr R P Prŷs-Jones has suggested to us that it results from Corn Buntings not making use of the spring flush of defoliating insects, as do the Yellowhammer and Reed Bunting (Prŷs-Jones 1977). More detailed studies would be needed to test these explanations.

Some regional differences in time of breeding are not unexpected. Thus Chaffinches breed later in more northerly Regions; Reed Buntings breed relatively late in Scotland and, to some extent, in Northern England (though this last depends on Altitude); Corn Buntings also breed relatively late in Scotland but not in Northern England (especially at high Altitudes). In contrast, Yellowhammers appear to breed earlier in the more northerly Regions - but this is probably because they are more likely to produce second broods in the south, which pushes the mean date of breeding back. The 5- and 95- percentiles suggest a relatively uniform start to the breeding season of this species but an earlier finish in northerly areas:

	Scotland	Northern England	Southeast	Southwest
5-percentile	29 April	29 April	3 May	28 April
95-percentile	26 June	7 July	22 July	30 July

Chaffinches, Greenfinches, and probably, Linnets fit in with what one might expect, in that they breed later at higher Altitudes. However, altitude has no clear effect on breeding time in Yellowhammers, while in the other two buntings differences in breeding time between Altitudes are not the same in different Regions. These birds may all be labelled 'seed-eaters' (so long as one does not forget that invertebrates are important food for most of them), but their ecologies are sufficiently different for them to respond differently to ecological factors that vary with Altitude or Region.

The species have also responded differently to temporal changes. Time of breeding of Chaffinch, Linnet and Reed Bunting has shown no long-term trends during 1962-89 but Greenfinches have tended to breed earlier and Yellowhammers later as the years have gone by (though these changes have themselves differed between Altitudes and Regions). Corn Buntings were different again, breeding earlier at the start and end of the study period than in the middle.

Clutch size variation in contrast to variation in time of breeding, has shown remarkable parallelism in Chaffinches, Greenfinches and Linnets, in terms both of differences between Regions and Altitude classes. Yellowhammers have also shown differences between Regions and Altitudes, but these are not parallel to those in the finches. In none of these species have there been long-term trends in clutch size and the same can be said of the Reed Bunting in terms of the national population, though this species has shown such trends within individual Regions. Thus declines in Linnet and Reed Bunting populations cannot be ascribed to fewer eggs being laid; and the stability of Chaffinch, Greenfinch, and Yellowhammer populations cannot be ascribed to increased reproductive output making up for difficulties at other stages in the life cycle.

Corn Bunting populations have declined through most of Britain but, although clutch sizes have declined in northern England, they have increased in the south and in Scotland. It again seems unlikely, therefore, that changes in clutch size have caused the population declines.

Daily rates of loss of nests do not, of course, translate directly through to losses over the entire nest period, since these depend also on the length of that period. Table 20 shows overall losses, calculated from the daily rates and the known incubation and fledging periods. It is clear that there is no correlation across the species between the rates of change of population size in recent decades and the average percentages of nests lost.

Nest losses have shown more long-term trends than clutch sizes and, although Altitude has affected rates of nest loss, this has not obscured the overall trends. In the Chaffinch, losses at the egg stage have declined (but not those at the chick stage or over the whole nest period); in the Greenfinch, losses at the egg stage and over the whole nest period declined during the 1960s but have been more stable since then; in the Yellowhammer, nest losses at all stages have decreased. The populations of all of these species have not increased, nor clutch sizes decreased, indicating that the increases in breeding success have been balanced by greater mortality at other stages in the life history (or by fewer nesting attempts being made).

The Linnet has, in contrast to these species, suffered increasing nest losses during incubation. Its population has declined. The two may be linked.

Another possible link occurs in the Reed Bunting. Losses of nests at the egg stage and over the whole nesting period declined from the early 1960s to the mid 1970s, when the population was increasing or stable; in interesting contrast, nest losses increased after 1975, while the population has declined. (The long-term decline in nest losses at the chick stage has been insufficient to counter the increased losses at the egg stage, which have driven the increased losses over the whole nest period).

The other declining species, Corn Bunting, has apparently not experienced greater nest losses at the same time as its population has declined. It is more likely, though the data are too few to draw firm conclusions, that rates of loss have declined.

Recalling that many of the causes of nest loss are more likely to occur when birds are short of food, one could reasonably argue that the increased nest losses in Linnets and Reed Buntings may be consequences of reduced food supplies.

It is thus possible that the changing fortunes of some of these species have resulted from changes in breeding output, but the picture is far from clear. Given that the approach is correlational rather than experimental (as it must be for studies on national populations), it would be valuable to extend the analysis to a wider suite of species, providing a larger and more diverse sample of Britain's avifauna.

In view of the current interest in long-term climatic changes, possibly caused by man, it would also be valuable to study the variations in breeding performance (and population level) from year to year in relation to annual fluctuations in the weather, to assess the extent to which they are determined by it and whether the long-term changes can be explained simply by changes in the weather. In the Song Thrush *Turdus philomelos* detailed study by BTO has shown that cold winters are an important determinant of annual population changes but that they cannot wholly explain a recent general decrease in the species' British population (Baillie 1990). It would be extremely valuable to carry out similar detailed studies on the birds considered in this report and on other species for which farmland or gardens are important. They require the bringing together of various BTO data sets, key factor analysis to determine the stages in the life-cycle that are particularly important in determining population changes, and the building of population models.

The assessment of the effects of agricultural practices on the population dynamics of the species living on farmland requires more detailed Regional study, in relation to Regional differences in the way that agriculture has changed. These were pioneered by O'Connor & Shrubb (1986a,b) but more comprehensive work is needed.

The evidence presented here suggests that differences in reproductive performance, themselves resulting from differences in feeding ecology, are responsible for some of the differences between the population trends of these species. Though not all seed-eating birds frequent gardens, this is an indication that the continued supply of high quality food in spring, through supplementary feeding in gardens, could be valuable for at least some birds.

APPENDIX: STATISTICAL METHODS

Date of First Egg and Clutch Size

These data are not Normally distributed but we have nonetheless used the usual parametric tests, since these can cope readily with the multifactorial models underlying the analysis. We have, therefore, been particularly careful to inspect the data, to check both on whether the effect apparently revealed by the significance tests is clearly reflected in the data and on the magnitude of the effect. (With large sample sizes even highly significant results can reflect quite trivial effects).

We have applied models in the SAS procedure GLM to these data, using the Type III sums of squares, which for any effect 'first removes any overlap with any other effect, then examines the relationship between the effect in question and the outcome variable. This provides what is called the "unique" contribution of each effect' (Cody & Smith 1987).

The independent variables considered were Year (Linear effect) (Y), Quadratic effect of year (ie. year squared) (Q), Region (R) and Altitude (A). We began by testing for differences between Regions in the slopes of any regression on Y, by fitting a model with the effects Y, A, R, YxA, AxR and YxR, using the F ratio of the last as our test statistic. (By running a model without the YxR term and comparing the difference between the two residual sums of squares, divided by the difference between their degrees of freedom, with the residual sum of squares from the first analysis, divided by its degrees of freedom, which is the appropriate test of YxR, we confirmed that this F ratio provided by GLM was the correct one for us to use).

We repeated the analysis with the effects of Q, QxA and QxR to test the latter as an indicator of differences between non-linear components of slopes between regions. Similar analyses were made to test differences between Altitudes.

Since we were interested only in the years for which we have data and not in extrapolating regressions on Y and Q more generally, it was appropriate to test the mean differences between Regions and between Altitudes (and their interaction) even where there were differences between Regions and Altitudes in the regression slopes. In many of our analyses it was also sensible to test the overall regressions since, even where there were significant differences in slopes between Regions or Altitudes, these were slight. We have therefore routinely tested the overall regressions, ignoring the results in cases where there were major differences in regression slopes between Regions or Altitudes. We began by fitting a model with Y, A, R, and RxA, using the F ratio for Y to test the overall linear regression. A model with Y, Q, A, R and RxA was then fitted and the F ratio for Q used to test whether there was an overall quadratic effect, over and above the linear - in other words, was there a non-linear trend? The F ratios for A and R were used to test for differences between Altitudes and between Regions, though these were ignored if the AxR F ratio showed a significant interaction which inspection of means showed to be stronger than the main effects of these variables.

Rates of loss of nests

As with time of breeding and clutch size, we have adopted the approach of fitting quadratic effects only after linear effects had been taken into account. We therefore fitted a model with linear effect of Year, effect of Region, and YxR interaction first, to test these three components. Then we fitted a model to which the quadratic effect of year and the interaction of that with Region had been added, to test these two components. As before, we used the Type III sums of squares for testing the effects. Parallel analyses were carried out for Altitude. The effects of Year were never identical in the two sets of analyses, even though they were based on the same raw data, because the GLM analyses used as their data the annual estimates of daily rates of nest loss, for which the sample sizes differed between Regions and between Altitude classes.

Because of small sample sizes, the variances associated with the estimates of rates of nest loss on a Regional or Altitudinal basis were occasionally rather large. Since all estimates were given equal weight in the analyses, it seemed likely that analyses that used separate Regional or Altitudinal estimates might sometimes result in temporal trends being lost in the error variance. We therefore also made estimates of the annual mean daily rates of loss for all Regions and Altitudes combined and used these to test for temporal trends. As expected, these sometimes gave significant results when the analyses based on separate Regional or Altitudinal estimates did not, though the form of the national trends revealed by the different analyses was never substantially different.

SUMMARY

The six species considered differ in time of breeding, average clutch size, and rate of loss of nests. All of these vary, within species, from year to year. During 1962-89 there have been longer-term variations in the timing of breeding in some species, as well as differences associated with Region and Altitude. (More often than not, breeding is later in the north and at higher Altitudes). Clutch size has also shown Regional and Altitudinal variation in most species, but no long-term trends.

In the three species whose populations have been stable (Chaffinch, Greenfinch and Yellowhammer), losses of nests declined during 1962-89. In Linnets and Reed Buntings, losses increased concurrent with population declines. But in Corn Buntings losses may have decreased rather than increased, even though the population has declined.

We conclude that it is likely that some of the differences between these species in the ways in which their populations have changed are the result of differences in their feeding ecologies, which have given rise to differences in reproductive performance, and that it may be important for them that supplementary feeding in gardens continues into the spring.

REFERENCES

Baillie, S.R. 1990. Integrated population monitoring of breeding birds in Britain and Ireland. *Ibis* 132: 151-166.

Cody, R.P. & Smith, J.K. 1987. *Applied Statistics and the SAS Programming Language* (2nd Edition). North Holland, New York.

Crick, H.Q.P., Gibbons, D.W. & Magrath, R.D. (in prep.). Seasonal changes in clutch size in British birds.

Johnson, D.H. 1979. Estimating nest success: the Mayfield method and an alternative. *Auk* 96: 651-661.

Klomp, H. 1970. The determination of clutch size in birds. *Ardea* 58: 1-124.

Lack, D. 1947. The significance of clutch size. *Ibis* 89: 302-352.

Lack, D. 1954. *The Natural Regulation of Animal Numbers*. Clarendon Press, Oxford.

Mayer Gross, H. 1970. *The Nest Record Scheme*. British Trust for Ornithology, Tring.

Mayfield, H.F. 1961. Nesting success calculated from exposure. *Wilson Bull*. 73: 255-261.

Mayfield, H.F. 1975. Suggestions for calculating nest success. *Wilson Bull*. 87: 456-466.

Newton, I. 1972. *Finches*. Collins, London.

O'Connor, R.J. 1988. Patterns of nesting mortality in British Passerines. Proc. 19th I.O.C.: 1457-1466.

O'Connor, R.J. & Morgan, R.A. 1982. Some effects of weather conditions on the breeding of the Spotted Flycatcher *Muscicapa striata* in Britain. *Bird Study* 29: 41-48.

O'Connor, R.J. & Shrubb, M. 1986. *Farming and Birds*. Cambridge University Press, Cambridge.

Perrins, C.M. 1970. The timing of birds' breeding seasons. *Ibis* 112: 242-255.

Perrins, C.M. 1979. *British Tits*. Collins, London.

Prŷs-Jones, R.P. 1977. Aspects of Reed Bunting ecology, with comparisons with the Yellowhammer. D.Phil. Thesis, University of Oxford.

SAS Institute Inc. (1985). *SAS User's Guide*. Version 5. SAS Institute Inc., Cary, N.C.

Yom-Tov, Y. in prep. The timing of breeding of British buntings.

Table 1 Sample sizes for analyses of time of breeding and clutch size. Percentages show the distribution of samples for time of breeding between Regions and between Altitudes; total shows the total sample size for time of breeding. The final row shows the percentage by which this total exceeds (or falls short of) the total sample size for clutch size (of which the Regional and Altitudinal distributions are similar to those for time of breeding). Altitudes are metres above sea level.

	Chaffinch	Greenfinch	Linnet	Yellow-hammer	Reed Bunting	Corn Bunting
TOTAL	2161	1944	2463	831	1730	261
REGIONAL PERCENTAGE						
Scotland	11	11	8	3	4	10
Northern England	22	18	21	16	19	11
Southeast England	45	55	59	65	66	68
Southwest England & Wales	22	15	12	16	11	11
ALTITUDINAL PERCENTAGE						
above 99m	30	19	19	34	16	65
50 - 99m	31	26	16	31	19	-
0 - 49m	39	54	65	36	65	35
EXCESS OVER CLUTCH	+33	+6	-1	-36	+9	+60

Table 2 Sample sizes for Mayfield analyses, for egg stage, chick stage and whole nest period. All Regions and Altitudes are combined.

	Egg	Chick	Whole
Chaffinch	3687	2229	4750
Greenfinch	2985	1993	3538
Linnet	3958	2582	4658
Yellowhammer	2620	1561	3405
Reed Bunting	1959	1740	2669
Corn Bunting	212	197	308

Table 3 Parameters of frequency distributions of Dates of First Egg during 1961-89 in all Regions and at all Altitudes. Dates are shown as day/month. The mode shown is the greater of the two, for those distributions that are bimodal. The co-efficient of skew is positive when the distribution has an extended upward tail, negative when there is an extended downward tail.

	Chaffinch	Greenfinch	Linnet	Yellow-hammer	Reed Bunting	Corn Bunting
Mean	10/5	22/5	23/5	2/6	20/5	13/6
Median	8/5	17/5	16/5	26/5	15/5	13/6
Mode	10/5	17/5	7/5	16/5	9/5	30/5
Standard Deviation	13.3	25.3	23.9	24.6	18.3	20.4
5-percentile	21/4	18/4	25/4	1/5	29/4	20/5
95-percentile	3/6	13/7	11/7	21/7	26/7	24/7
Earliest	3/4	21/3	29/3	5/4	4/4	22/4
Latest	16/7	28/8	20/8	22/8	2/8	13/8
Skew	0.61	0.87	1.02	0.86	1.15	-0.05
Sample Size	2161	3677	2463	831	1730	261

Table 4 Results of tests of differences between Regions and between Altitudes in the slopes of regressions of Date of First Egg on Year. Probabilities are those associated with the departure of the variance ratio (F) from 1.0, testing the null hypothesis that there are no differences between Regions or between Altitudes in regression slopes. Linear indicates that a linear regression model was fitted; quadratic indicates the additional effect of fitting a quadratic component. The degrees of freedom shown are those for the residual mean squares for the linear regressions (identical for Regions and Altitudes); those for the quadratic regressions are 6 less (5 less for Corn Bunting); the numerator degrees of freedom for the interaction mean squares were 3 for regions (both linear and quadratic) and 2 for altitudes (both linear and quadratic), except for Corn Bunting where there was only 1 d.f. for altitude. Asterisks pick out results significant at the 5% level.

	Chaffinch	Greenfinch	Linnet	Yellow-hammer	Reed Bunting	Corn Bunting
VARIANCE RATIO						
Region Linear	0.03	0.34	1.38	7.05*	2.08	0.76
Altitude Linear	0.39	1.35	0.71	0.54	0.79	1.14
Region Quadratic	0.35	1.49	3.14*	0.93	1.69	0.70
Altitude Quadratic	0.06	3.57*	0.39	0.33	2.68	0.31
PROBABILITY						
Region Linear	0.99	0.79	0.25	0.0001*	0.10	0.76
Altitude Linear	0.68	0.26	0.49	0.58	0.45	0.29
Region Quadratic	0.79	0.22	0.024*	0.43	0.17	0.55
Altitude Quadratic	0.94	0.028*	0.68	0.72	0.069	0.31
DEGREES OF FREEDOM	2015	1835	2235	683	1578	211

Table 5 Results of tests of the effects on Date of First Egg of Year (Linear regression), Year (Quadratic regression, Altitude, Region, and Altitude x Region Interaction). Probabilities are those associated with the departure of the variance ratio (F) from 1.0, testing the null hypotheses that there are no systematic effects of the variables. The degrees of freedom for the residual mean squares are 4 more than those in Table 4 (3 more for Year (Linear), 3 and 2 more respectively for Corn Bunting); the numerator degrees of freedom for the mean squares of the various effects were 1, 1, 2, 3 and 6 respectively (1, 1, 1, 3 and 3 for Corn Bunting). Asterisks pick out results significant at the 5% level.

	Chaffinch	Greenfinch	Linnet	Yellow-hammer	Reed Bunting	Corn Bunting
VARIANCE RATIO						
Year (Linear)	0.40	13.29*	0.23	0.64	0.17	6.90*
Year (Quadratic)	11.00*	0.68	0.01	1.94	2.19	4.83*
Altitude	24.78*	8.72*	1.30	0.51	0.33	0.01
Region	16.94*	1.20	1.79	7.25*	5.24*	3.29*
Altitude x Region	2.44*	1.84	1.97	1.11	3.82*	4.89*
PROBABILITY						
Year (Linear)	0.53	0.0003*	0.63	0.42	0.68	0.0093*
Year (Quadratic)	0.0009*	0.41	0.91	0.16	0.14	0.029*
Altitude	0.0001*	0.0002*	0.27	0.60	0.72	0.93
Region	0.0001*	0.31	0.15	0.0001*	0.0013*	0.022*
Altitude x Region	0.0237*	0.09	0.066	0.35	0.0009*	0.0084*

Table 6 Mean Dates in May (or June - J) of First Egg according to Altitude and Region. Altitudes are metres above sea level.

	N.England	Scotland	Southeast	Southwest
Chaffinch				
0 - 49m	8	13	8	5
50 - 99m	10	13	8	8
above 99m	16	18	10	10
Greenfinch				
0 - 49m	18	20	20	20
50 - 99m	17	15	25	20
above 99m	29	27	26	29
Linnet				
0 - 49m	23	19	23	22
50 - 99m	24	26	23	23
above 99m	31	23	22	19
Yellowhammer				
0 - 49m	26	22	30	7J
50 - 99m	21	30	5J	31
above 99m	22	16	4J	30
Reed Bunting				
0 - 49m	18	27	18	21
50 - 99m	18	1J	23	17
above 99m	26	27	17	14
Corn Bunting				
0 - 49m	13J	24J	16J	14J
above 49m	31	-	30J	7J

Table 7 Parameters of frequency distributions of Clutch Size during 1961-89 in all Regions and all Altitudes. For explanation, see notes for Table 3.

	Chaffinch	Greenfinch	Linnet	Yellow-hammer	Reed Bunting	Corn Bunting
Mean	4.27	4.70	4.71	3.42	4.48	4.18
Median	4.37	4.82	4.83	3.41	4.60	4.23
Mode	5	5	5	3	5	4
Standard Deviation	0.83	0.81	0.70	0.73	0.72	0.91
Range	1-6	1-7	1-7	1-6	1-8	1-7
Skew	-1.07	-1.09	-1.31	-0.09	-0.96	-0.17
Sample Size	1634	1830	2477	1388	1587	160

Table 8 Results of tests of differences between Regions and between Altitudes in the slopes of regressions of Clutch Size on Year. For explanation, see notes for Table 4.

	Chaffinch	Greenfinch	Linnet	Yellow-hammer	Reed Bunting	Corn Bunting
VARIANCE RATIO						
Region Linear	0.41	2.16	1.59	2.01	0.24	4.30*
Altitude Linear	5.62*	3.37*	1.00	0.06	1.01	0.01
Region Quadratic	1.14	1.45	0.41	0.12	2.77*	0.90
Altitude Quadratic	0.19	3.31*	5.18*	2.81	2.01	8.01*
PROBABILITY						
Region Linear	0.74	0.091	0.19	0.11	0.87	0.0063*
Altitude Linear	0.0037*	0.035*	0.37	0.94	0.36	0.94
Region Quadratic	0.33	0.22	0.74	0.95	0.040*	0.45
Altitude Quadratic	0.83	0.037*	0.0057*	0.061	0.13	0.0054*
DEGREES OF FREEDOM						
Linear	1497	1722	2253	1101	1441	131
Quadratic	1491	1716	2247	1095	1435	126

Table 9 Results of tests of the effects on Clutch Size of Year (Linear regression), Year (Quadratic regression), Altitude, Region, and Altitude x Region interaction. For explanation, see notes for Table 5.

	Chaffinch	Greenfinch	Linnet	Yellow-hammer	Reed Bunting	Corn Bunting
VARIANCE RATIO						
Year (Linear)	0.56	0.02	0.80	2.40	1.77	6.34*
Year (Quadratic)	2.11	0.53	0.16	2.01	2.02	0.63
Altitude	0.57	3.99*	0.28	0.14	1.63	0.04
Region	1.17	0.14	3.18*	3.70*	3.12*	1.26
Altitude x Region	2.80*	2.83*	3.88*	2.95*	2.57*	0.31
PROBABILITY						
Year (Linear)	0.45	0.88	0.37	0.12	0.18	0.013*
Year (Quadratic)	0.15	0.47	0.69	0.16	0.16	0.43
Altitude	0.56	0.019*	0.76	0.87	0.20	0.83
Region	0.32	0.94	0.023*	0.011*	0.025*	0.29
Altitude x Region	0.010*	0.0096*	0.0007*	0.007*	0.018*	0.73
DEGREES OF FREEDOM	1501	1726	2257	1105	1445	134

Table 10 Mean Clutch Sizes according to Altitude and Region. Altitudes are metres above sea level.

	N.England	Scotland	Southeast	Southwest
Chaffinch				
0 - 49m	4.31	4.18	4.13	4.44
50 - 99m	4.19	4.29	4.41	4.29
above 99m	4.38	4.09	4.27	4.22
Greenfinch				
0 - 49m	4.52	4.61	4.73	4.73
50 - 99m	4.88	5.00	4.71	4.72
above 99m	4.82	4.48	4.76	4.65
Linnet				
0 - 49m	4.68	4.70	4.71	4.78
50 - 99m	4.72	4.75	4.61	4.84
above 99m	4.97	4.35	4.75	4.68
Yellowhammer				
0 - 49m	3.44	3.22	3.40	3.58
50 - 99m	3.22	3.25	3.54	3.44
above 99m	3.23	3.56	3.50	3.31
Reed Bunting				
0 - 49m	4.49	4.17	4.47	4.39
50 - 99m	4.63	4.33	4.44	4.49
above 99m	4.52	4.40	4.80	4.33
Corn Bunting				
0 - 49m	3.69	4.23	4.10	4.40
50 - 99m	-	-	-	-
above 99m	4.00	-	4.30	4.12

Table 11 Mean daily rates of loss of nests during 1962-89 in all species, at egg stage, at chick stage, and over the whole nest period.

MEANS	Egg	Chick	Whole
Chaffinch	0.0304	0.0327	0.0376
Greenfinch	0.0241	0.0214	0.0285
Linnet	0.0249	0.0210	0.0264
Yellowhammer	0.0452	0.0452	0.0462
Reed Bunting	0.0108	0.0255	0.0245
Corn Bunting	0.0565	0.0299	0.0404
STANDARD ERRORS			
Chaffinch	0.0068	0.0111	0.0059
Greenfinch	0.0042	0.0075	0.0033
Linnet	0.0057	0.0070	0.0051
Yellowhammer	0.0111	0.0163	0.0068
Reed Bunting	0.0050	0.0100	0.0070
Corn Bunting	0.1152	0.0497	0.0700

Table 12 Results for Chaffinch of tests of regression of rates of nest loss on Year and of the differences in mean rates and in regression slopes between different Regions and Altitudes. Results are quoted for egg stage, for chick stage, and for the whole nest period. Within each, Year effects (both linear and quadratic) were tested over all Regions and Altitudes combined as well as when taking Region and Altitude into account, i.e. when both the main effects of Region and Altitude and their interactions with Year (both linear and quadratic) were also tested. Note that interactions of Region with Altitude were not tested. Asterisks pick out results significant at the 5% level. For further explanation, see Methods and Appendix.

	F-ratio			Probability		
	Overall	Region	Altitude	Overall	Region	Altitude
EGG STAGE						
Year, Linear	9.32*	7.73*	9.47*	0.0052*	0.0064*	0.0029*
Year, Quadratic	0.29	0.11	0.96	0.60	0.74	0.33
Region or Altitude	-	1.03	2.27	-	0.38	0.11
Interaction, Linear	-	0.87	2.33	-	0.46	0.10
Interaction, Quadratic	-	0.01	0.26	-	1.00	0.77
CHICK STAGE						
Year, Linear	0.02	0.29	0.01	0.90	0.59	0.91
Year, Quadratic	0.72	1.51	4.22*	0.40	0.22	0.044*
Region or Altitude	-	1.47	1.33	-	0.23	0.27
Interaction, Linear	-	1.11	0.25	-	0.35	0.78
Interaction, Quadratic	-	0.36	4.98*	-	0.78	0.0093*
WHOLE NEST PERIOD						
Year, Linear	0.06	1.22	0.12	0.81	0.27	0.73
Year, Quadratic	1.80	0.83	0.93	0.19	0.36	0.34
Region or Altitude	-	1.75	4.69*	-	0.16	0.012*
Interaction, Linear	-	1.59	4.70*	-	0.20	0.012*
Interaction, Quadratic	-	0.20	1.49	-	0.89	0.23

Table 13 Mean daily rates of loss of nests in different Regions during 1962-89, at egg stage, at chick stage, and over the whole nest period. Sample sizes for Corn Bunting were too small to allow reliable estimates to be made.

	Chaffinch	Greenfinch	Linnet	Yellowhammer	Reed Bunting
EGG STAGE					
Scotland	0.0261	0.0322	0.0374	0.0935	0.0145
Northern England	0.0333	0.0283	0.0229	0.0489	0.0152
Southeast England	0.0316	0.0232	0.0240	0.0435	0.0109
Southwest England & Wales	0.0311	0.0256	0.0311	0.0518	0.0176
CHICK STAGE					
Scotland	0.0260	0.0171	0.0516	0.0411	0.0208
Northern England	0.0307	0.0144	0.0162	0.0563	0.0180
Southeast England	0.0339	0.0238	0.0225	0.0454	0.0296
Southwest England & Wales	0.0464	0.0237	0.0169	0.0482	0.0277
WHOLE PERIOD					
Scotland	0.0308	0.0323	0.0437	0.0439	0.0256
Northern England	0.0307	0.0298	0.0254	0.0484	0.0236
Southeast England	0.0395	0.0295	0.0271	0.0453	0.0261
Southwest England & Wales	0.0402	0.0271	0.0265	0.0492	0.0269

Table 14 Mean daily rates of loss of nests at different Altitudes during 1962-89, at egg stage, at chick stage, and over the whole nest period. Sample sizes for Corn Bunting were too small to allow reliable estimates to be made. Altitudes are metres above sea level.

	Chaffinch	Greenfinch	Linnet	Yellowhammer	Reed Bunting
EGG STAGE					
above 99m	0.0306	0.0280	0.0258	0.0512	0.0169
50 - 99m	0.0302	0.0249	0.0250	0.0486	0.0106
0 - 49m	0.0313	0.0241	0.0248	0.0434	0.0100
CHICK STAGE					
above 99m	0.0406	0.0181	0.0200	0.0450	0.0292
50 - 99m	0.0350	0.0230	0.0291	0.0522	0.0227
0 - 49m	0.0307	0.0227	0.0214	0.0418	0.0282
WHOLE PERIOD					
above 99m	0.0380	0.0295	0.0268	0.0499	0.0306
50 - 99m	0.0390	0.0301	0.0291	0.0490	0.0216
0 - 49m	0.0369	0.0291	0.0258	0.0429	0.0252

Table 15 Results for Greeenfinch of tests of regression of rates of nest loss on Year and of the differences in mean rates and in regression slopes between different Regions and Altitudes. For further explanation, see notes to Table 12.

	F-ratio			Probability		
	Overall	Region	Altitude	Overall	Region	Altitude
EGG STAGE						
Year, Linear	15.76*	5.71*	4.69*	0.0005*	0.019*	0.033*
Year, Quadratic	6.84*	1.80	5.52*	0.015*	0.18	0.021*
Region or Altitude	-	0.39	0.15	-	0.76	0.86
Interaction, Linear	-	0.36	0.17	-	0.78	0.84
Interaction, Quadratic	-	0.56	1.13	-	0.64	0.33
CHICK STAGE						
Year, Linear	0.01	0.06	0.72	0.94	0.81	0.40
Year, Quadratic	0.67	0.01	0.25	0.42	0.93	0.62
Region or Altitude	-	1.35	0.96	-	0.26	0.39
Interaction, Linear	-	1.06	0.80	-	0.37	0.45
Interaction, Quadratic	-	1.73	0.89	-	0.17	0.42
WHOLE NEST PERIOD						
Year, Linear	8.07*	2.46	1.97	0.0086*	0.12	0.16
Year, Quadratic	0.13	0.07	1.88	0.72	0.78	0.17
Region or Altitude	-	0.72	0.08	-	0.54	0.92
Interaction, Linear	-	0.82	0.52	-	0.49	0.60
Interaction, Quadratic	-	0.10	1.92	-	0.96	0.15

Table 16 Results for Linnet of tests of regression of rates of nest loss on Year and of the differences in mean rates and in regression slopes between different Regions and Altitudes. For further explanation, see notes to Table 12.

	F-ratio			Probability		
	Overall	Region	Altitude	Overall	Region	Altitude
EGG STAGE						
Year, Linear	4.75*	0.00	0.44	0.039*	0.94	0.51
Year, Quadratic	1.32	1.28	0.28	0.26	0.26	0.60
Region or Altitude	-	1.47	0.06	-	0.23	0.94
Interaction, Linear	-	1.19	0.39	-	0.32	0.68
Interaction, Quadratic	-	0.85	3.75*	-	0.47	0.028*
CHICK STAGE						
Year, Linear	0.80	1.06	0.12	0.36	0.31	0.73
Year, Quadratic	1.18	0.33	2.39	0.29	0.57	0.13
Region or Altitude	-	1.76	0.43	-	0.16	0.65
Interaction, Linear	-	1.30	0.49	-	0.28	0.61
Interaction, Quadratic	-	0.13	0.18	-	0.94	0.83
WHOLE NEST PERIOD						
Year, Linear	8.60*	0.09	5.17*	0.0069*	0.77	0.026*
Year, Quadratic	0.59	0.06	0.43	0.45	0.81	0.52
Region or Altitude	-	0.78	2.78	-	0.51	0.068
Interaction, Linear	-	0.51	2.84	-	0.68	0.064
Interaction, Quadratic	-	0.25	0.05	-	0.86	0.95

Table 17 Results for Yellowhammer of tests of regression of rates of nest loss on Year and of the differences in mean rates and in regression slopes between different Regions and Altitudes. For further explanation, see notes to Table 12.

	F-ratio			Probability		
	Overall	Region	Altitude	Overall	Region	Altitude
EGG STAGE						
Year, Linear	49.14*	1.51	24.70*	0.0001*	0.22	0.0001*
Year, Quadratic	0.39	0.46	1.05	0.54	0.50	0.36
Region or Altitude	-	0.03	0.20	-	0.99	0.65
Interaction, Linear	-	0.06	1.09	-	0.98	0.34
Interaction, Quadratic	-	0.46	0.26	-	0.71	0.77
CHICK STAGE						
Year, Linear	13.19*	6.70*	8.14*	0.0012*	0.011*	0.0049*
Year, Quadratic	1.46	0.01	0.63	0.24	0.94	0.43
Region or Altitude	-	0.53	6.11*	-	0.66	0.0034*
Interaction, Linear	-	0.47	5.98*	-	0.70	0.0038*
Interaction, Quadratic	-	0.57	0.18	-	0.63	0.83
WHOLE NEST PERIOD						
Year, Linear	39.48*	6.21*	15.69*	0.0001*	0.014*	0.0002*
Year, Quadratic	0.46	0.24	0.58	0.50	0.62	0.45
Region or Altitude	-	0.44	0.87	-	0.73	0.42
Interaction, Linear	-	0.41	1.13	-	0.75	0.33
Interaction, Quadratic	-	0.22	0.79	-	0.88	0.46

Table 18 Results for Reed Bunting of tests of regression of rates of nest loss on Year and of the differences in mean rates and in regression slopes between different Regions and Altitudes. For further explanation, see notes to Table 12.

	F-ratio			Probability		
	Overall	Region	Altitude	Overall	Region	Altitude
EGG STAGE						
Year, Linear	0.49	0.02	0.01	0.49	0.88	0.94
Year, Quadratic	4.57*	1.93	0.10	0.042*	0.17	0.75
Region or Altitude	-	0.12	0.69	-	0.95	0.50
Interaction, Linear	-	0.02	0.55	-	1.00	0.58
Interaction, Quadratic	-	1.79	0.77	-	0.15	0.47
CHICK STAGE						
Year, Linear	5.73*	1.25	0.09	0.024*	0.27	0.76
Year, Quadratic	0.03	3.06	0.27	0.86	0.083	0.61
Region or Altitude	-	1.01	3.39*	-	0.39	0.039*
Interaction, Linear	-	1.07	3.48*	-	0.36	0.036*
Interaction, Quadratic	-	1.04	0.30	-	0.38	0.74
WHOLE NEST PERIOD						
Year, Linear	0.17	0.96	0.11	0.68	0.33	0.74
Year, Quadratic	5.48*	1.49	1.05	0.028*	0.22	0.31
Region or Altitude	-	0.35	0.54	-	0.79	0.58
Interaction, Linear	-	0.33	0.42	-	0.81	0.66
Interaction, Quadratic	-	3.35*	0.36	-	0.022*	0.70

Table 19 Results for Corn Bunting of tests of regression of rates of nest loss on year. Because small sample sizes render them so insensitive, results of tests involving differences between Regions and Altitudes are omitted. For further explanation, see notes to Table 12.

	F-ratio	Probability
EGG STAGE		
Linear	0.01	0.91
Quadratic	0.30	0.59
CHICK STAGE		
Linear	3.22	0.085
Quadratic	0.01	0.91
OVERALL		
Linear	0.47	0.50
Quadratic	0.07	0.80

Table 20 Percentage losses of nests during the whole of the egg stage, chick stage, and whole nest period. The values are calculated from the estimates of daily rates in Table 11, using the incubation and nestling periods shown here. Note that, since the estimates presented here for the whole nest period are based on larger samples than those for the egg and chick periods, they are better estimates than could be obtained by combining the estimates for egg and chick periods.

	Losses			Periods (days)	
	Egg	Chick	Whole	Incubation	Nestling
Chaffinch	39	37	68	16	14
Greenfinch	34	28	60	17	15
Linnet	36	24	56	18	13
Yellowhammer	40	50	71	11	15
Reed Bunting	15	27	49	15	12
Corn Bunting	65	31	71	18	12

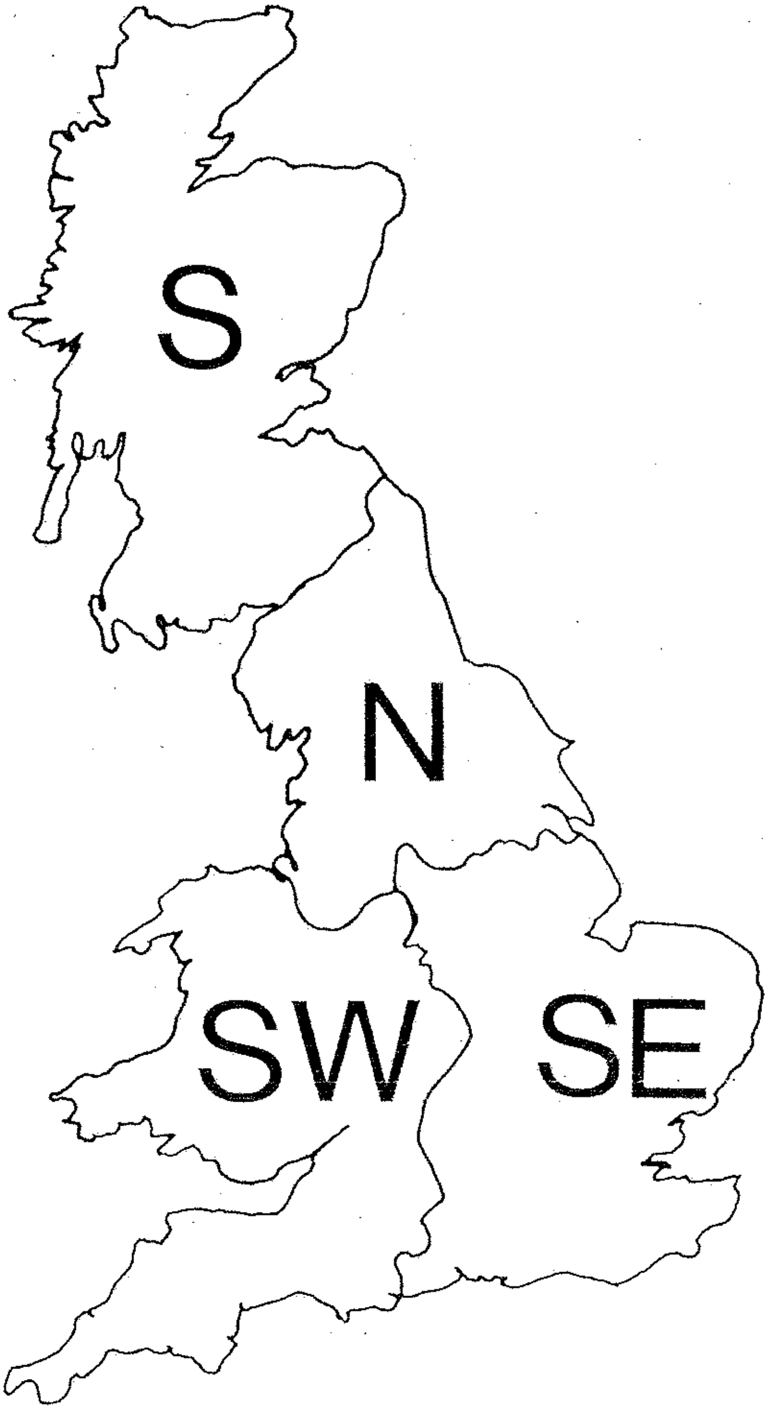


Figure 1 The regional divisions used in this study. S = Scotland, N = Northern England, SW = Southwest England and Wales, SE = Southeast England. Offshore islands were included in the nearest mainland region.

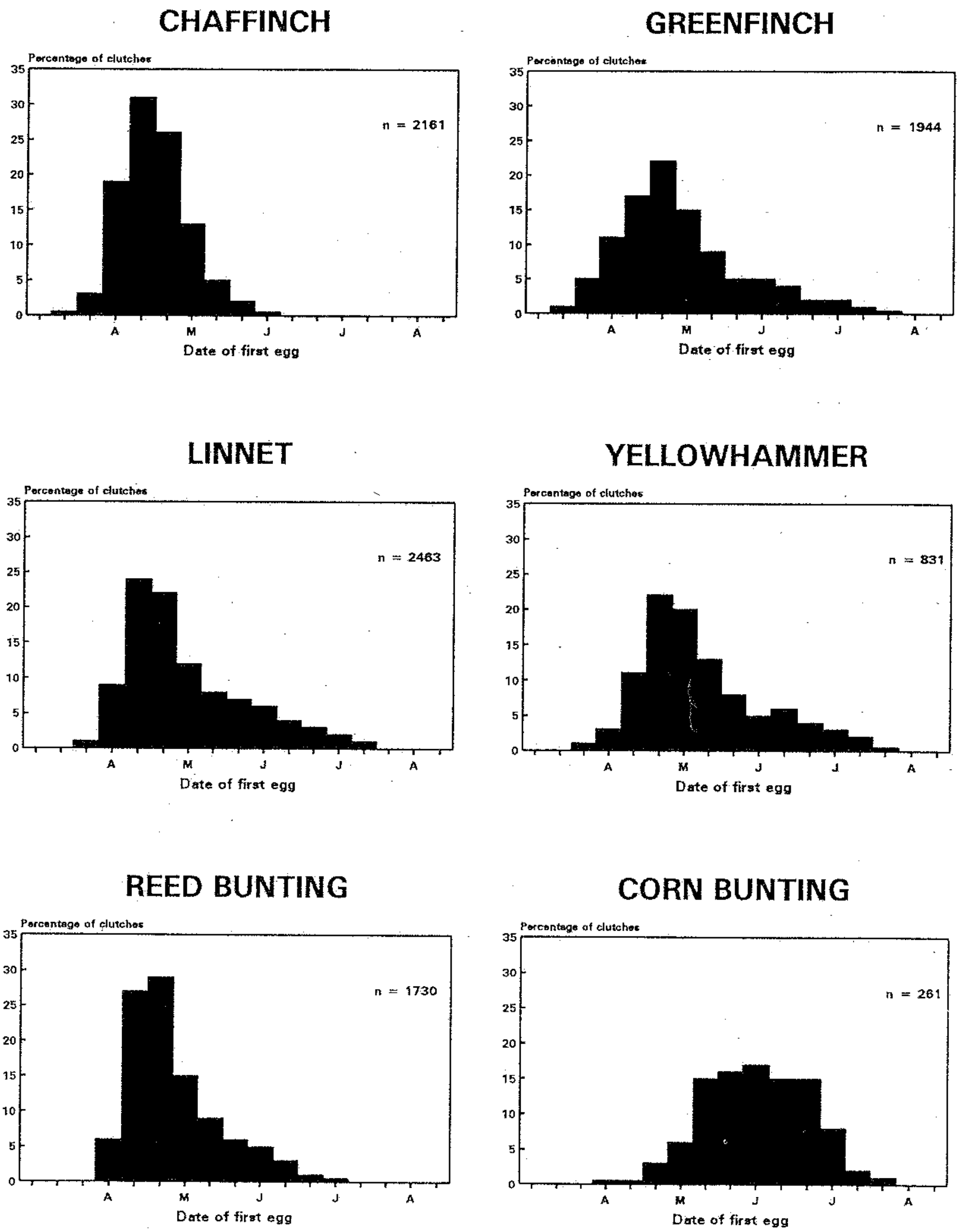
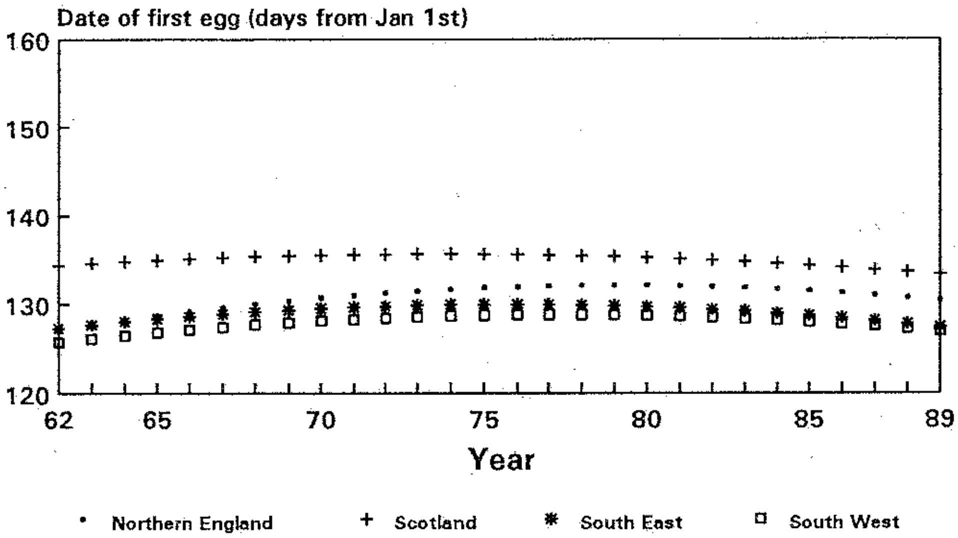


Figure 2 Frequency distributions of Date of First Egg during 1962-89, in all Regions and Altitudes combined. Letters indicate approximate midpoints of months.

CHAFFINCH

Regional trends in date of first egg



Altitudinal trends in date of first egg

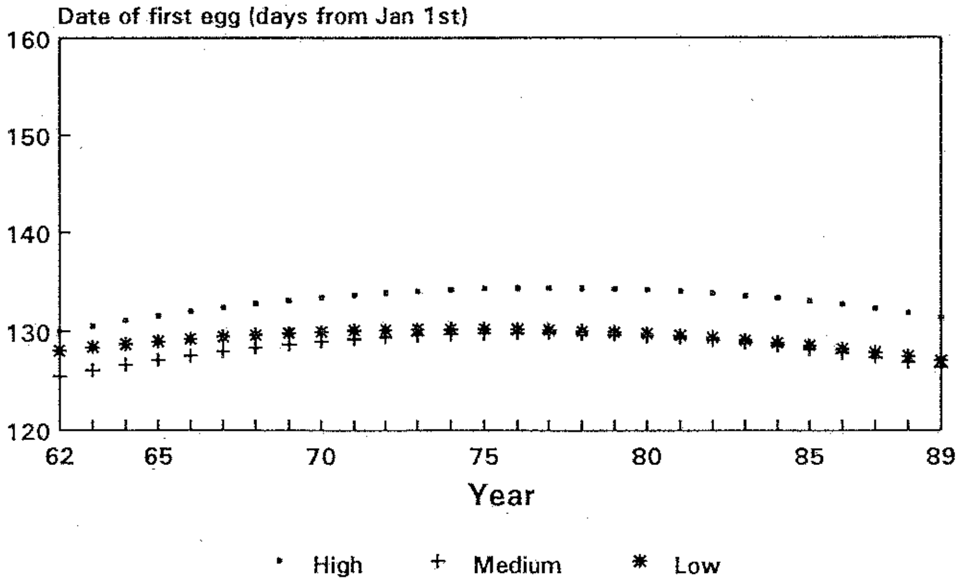
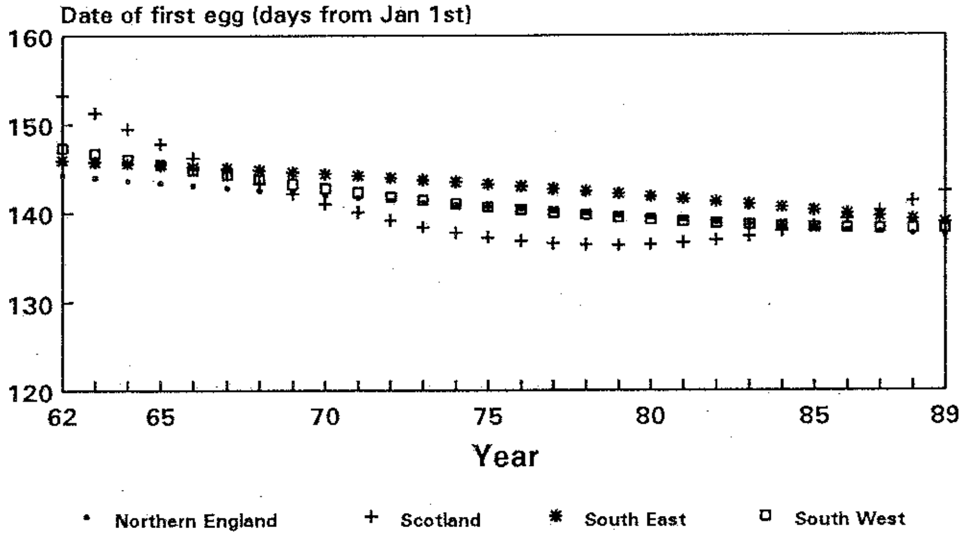


Figure 3 Temporal trends in Date of First Egg for Chaffinch and year during 1962-89 for various Regions (upper) and Altitudes (lower). Curves fitted by quadratic regression. Note that day 140 is 20 May.

GREENFINCH

Regional trends in date of first egg



Altitudinal trends in date of first egg

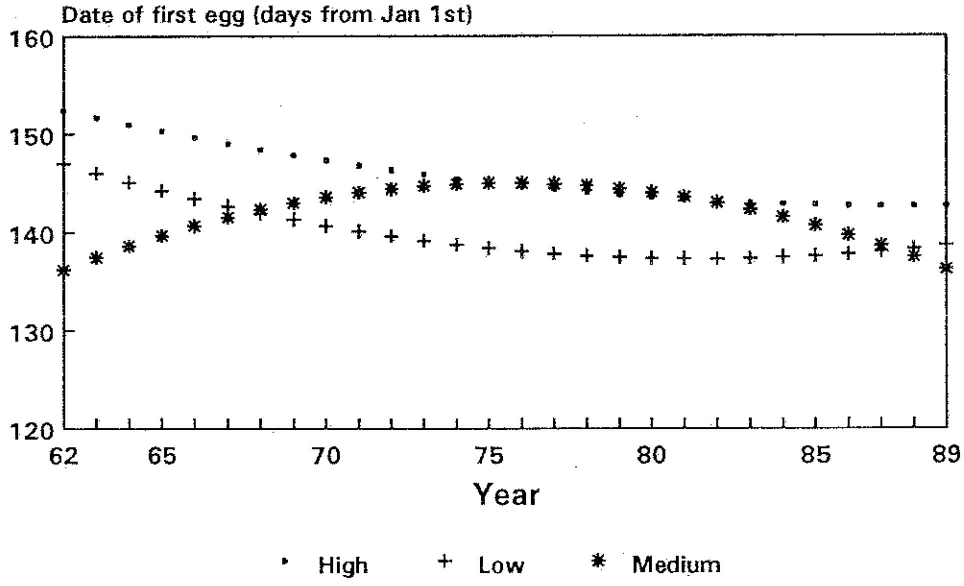
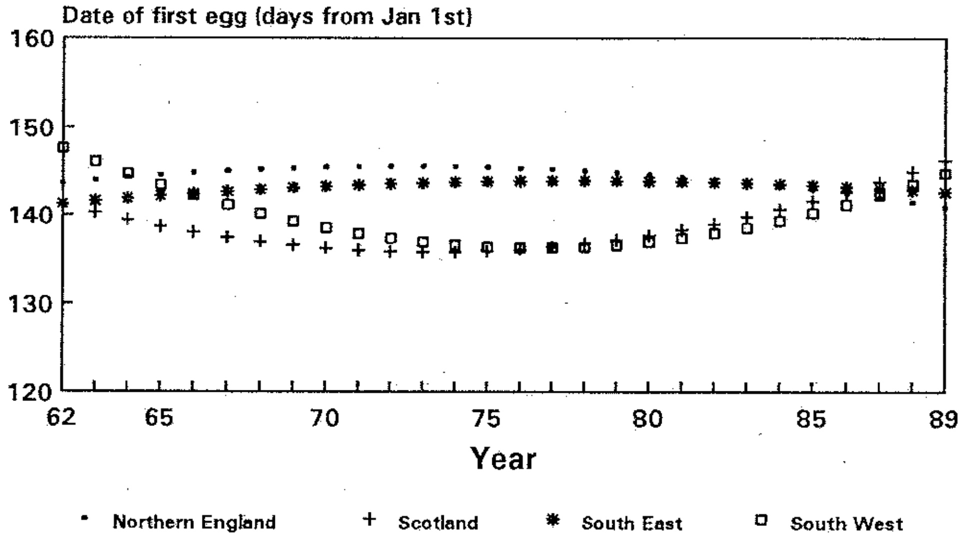


Figure 4 Temporal trends in Date of First Egg for Greenfinch and year during 1962-89 for various Regions (upper) and Altitudes (lower). Curves fitted by quadratic regression. Note that day 140 is 20 May.

LINNET

Regional trends in date of first egg



Altitudinal trends in date of first egg

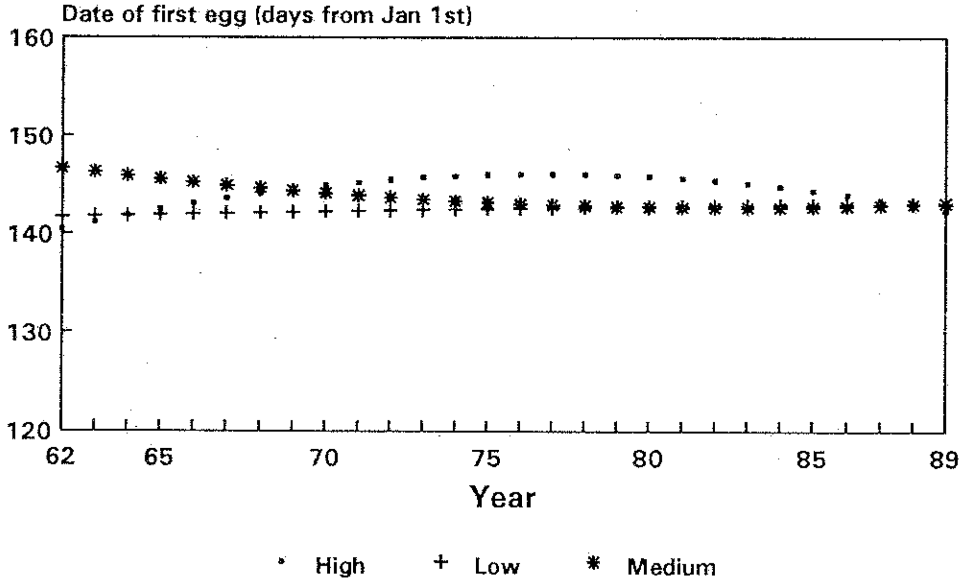
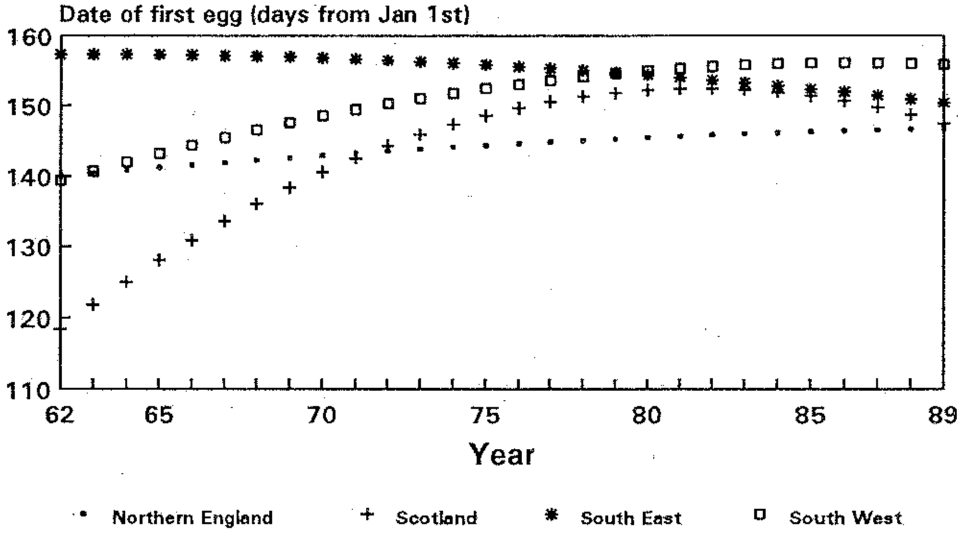


Figure 5 Temporal trends in Date of First Egg for Linnet and year during 1962-89 for various Regions (upper) and Altitudes (lower). Curves fitted by quadratic regression. Note that day 140 is 20 May.

YELLOWHAMMER

Regional trends in date of first egg



Altitudinal trends in date of first egg

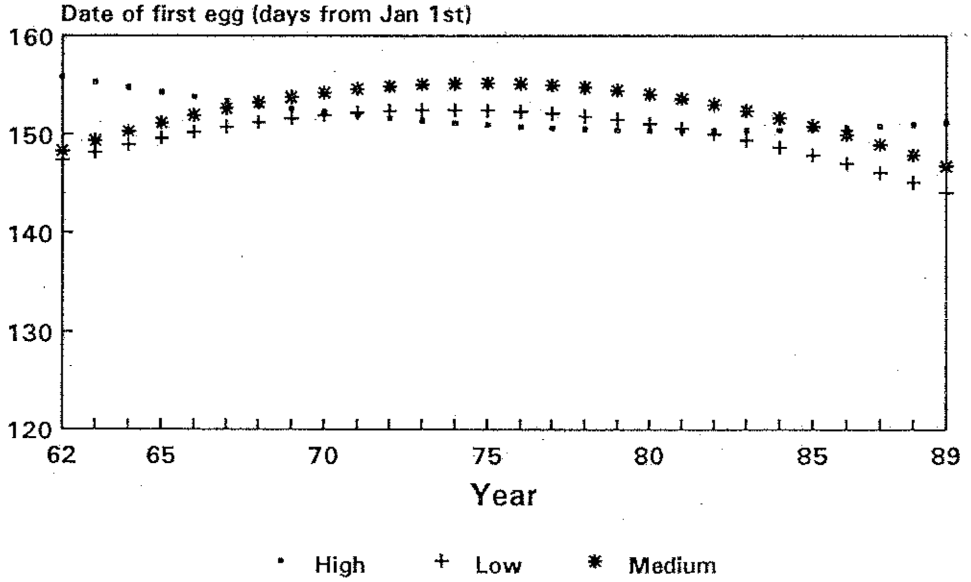
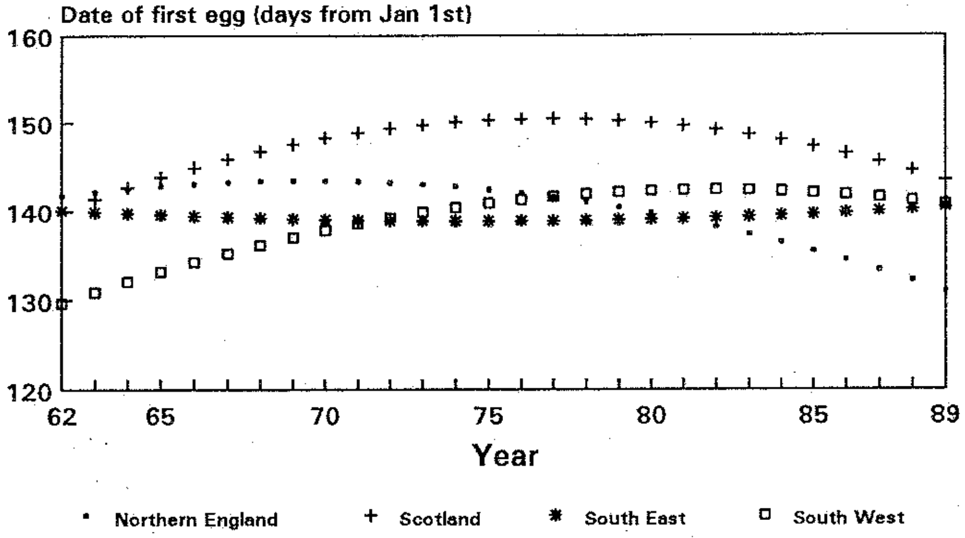


Figure 6 Temporal trends in Date of First Egg for Yellowhammer and year during 1962-89 for various Regions (upper) and Altitudes (lower). Curves fitted by quadratic regression. Note that day 140 is 20 May.

REED BUNTING

Regional trends in date of first egg



Altitudinal trends in date of first egg

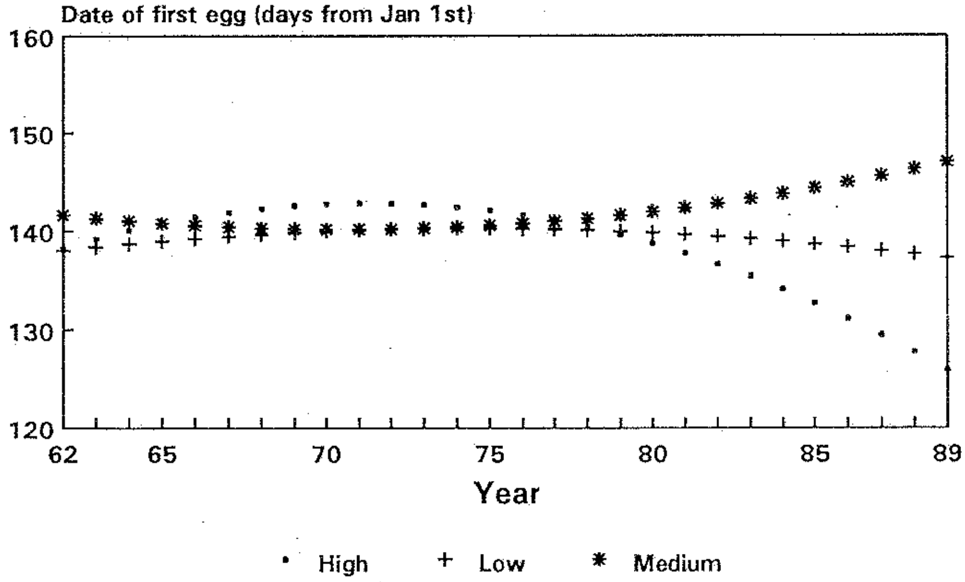
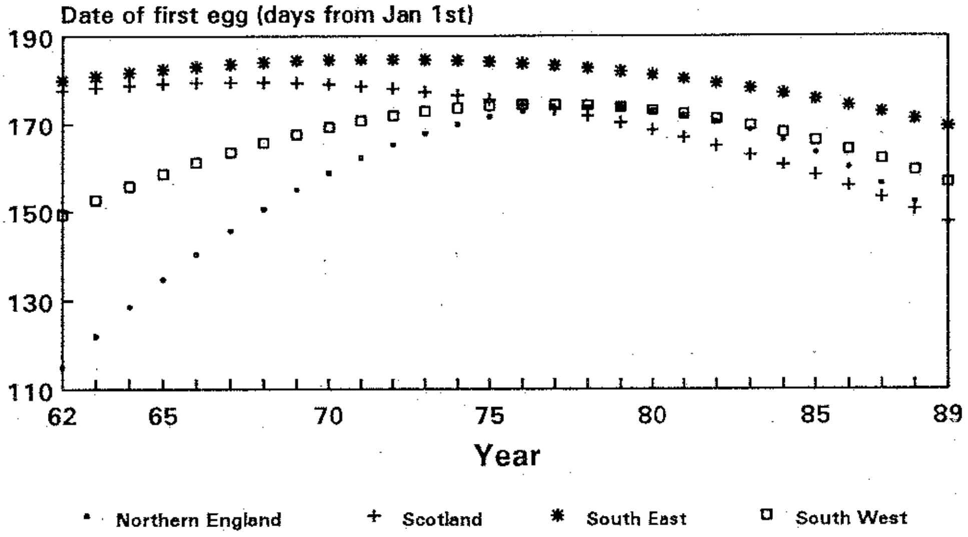


Figure 7 Temporal trends in Date of First Egg for Reed Bunting and year during 1962-89 for various Regions (upper) and Altitudes (lower). Curves fitted by quadratic regression. Note that day 140 is 20 May.

CORN BUNTING

Regional trends in date of first egg



Altitudinal trends in date of first egg

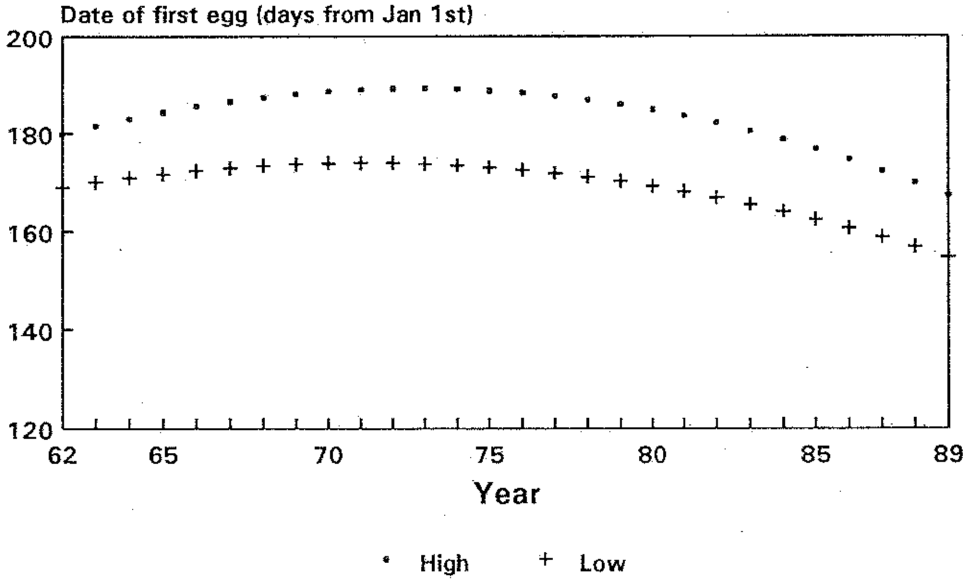
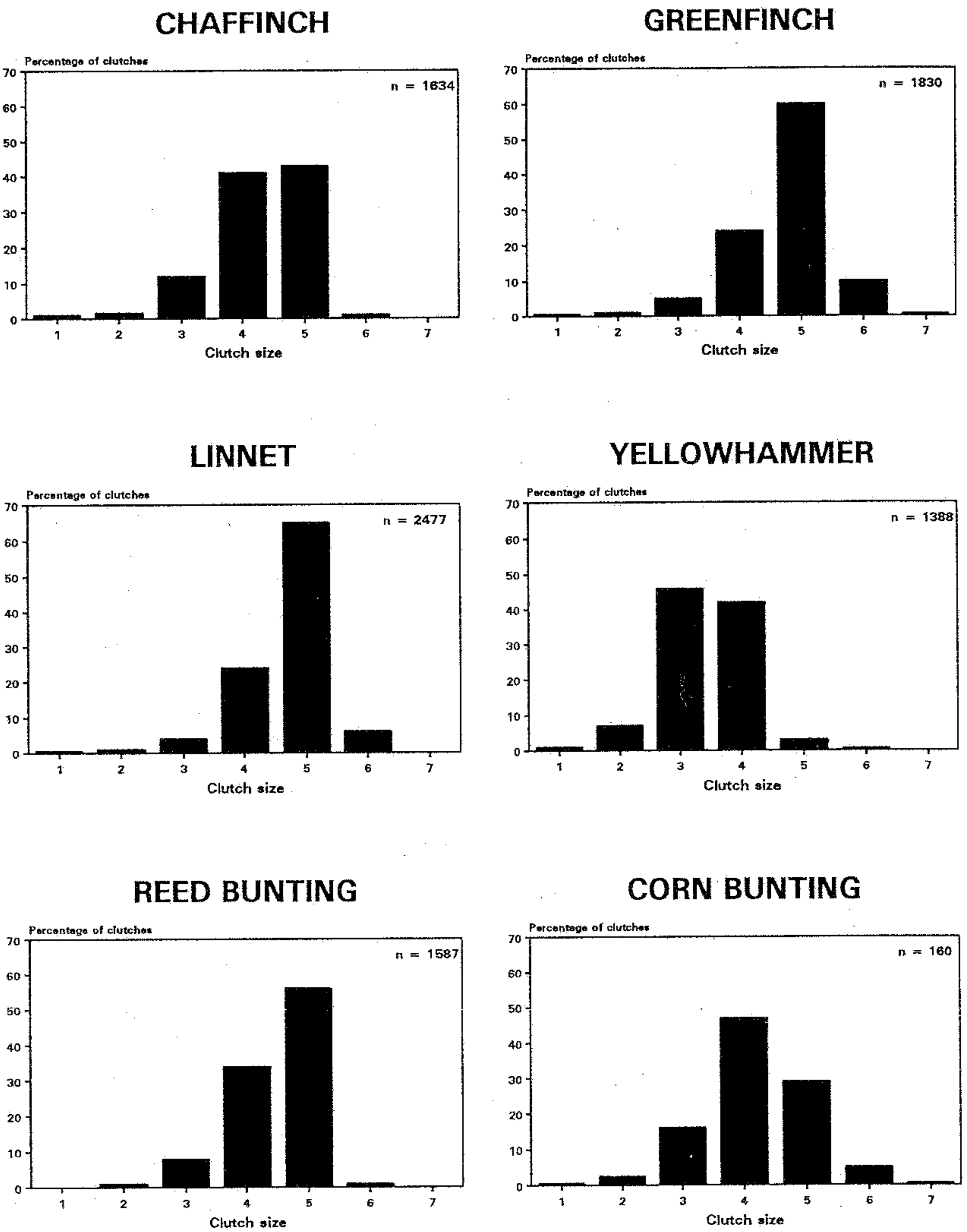


Figure 8 Temporal trends in Date of First Egg for Corn Bunting and year during 1962-89 for various Regions (upper) and Altitudes (lower). Curves fitted by quadratic regression. Note that day 140 is 20 May.



CHAFFINCH

GREENFINCH

LINNET

YELLOWHAMMER

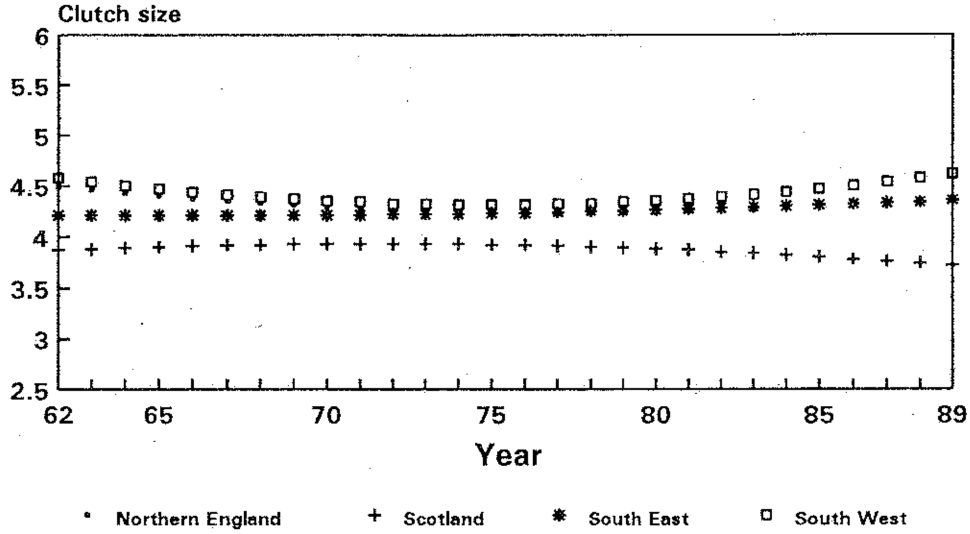
REED BUNTING

CORN BUNTING

Figure 9 Frequency distributions of Clutch Size during 1962-89, in all Regions and Altitudes combined.

CHAFFINCH

Regional trends in clutch size



Altitudinal trends in clutch size

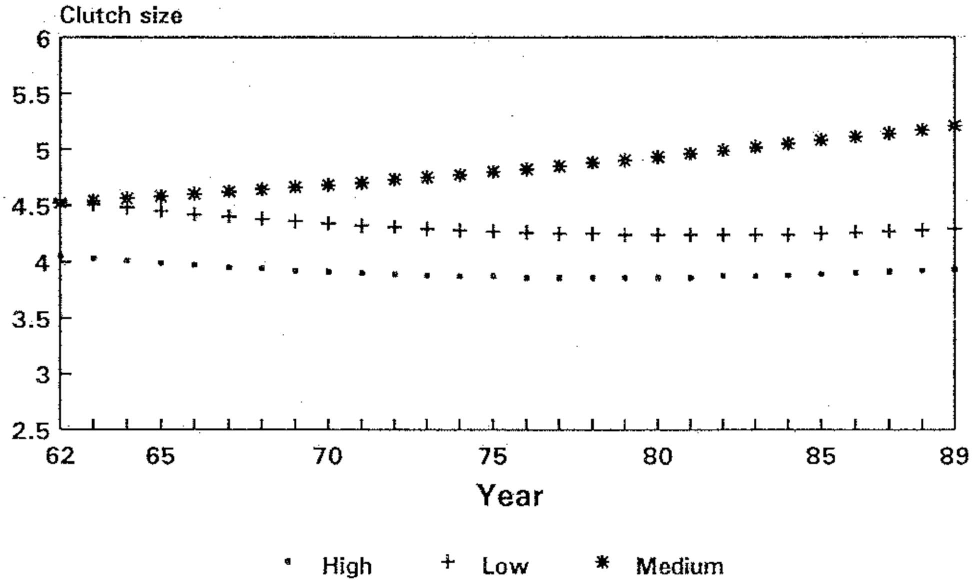
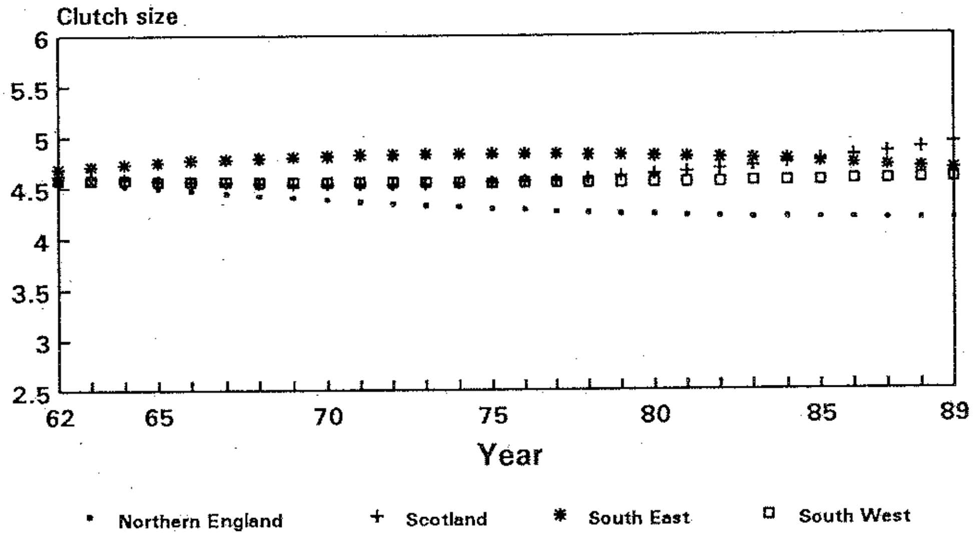


Figure 10 Temporal trends in Clutch Size of Chaffinch during 1962-89 for various Regions (upper) and Altitudes (lower). Curves fitted by quadratic regression.

GREENFINCH

Regional trends in clutch size



Altitudinal trends in clutch size

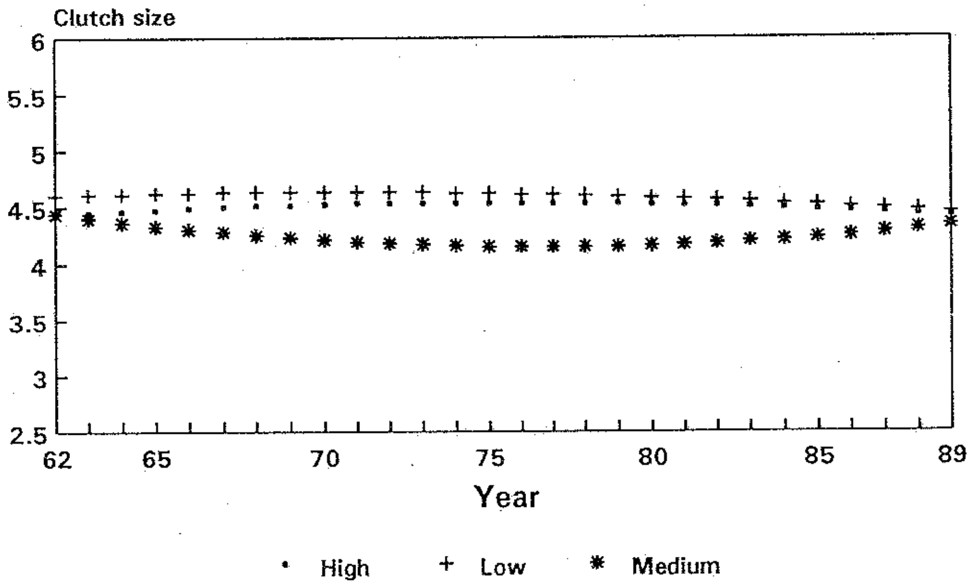
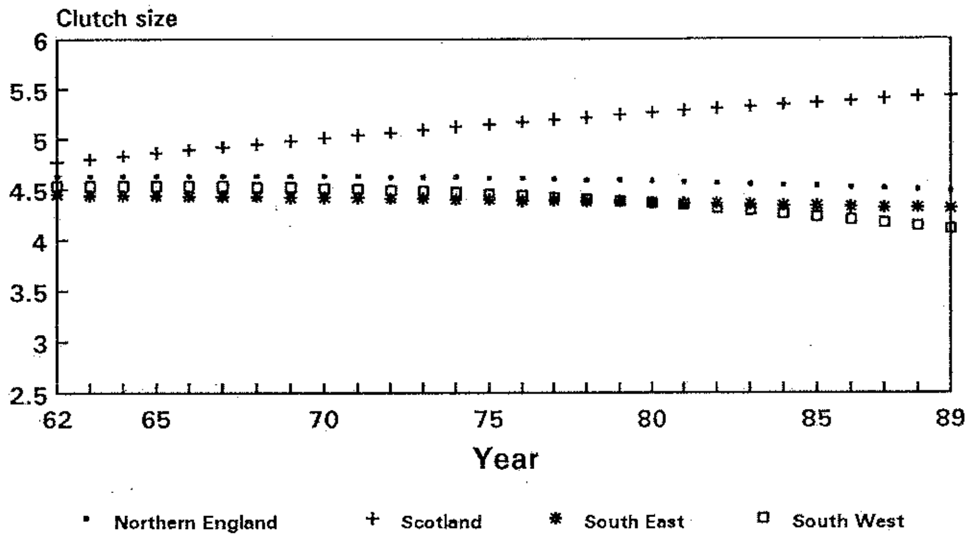


Figure 11 Temporal trends in Clutch Size of Greenfinch during 1962-89 for various Regions (upper) and Altitudes (lower). Curves fitted by quadratic regression.

LINNET

Regional trends in clutch size



Altitudinal trends in clutch size

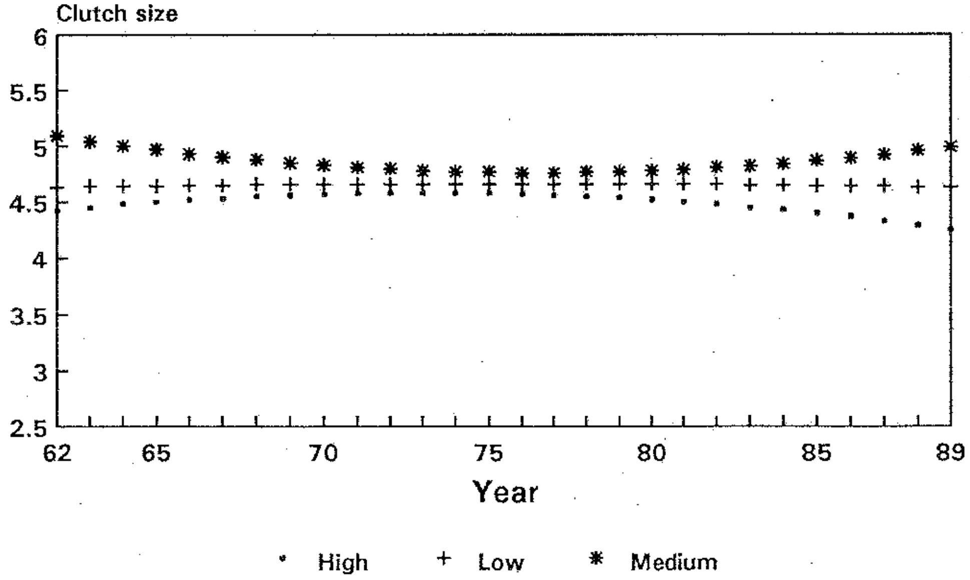
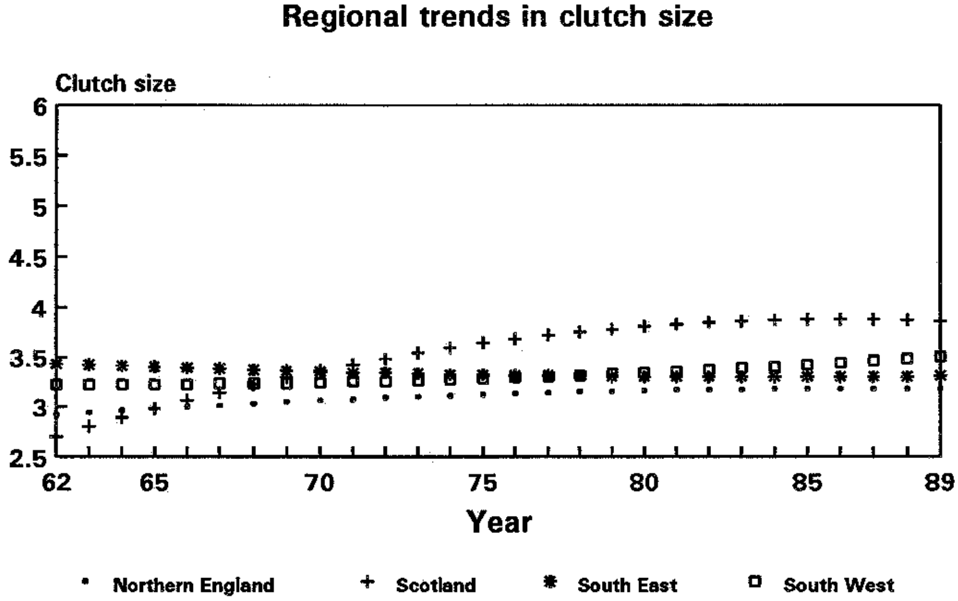


Figure 12 Temporal trends in Clutch Size of Linnet during 1962-89 for various Regions (upper) and Altitudes (lower). Curves fitted by quadratic regression.

YELLOWHAMMER



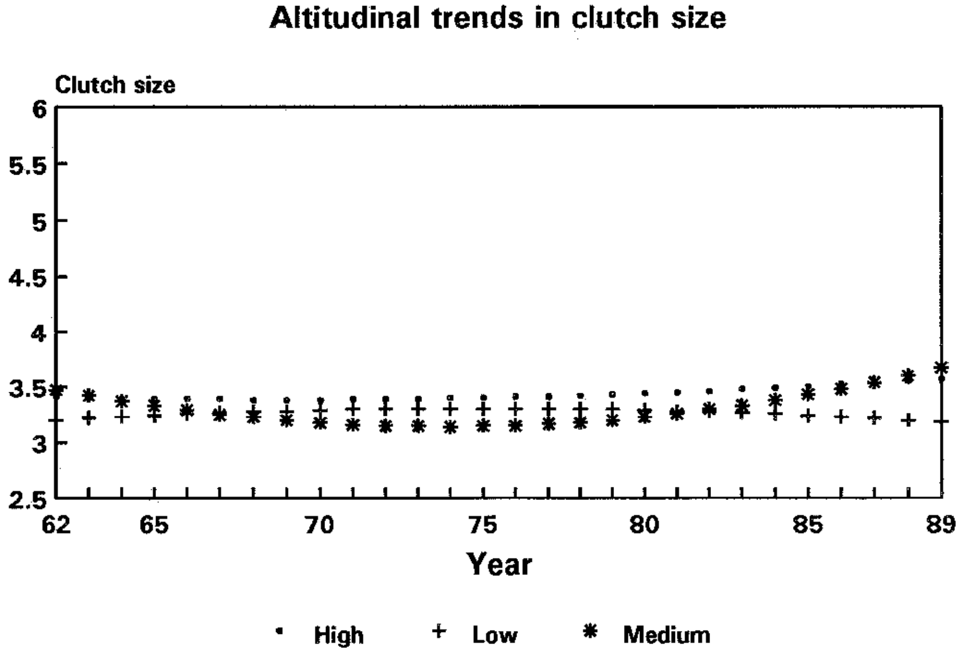
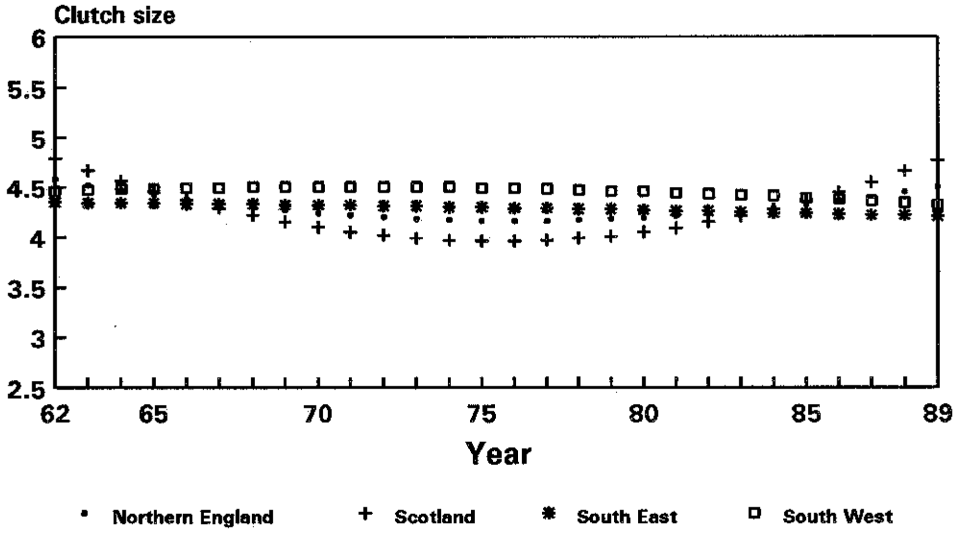


Figure 13 Temporal trends in Clutch Size of Yellowhammer during 1962-89 for various Regions (upper) and Altitudes (lower). Curves fitted by quadratic regression.

REED BUNTING

Regional trends in clutch size



Altitudinal trends in clutch size

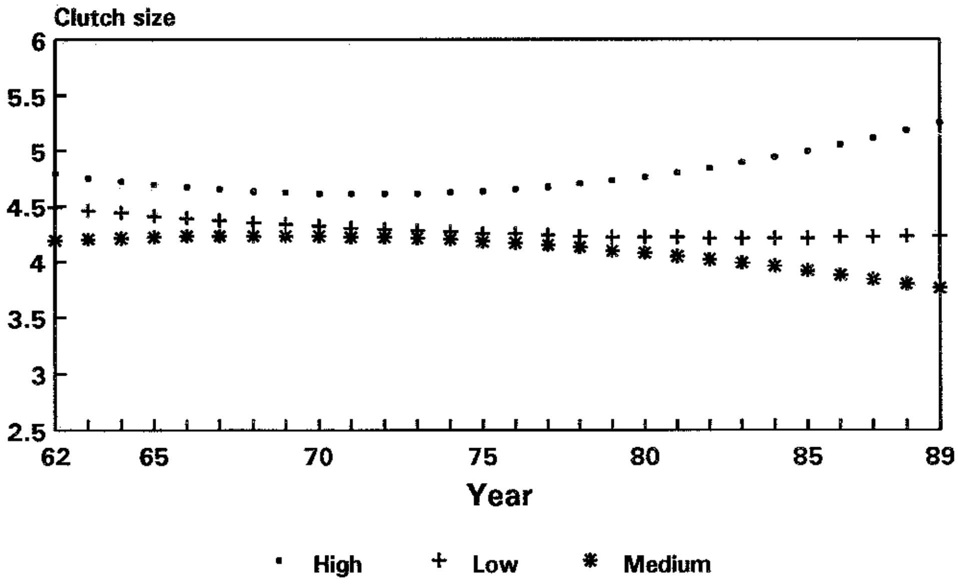
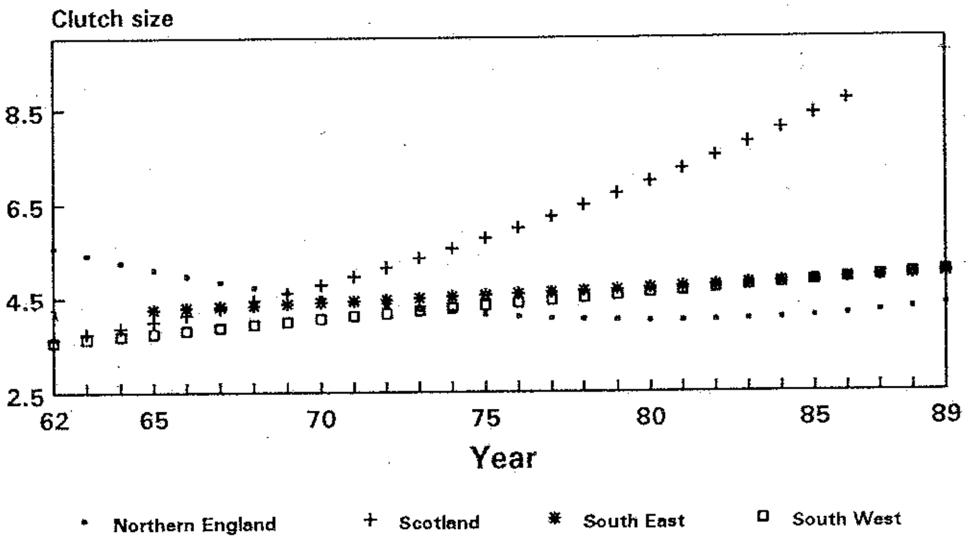


Figure 14 Temporal trends in Clutch Size of Reed Bunting during 1962-89 for various Regions (upper) and Altitudes (lower). Curves fitted by quadratic regression.

CORN BUNTING

Regional trends in clutch size



Altitudinal trends in clutch size

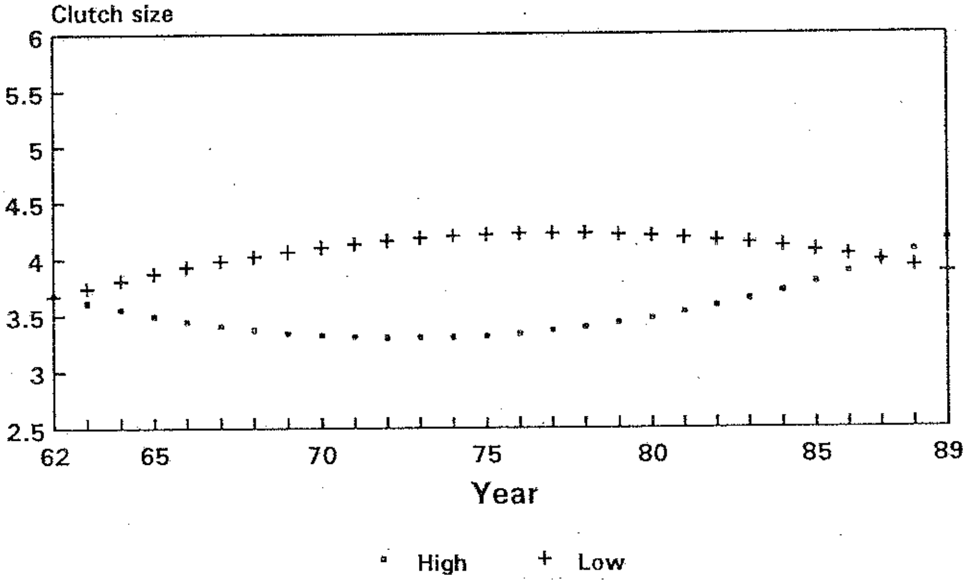


Figure 15 Temporal trends in Clutch Size of Corn Bunting during 1962-89 for various Regions (upper) and Altitudes (lower). Curves fitted by quadratic regression.

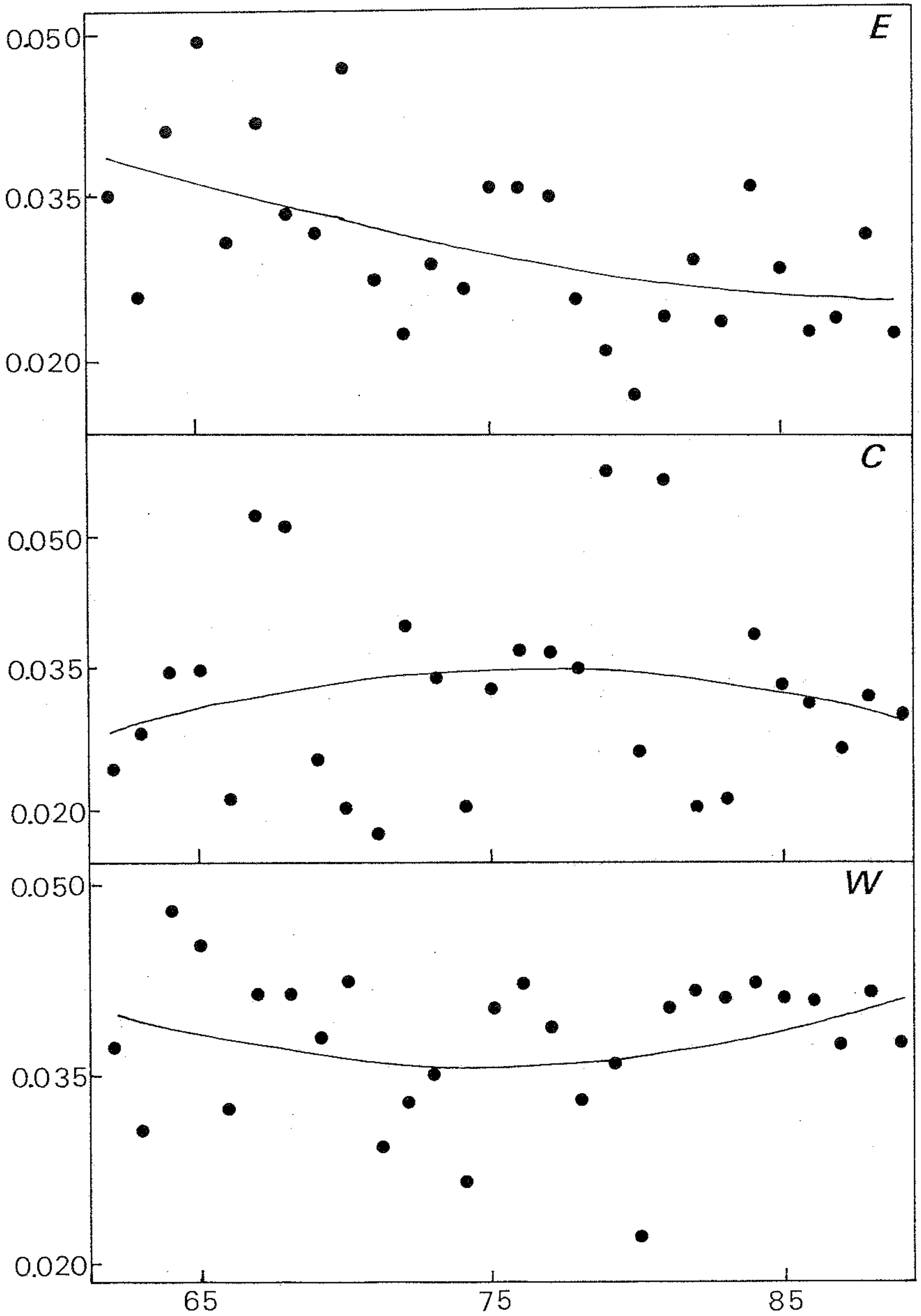


Figure 16 Temporal trends in daily rates of nest losses for Chaffinch during 1962-89 for all Regions and Altitudes combined. E = egg stage, C = chick stage, W = whole nest period. Points show annual values; curves fitted by quadratic regression.

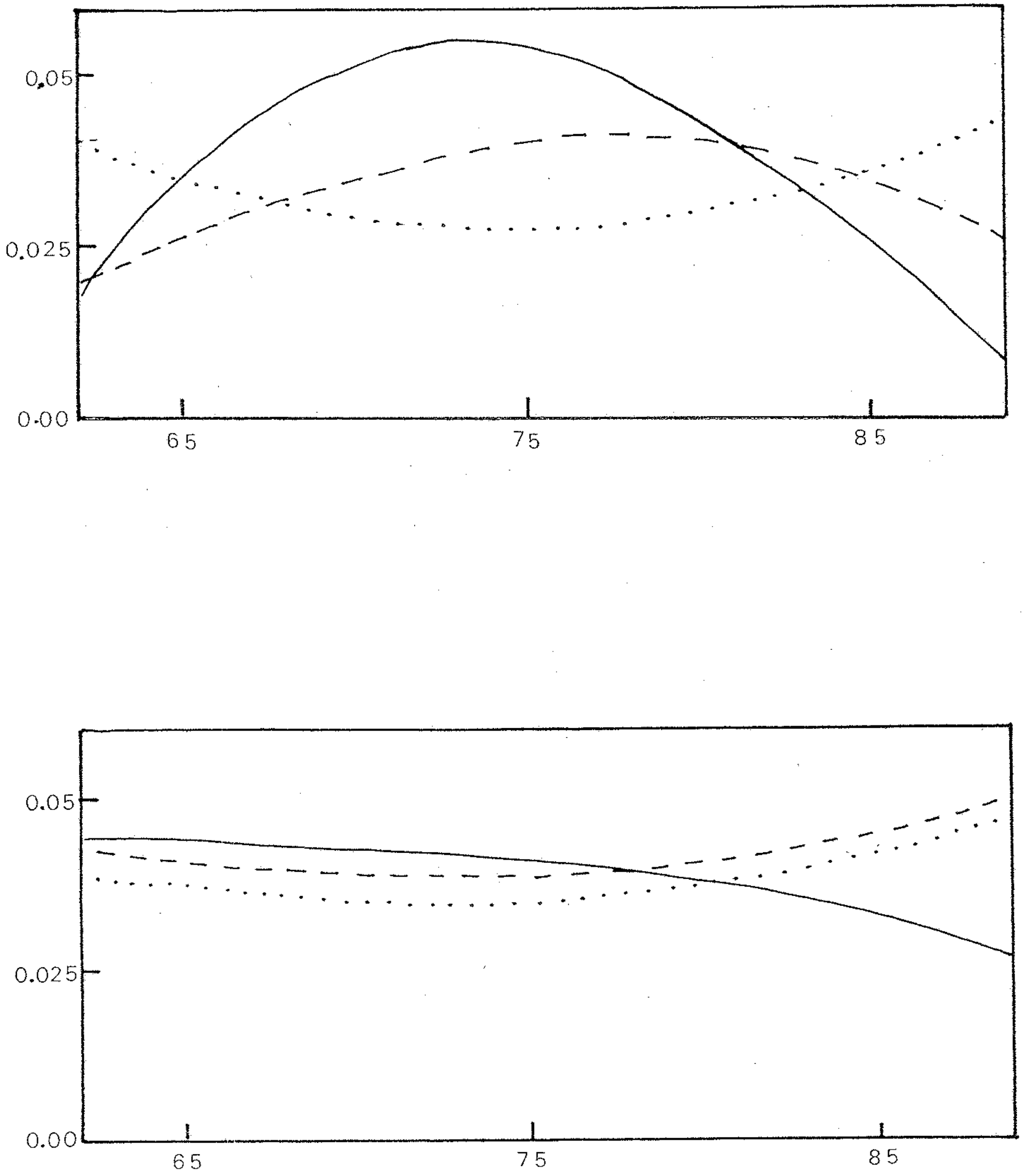


Figure 17 Temporal trends in daily rates of loss of nests of Chaffinches in the three Altitude classes, shown by fitted quadratic regressions. (continuous line, High; pecked line, Medium; dotted line, Low). The upper figure shows losses at the chick stage, the lower those over the whole nest period.

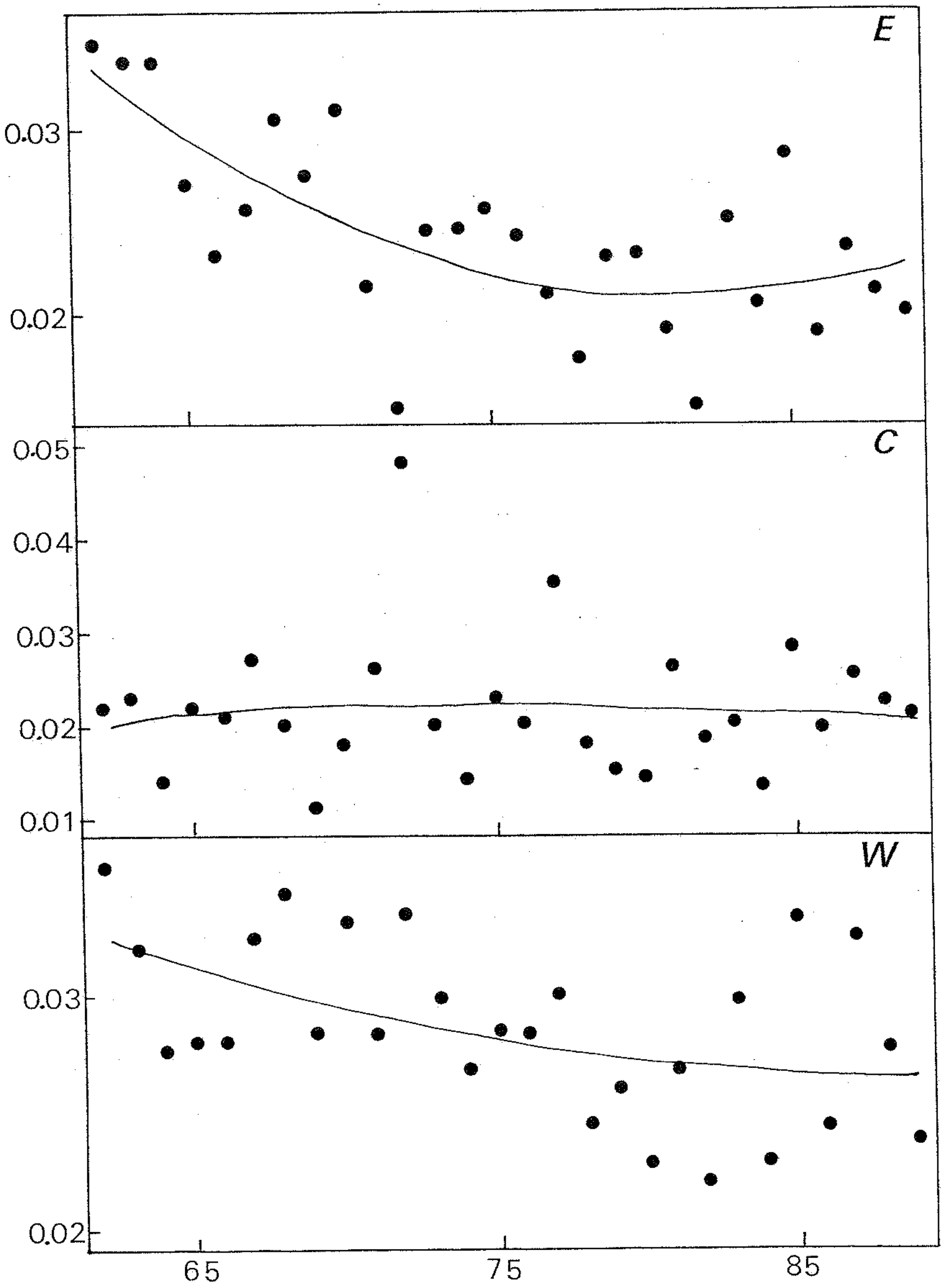


Figure 18 Temporal trends in daily rates of nest losses for Greenfinch during 1962-89 for all Regions and Altitudes combined. E = egg stage, C = chick stage, W = whole nest period. Points show annual values; curves fitted by quadratic regression.

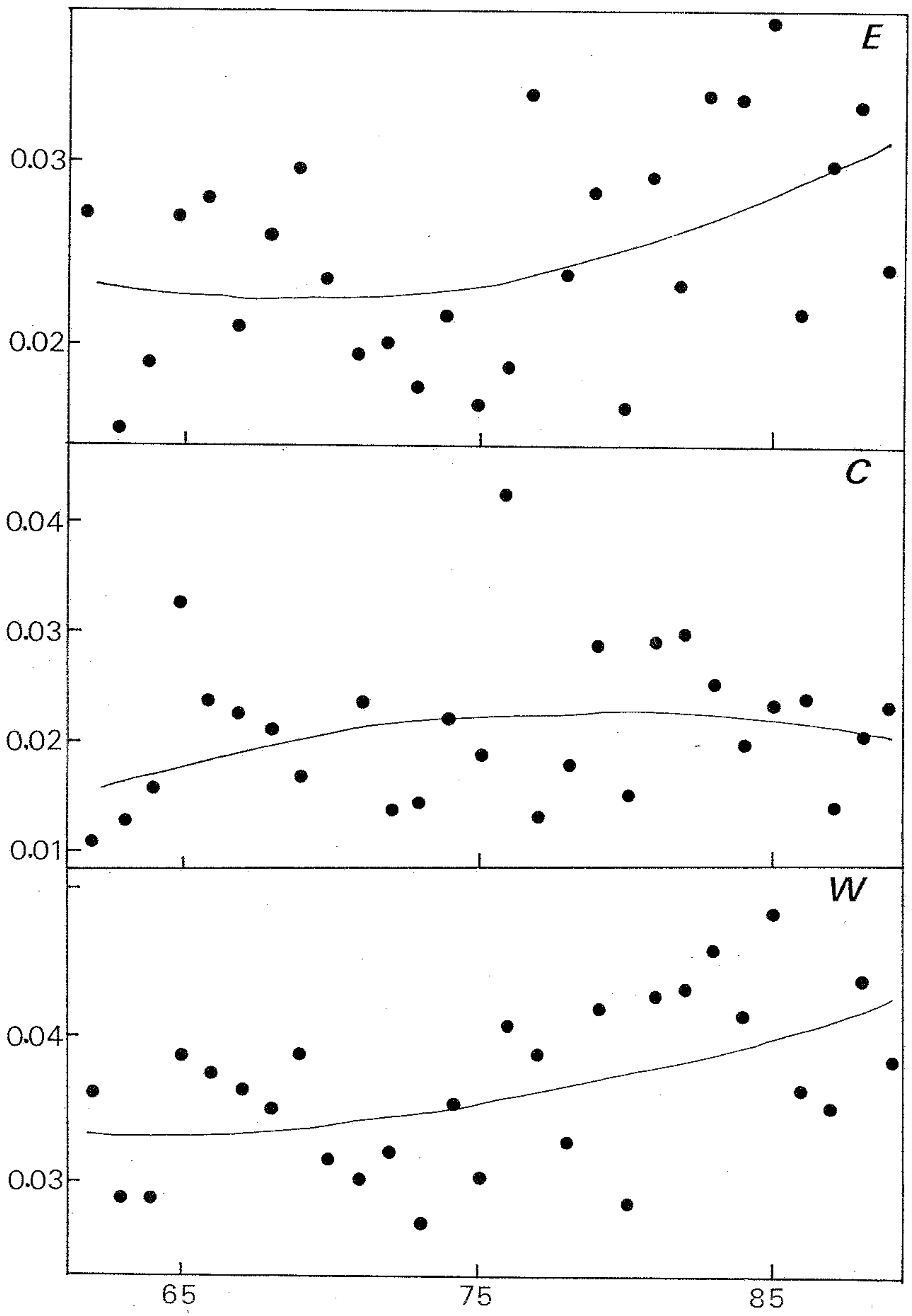


Figure 19 Temporal trends in daily rates of nest losses for Linnet during 1962-89 for all Regions and Altitudes combined. E = egg stage, C = chick stage, W = whole nest period. Points show annual values; curves fitted by quadratic regression.

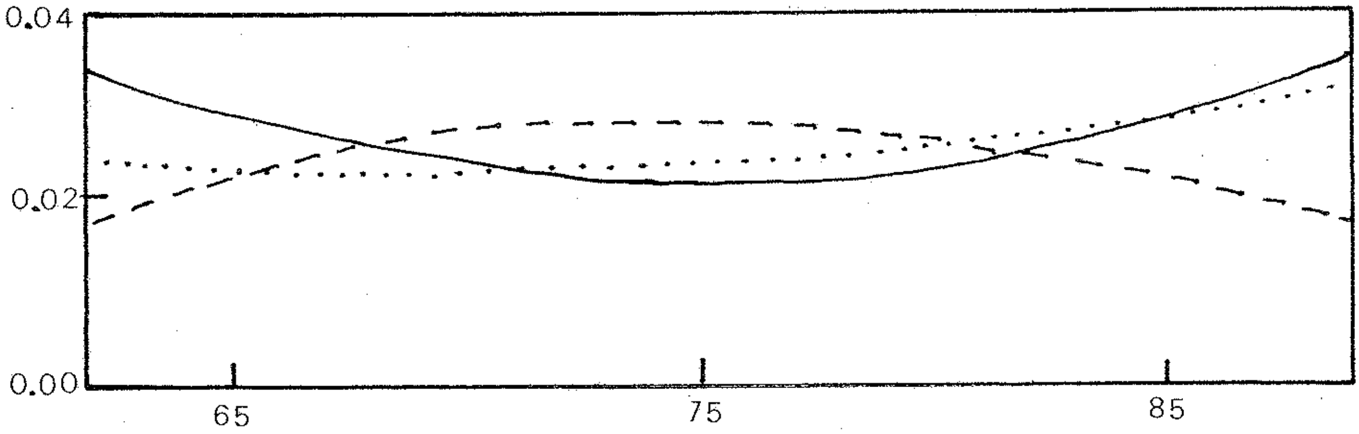


Figure 20 Temporal trends in daily rates of loss of nests of Linnets at the egg stage in the three Altitude classes, shown by fitted quadratic regressions (continuous line, High; pecked line, Medium; dotted line, Low).

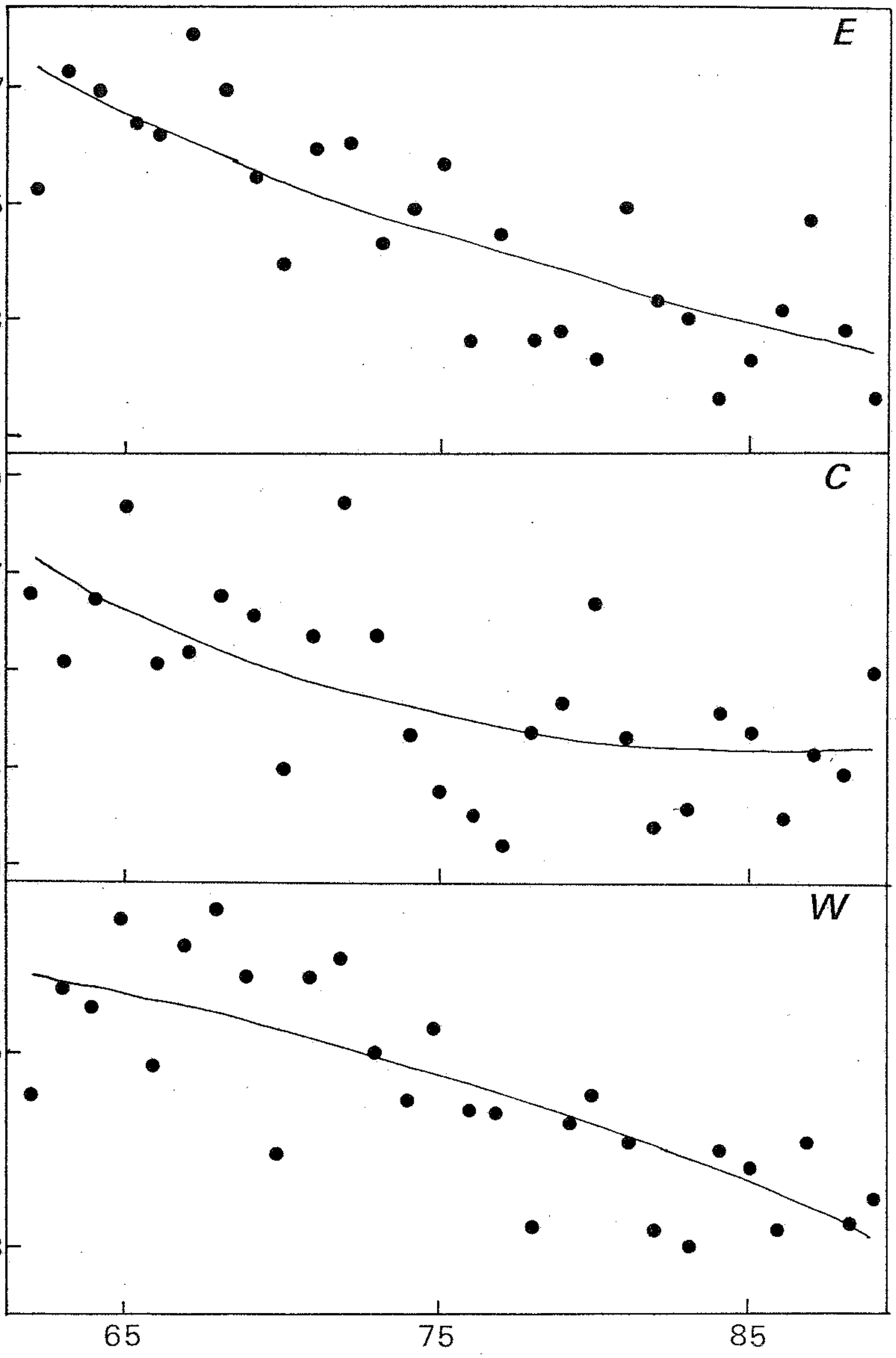


Figure 21 Temporal trends in daily rates of nest losses for Yellowhammer during 1962-89 for all Regions and Altitudes combined. E = egg stage, C = chick stage, W = whole nest period. Points show annual values; curves fitted by quadratic regression.

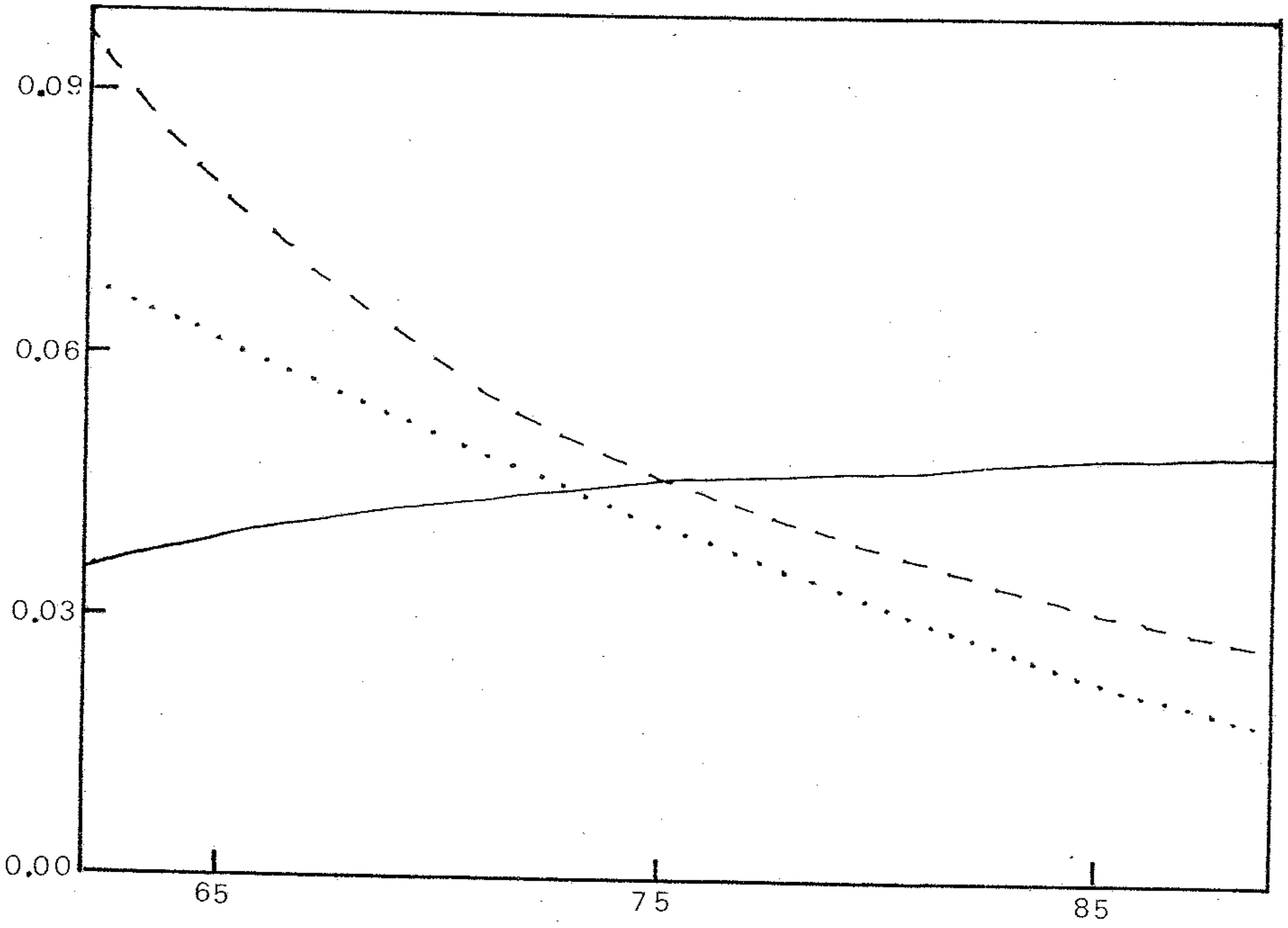


Figure 22 Temporal trends in daily rates of loss of nests of Yellowhammers at the chick stage in the three Altitude classes, shown by fitted quadratic regressions (continuous line, High; pecked line, Medium, dotted line, Low).

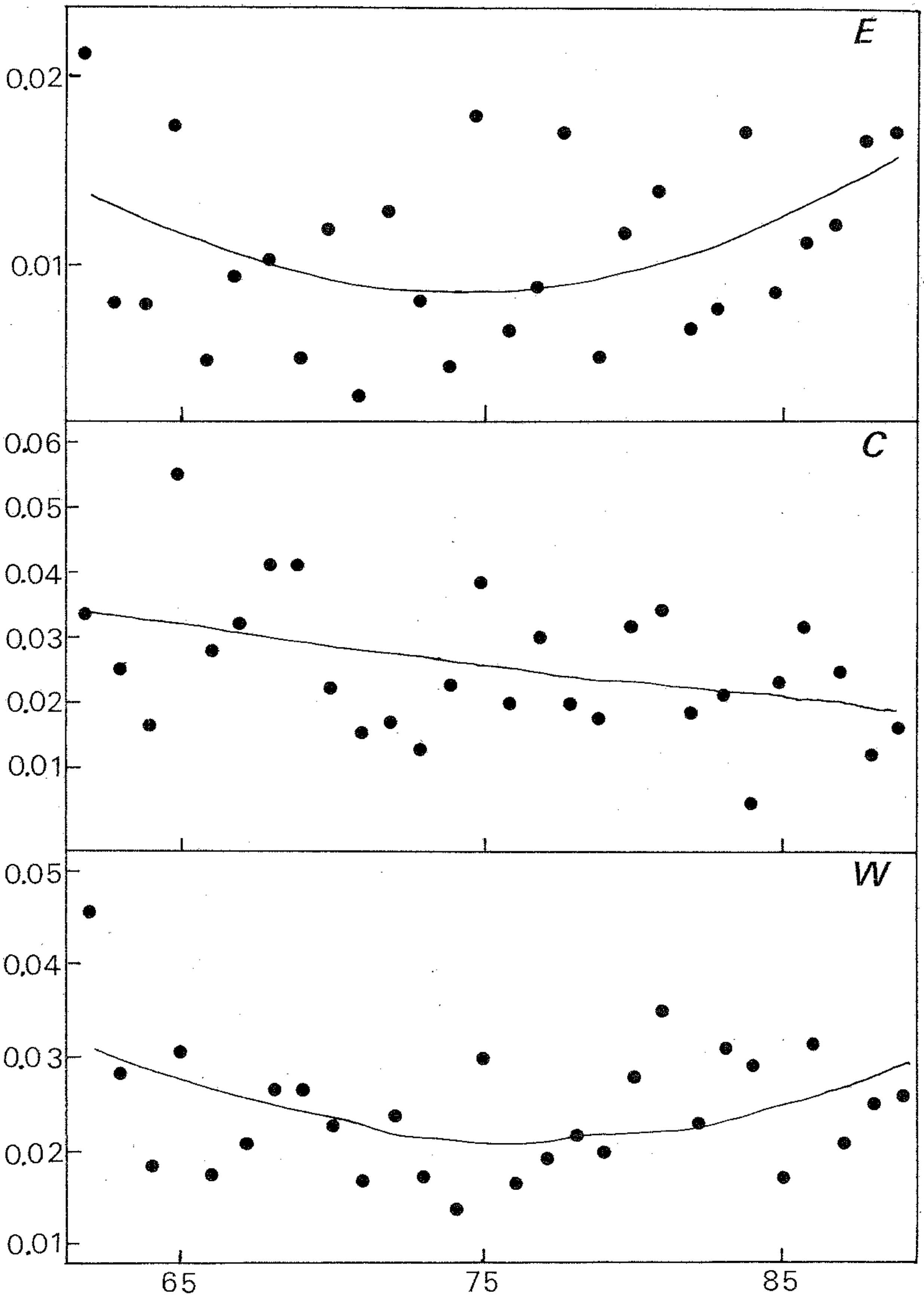


Figure 23 Temporal trends in daily rates of nest losses for Reed Bunting during 1962-89 for all Regions and Altitudes combined. E = egg stage, C = chick stage, W = whole nest period. Points show annual values; curves fitted by quadratic regression.

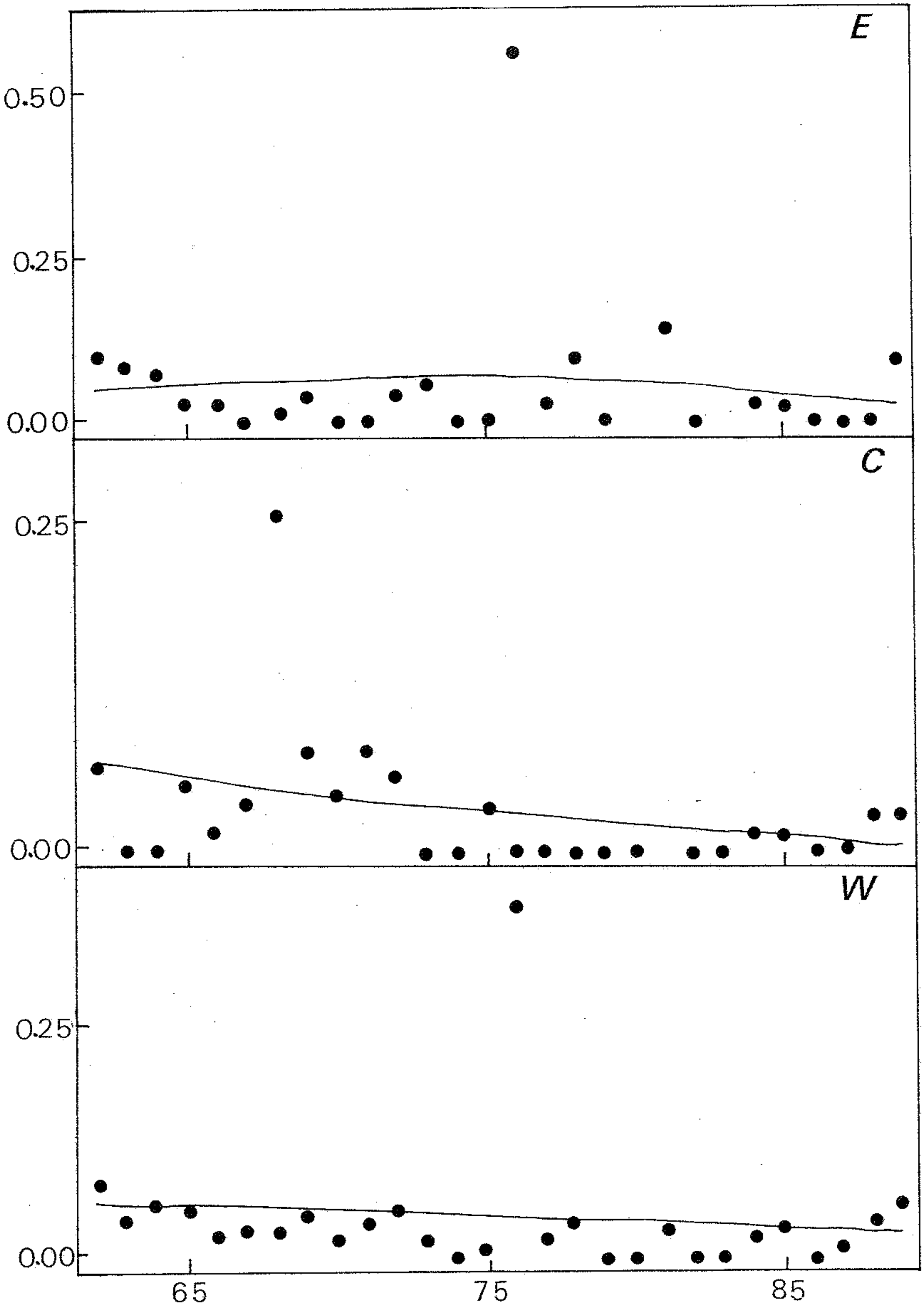


Figure 24 Temporal trends in daily rates of nest losses for Corn Bunting during 1962-89 for all Regions and Altitudes combined. E = egg stage, C = chick stage, W = whole nest period. Points show annual values; curves fitted by quadratic regression. Curves have been drawn only over that domain of years for which there were data.

CHAPTER 4

SEASONAL PATTERNS IN APPARENT MORTALITY RATES OF SOME SEED-EATING BIRDS

INTRODUCTION

The sizes of British populations of a small number of birds, such as Quail *Coturnix coturnix* and Common Crossbill *Loxia curvirostra* are strongly dependent on irruptive invasions from continental Europe (Marchant *et al*. 1990). In addition, it has recently been argued (Summers-Smith 1989) that medium-term changes in the size of the British population of Tree Sparrows *Passer montanus* have been greatly influenced by massive immigration. But for most bird populations, while immigration and emigration may be important at the local level, birth-rates and death-rates are probably the major factors influencing British population sizes.

Because birds breed in nests that are relatively easy to find, their birth-rates are easier to study than those of many wild animals. Information of that sort has been considered in Chapter 3. Here we concentrate on death-rates, which are less easy to study because deaths are difficult to observe directly in a systematic and unbiased fashion.

There is no systematic programme for recording the numbers of birds found dead but there is a source of information for a subset of birds - those that have been ringed in the BTO ringing scheme. If such birds are found dead, sick or injured, then they may be reported, since the rings carry a return address. The pattern of such 'recoveries' throughout the year can give an indication of the seasonal pattern of mortality, though it is clearly likely to be biased by seasonal changes in the ease with which dead birds can be found and changes in human out-of-doors activity. This chapter is concerned with such seasonal patterns of recoveries, as a means of assessing the likely times of stress for the study species, particularly that resulting from food shortage. It is widely believed that winter is the critical period. For that reason, many people feed their garden birds only at that season, so it is important to discover whether that widespread belief is supported by the facts.

We also consider whether different age groups have different patterns and, in relation to the possible effects of agricultural changes, whether the seasonal patterns have changed historically.

It is well known that severe winter weather may be important in determining the numbers of birds in British breeding populations because it causes numbers of birds to die (Dobinson & Richards 1964, Cawthorne & Marchant 1980, Elkins 1983, Baillie *et al.* 1986, Greenwood & Baillie 1991). It is not surprising that this is so: cold weather (and wind and rain) mean that birds need to eat well if they are to maintain their body temperatures, yet days are short (restricting foraging time), insects are generally scarce, and it is rare for food supplies to be renewed during winter (since most prey animals do not breed then and plants do not fruit). Yet winter may not be the only time of stress: renewal of food supplies may lag well behind rising temperatures in spring, so that some species may be faced with dwindling food stocks until late spring or summer. This is especially true of seed-eaters, since seeds are not produced until late spring or summer. Furthermore, though birds often time their breeding seasons to coincide with peak food availability (Perrins 1985), the demands made on birds by the production of eggs and the feeding of chicks are considerable - to the extent that individuals that produce more young than average may reduce their own subsequent survival to a measurable extent (Nur 1988, Partridge 1989, Bryant & Tatner 1988, 1991). After the chicks have fledged, they have to learn to feed - at a time when they are also having to cope with many other problems caused by inexperience. In late summer, most such young birds undergo at least a partial moult and their parents undergo a complete moult, a potentially demanding process requiring the production of large amounts of sulphur-rich proteins and perhaps a marked increase in the metabolic rate (Evans 1985), though some recent measurements suggest that the energy demand may be slight in at least some species (Bryant & Tatner 1988).

Considering all these matters, one would not be surprised to find peak mortality of seed-eaters occurring at any time of year except autumn (when the moult is over but seed supplies should still be reasonably plentiful and the weather relatively benign). The aim of this Chapter is to use the seasonal pattern of recoveries to discover when peak mortalities actually occur.

MATERIAL AND METHODS

The study species were those determined in Chapter 2: Chaffinch *Fringilla coelebs*, Greenfinch *Carduelis chloris*, Linnet *Carduelis* *cannabina*, Yellowhammer *Emberiza citrinella*, Reed Bunting *Emberiza schoeniclus*, and Corn Bunting *Miliaria calandra*. Recoveries used were those from 1909 to 1989 inclusive, except for Linnet, for which the data prior to 1986 have yet to be computerised. For the other species, the data were divided into those up to and including 1970 and those for 1971 and later, this date being appropriate to look for changes in the seasonal patterns that might have been a consequence of recent agricultural changes (O'Connor & Shrubb 1986). If possible, birds were divided into those less than or greater than 12 months old (approximately) at the time of death, to look for age-related differences.

Many birds are recaptured by ringers (either the original ringer or someone else). Since we were trying to determine mortality patterns, such birds have been excluded from the analysis, as have all birds found in a healthy condition. Sick or wounded birds were included, as they would probably have died had they not been caught. We excluded birds reported to have been long dead at the time they were found.

Because we wished to concentrate on birds that might have starved to death, we divided the recoveries into those for which the cause of death (or sickness) was 'traumatic' and others. Traumatic causes included:

killed by man, deliberately or accidentally;

accidents induced by human activity, such as collisions with cars or overhead wires;

natural accidents, such as drowning, tangling in vegetation;

predation, including that by domestic animals;

disease.

Non-traumatic causes included:

starvation;

cold weather (because, although cold itself rarely kills birds in Britain, it causes starvation by rendering food inaccessible or by raising energy demands higher than can be satisfied by the food available);

all unknown causes (which will include most cases of starvation but many others as well).

Sample sizes are shown in Table 1.

Data were tabulated and inspected. If there appeared to be age-related or year-related effects, they were tested by using the usual G-test (log likelihood ratio test) for contingency tables.

RESULTS: HISTORICAL CHANGES

In all species, non-traumatic causes of death were more commonly reported before 1971 but we regard this as an artefact, the cause of death being less commonly recorded in the earlier years, even when traumatic.

There were no clear differences, in any species, between the two periods in the seasonal pattern of recoveries.

Only in the Chaffinch was there any sign that the seasonal pattern of recoveries that were ascribed to non-traumatic causes was different in the two periods considered (Fig. 1). The difference is highly significant (three-way interaction in the contingency table of Periods x Months x Mortality causes: $G = 123$, 11 d.f., $P<0.0001$). In earlier years, non-traumatic mortality was high during October to May, low during June to September; in later years it has been high during January to May, low during June to December: relatively speaking, early winter is now less important and late winter and spring more important for non-traumatic mortality.

RESULTS: DIFFERENCES BETWEEN AGE GROUPS

There were no clear differences between age groups in the proportion of recoveries ascribed to non-traumatic causes, in the seasonal pattern of recoveries, or in the seasonal pattern of the proportion of the recoveries that was ascribed to non-traumatic causes.

RESULTS: DIFFERENCES BETWEEN SEASONS

To test for broad seasonal patterns, the data were grouped into 3-month periods (Jan-Mar, Apr-Jun, Jul-Sep, Oct-Dec). The differences between species in seasonal pattern of recoveries were clearly significant (G = 52, d.f. = 15, P<0.0001), as were the differences in seasonal pattern of the proportion of non-traumatic recoveries (G = 241, d.f. = 15, P<0.0001).

Chaffinch recoveries clearly peaked in April, with 50% of the total during March to May inclusive. Monthly recovery rates were above average from February to June inclusive (Fig. 1). But there was little substantial variation over the year in the proportion of recoveries that were from non-traumatic causes (Fig. 1).

The annual pattern of recoveries of Greenfinches was similar to that of Chaffinches but the spring peak extended further into the early summer, with July added to the months in which recovery rate was above average (Fig. 2). The proportion of non-traumatic recoveries varied markedly in this species, from over 50% in January to April to under 40% in June to September (Fig. 2).

In the Linnet, the seasonal peak of recoveries was shifted even further back: 46% of recoveries were in May and June and the period in which the monthly rate was above average was April to August (Fig. 3). Because sample sizes were small, the seasonal pattern in proportion of non-traumatic recoveries was erratic.

The seasonal pattern of Yellowhammer recoveries was similar to that of the Greenfinch, with 54% of the recoveries in March to June and with March to July inclusive having above-average recovery rates (Fig. 4). Seasonal changes in proportion of recoveries that were non-traumatic were on the same scale as in the Greenfinch (allowing for fluctuations resulting from smaller sample sizes) but the spring decline was less sharp (Fig. 4).

Reed Buntings had the earliest peak of recoveries, with nearly as many in March as in April, these two months accounting for 45% of all recoveries (Fig. 5). Above-average monthly rates occurred during January to May. The pattern of non-traumatic recoveries was different in this species from that in all the others under consideration, with peaks in April and late autumn (Fig. 5).

The peak of Corn Bunting recoveries was even later than that of Linnets, being clearly in June (Fig. 6). May to July provided 59% of the recoveries of this species and were the only months apart from January with recovery rates above the monthly average. The January 'peak' is probably an artefact of the small sample size for this species but the mid-summer peak is unlikely to be so: arbitrarily grouping the data into 3-month periods and testing the numbers against the expectation of equal distribution over the four periods gave a highly significant result ($G = 19.1$, $df = 3$, $P<0.001$). As with the Linnet, however, sample sizes are too small for the pattern of non-traumatic recoveries to be other than erratic (Fig. 6).

DISCUSSION

Seasonal patterns of recoveries depend not only on seasonal variations in death rates but also on seasonal changes in the likelihood of dead birds being found. One could perhaps argue that birds are more likely to be found in summer than in winter. Not only do people spend more time out of doors then but so do their domestic cats, a major contributor to the recoveries total.

Even motor vehicles, another important cause of deaths that give rise to recoveries (since dead birds are easily found on or beside roads), are more active in summer. People interested in wildlife, however, who are the ones most likely to find and report dead birds, may be less seasonal in their activity patterns than the general populace, reducing this bias. Furthermore, birds that move into gardens in winter are more likely to be found if they die there than if they die in the countryside in which they may spend the summer. In addition, dead birds are consumed much more slowly by insects and microbes in winter than in summer and they are less likely to be hidden by vegetation. The fact that there is no peak in recoveries of young birds in mid to late summer (except in Corn Buntings, where there is also such a peak in adults) suggests indeed that birds dying in summer are less likely to be found than those dying at other times, since intensive studies of individual species of small birds uniformly show that death-rates are very high during the period of weeks after leaving the nest (Mead 1985). Thus the assumption that dead birds are less likely to be found in winter than in summer may actually be the reverse of the truth.

It is difficult to avoid the conclusion that, even if the recoveries markedly underestimate winter death rates, the spring and early summer are difficult periods for seed-eating birds.

The differences between the species considered here almost certainly reflect differences in seasonal mortality patterns. It might be possible to think of ways in which different biases operate on different species to produce these patterns but such explanations do not readily spring to mind. It is striking that the seasonal peak in recoveries is earliest for those species that include most insects in their spring diets (Chaffinch and Reed Bunting), suggesting that the spring flush of insects compensates for the still-declining seed stocks in these species. Note also that Corn Bunting recoveries peak particularly late, like the breeding of this species, suggesting that breeding is, indeed, stressful.

The differences in timing of the mortality peaks of the various species is further evidence that they are not artifacts produced by variations in the probability of dead birds being found and reported.

It would be useful to extend these analyses to a wider range of species, with a wider range of diets but likely to be subject to similar biases in their recovery rates. If the spring and summer peaks in recoveries found here are partly a reflection of food shortages, one would expect other granivores to show similar peaks and insectivores to show peaks in winter (or, at least, lower peaks in spring and summer).

If food shortages are partly responsible for seasonal peaks in mortality, one would expect that the proportion of recoveries ascribed to non-traumatic causes to show peaks at the most stressful periods. However, these proportions will also be seasonally biased: while birds killed by cats, by traffic, or by flying into windows are likely to be discovered quickly, those starving to death will be less obvious, making it likely that in the warmer months they will be consumed by insects and microbes before they are found. Furthermore, food shortage may increase the likelihood of a bird dying from traumatic causes as well as the likelihood of it simply starving; a bird that is short of food may be less vigilant, less concerned about the risks of predation, and less likely to be able to move quickly enough to evade predators, for example. Thus the proportion of deaths ascribed to non-traumatic causes may not be an unbiased index of the proportion resulting from food shortages.

Taking the seasonal patterns of non-traumatic recoveries at their face values, it is clear that, although most of the species considered show peaks in winter, rates in March and April are almost as high as those in January and February. This confirms the view that spring may be a time of stress for seed-eating birds, probably resulting from shortage of food and the demands of the breeding season. That being so, continued supplementary feeding in gardens through the spring could be valuable for those species that enter gardens to feed.

SUMMARY

Recoveries of dead or dying seed-eating birds reported to the BTO Ringing Scheme peak between April and June. Because of seasonal biases, such recoveries may not accurately reflect mortality but the pattern suggests that spring and early summer are stressful periods for these birds. It is likely that food supplies for seed-eaters remain poor through spring, until new seeds are produced. Differences between species in the timing of the peak of recoveries may be linked with their diets and the timing of their breeding seasons.

The proportion of recoveries ascribed to non-traumatic causes tends to be highest in winter, but levels also tend to be high in spring, supporting the view that starvation-induced mortality may be important at that time and that continuation of supplementary feeding of garden birds through the spring may be valuable.

REFERENCES

Baillie, S.R., Clark, N.A. & Ogilvie, M.A. 1986. Cold weather movements of waterfowl and waders: an analysis of ringing recoveries. BTO Research Report No. 19.

Bryant, D.M. & Tatner, P. 1988. The costs of brood provisioning: effects of brood size and food supply. *Acta XIX Congressus Internationalis Ornithologici* (Ed. H. Ouellet), pp. 364-379, University of Ottawa Press, Ottawa.

Bryant, D.M. & Tatner, P. 1991. Intraspecies variation in avian energy expenditure: correlates and constraints. *Ibis* 133: 236-245.

Cawthorne, R.A. & Marchant, J.H. 1980. The effects of the 1978/79 winter on British bird populations. *Bird Study* 27: 163-172.

Dobinson, H.M. & Richards, A.J. 1964. The effects of the severe winter of 1962/63 on birds in Britain. *British Birds* 57: 373-434.

Elkins, N. 1983. *Weather and Bird Behaviour*. T. & A.D. Poyser, Calton.

Evans, P.R. 1985. Moult. In B. Campbell & E. Lack (eds.). *A Dictionary of Birds*. pp. 361-4. T. & A. D. Poyser, Calton.

Greenwood, J.J.D. & Baillie, S.R. 1991. Effects of density-dependence and weather on population changes of English passerines using a non-experimental paradigm. *Ibis* 133 suppl.1: 121-133.

Mead, C.J. 1985. Age In *A Dictionary of Birds* (Eds. B. Campbell & E. Lack), pp. 5-7. T. & A.D. Poyser, Calton.

Nur, N. 1988. The cost of reproduction in birds: an examination of the evidence. *Ardea* 76: 155-168.

O'Connor, R.J. & Shrubb, M. 1986. *Farming and Birds*. Cambridge University Press, Cambridge.

Partridge, L. 1989. Lifetime reproductive success and life-history evolution. In I. Newton (Ed.) *Lifetime Reproduction in Birds*: 421-440. Academic Press, London.

Perrins, C.M. 1985. Breeding Season. In B. Campbell & E. Lack (eds.). *A Dictionary of Birds*. pp. 63-5. T. & A.D. Poyser, Calton.

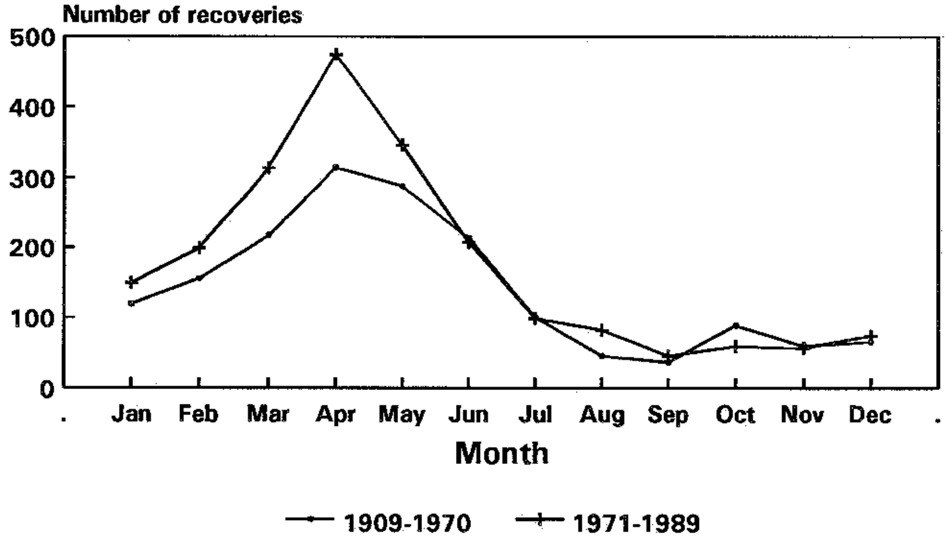
Summers-Smith, D. 1989. A history of the status of the Tree Sparrow *Passer montanus* in the British Isles. *Bird Study* 36: 23-31.

Table 1 Sample sizes available for analysis. Unknown = unknown age; Young = younger than 12 months old at time of death; Adult = older than 12 months.

		Chaffinch	Greenfinch	Linnet	Yellow hammer	Reed Bunting	Corn Bunting
BEFORE 1971							
Unknown	non-traumatic	141	325	0	19	29	2
	traumatic	121	252	0	24	31	3
Young	non-traumatic	182	494	0	27	40	4
	traumatic	159	356	0	21	34	4
Adult	non-traumatic	646	2143	0	69	82	5
	traumatic	457	1853	0	93	52	10
AFTER 1970							
Unknown	non-traumatic	40	68	1	3	20	1
	traumatic	56	93	2	13	32	7
Young	non-traumatic	217	765	11	25	83	0
	traumatic	378	1042	30	46	120	0
Adult	non-traumatic	579	3301	10	57	122	6
	traumatic	836	4595	11	116	173	11

CHAFFINCH

Number of recoveries in each month



Percentage of non-traumatic recoveries

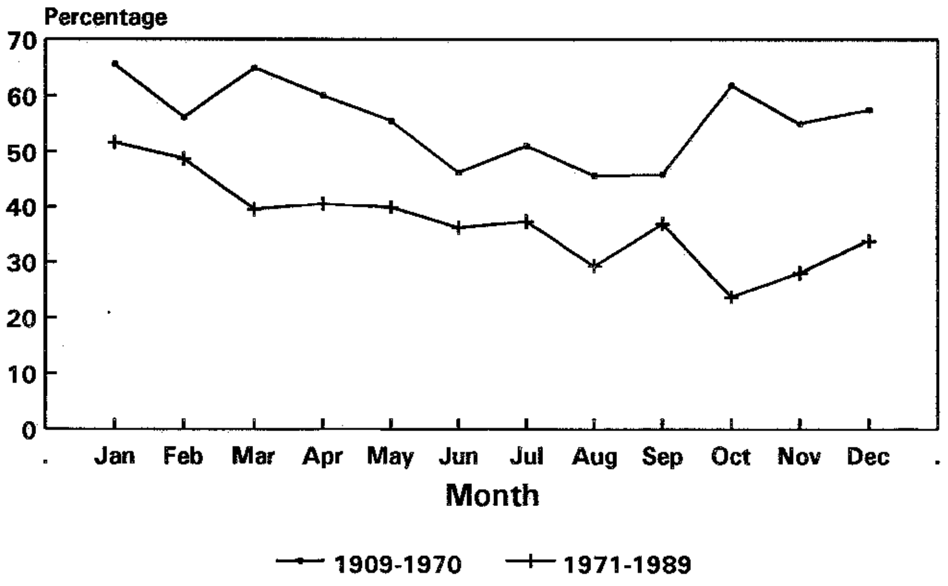
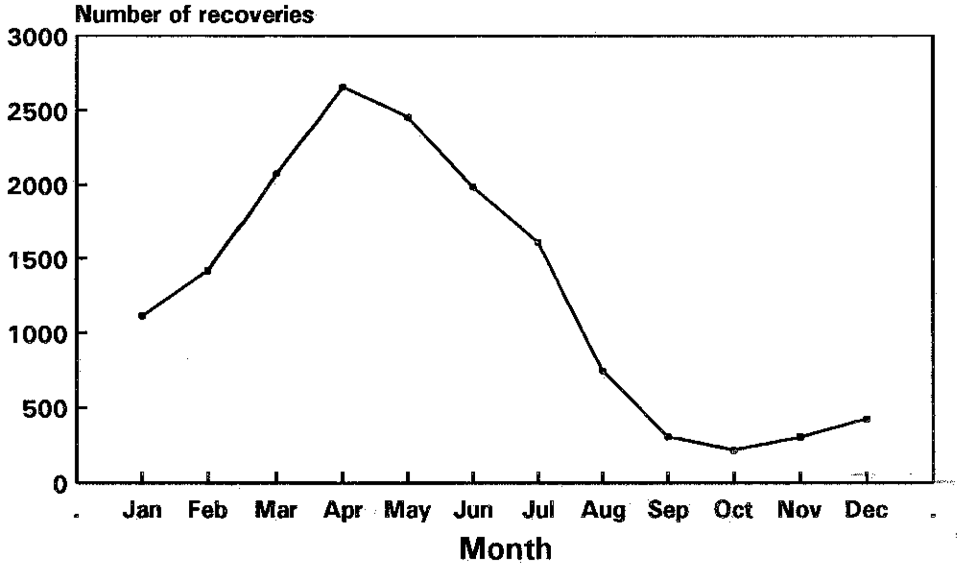


Figure 1 Seasonal distributions of all recoveries (upper) and of proportion of recoveries ascribed to non-traumatic causes (lower) for the Chaffinch.

GREENFINCH

Number of recoveries in each month



Percentage of non-traumatic recoveries

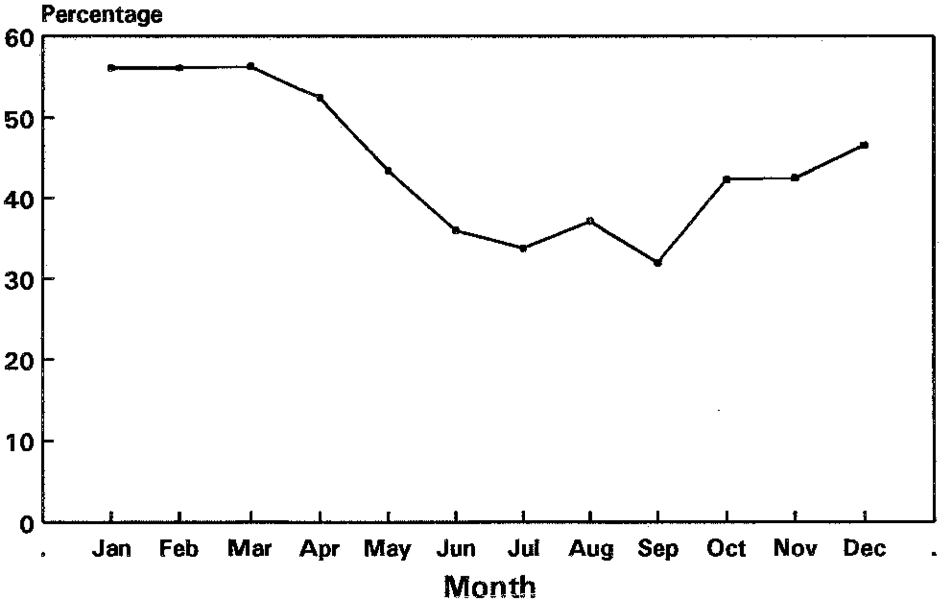
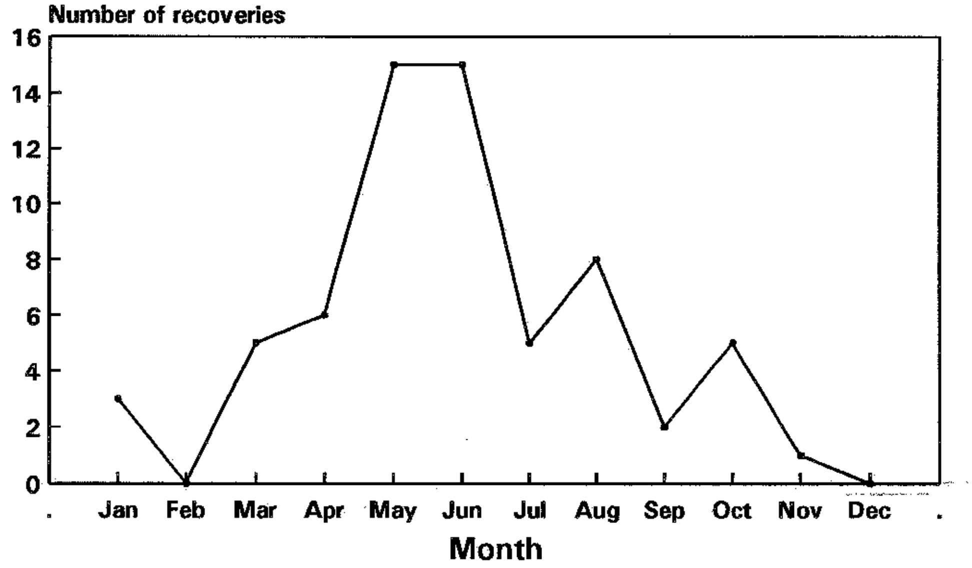


Figure 2 Seasonal distributions of all recoveries (upper) and of proportion of recoveries ascribed to non-traumatic causes (lower) for the Greenfinch.

LINNET

Number of recoveries in each month



Percentage of non-traumatic recoveries

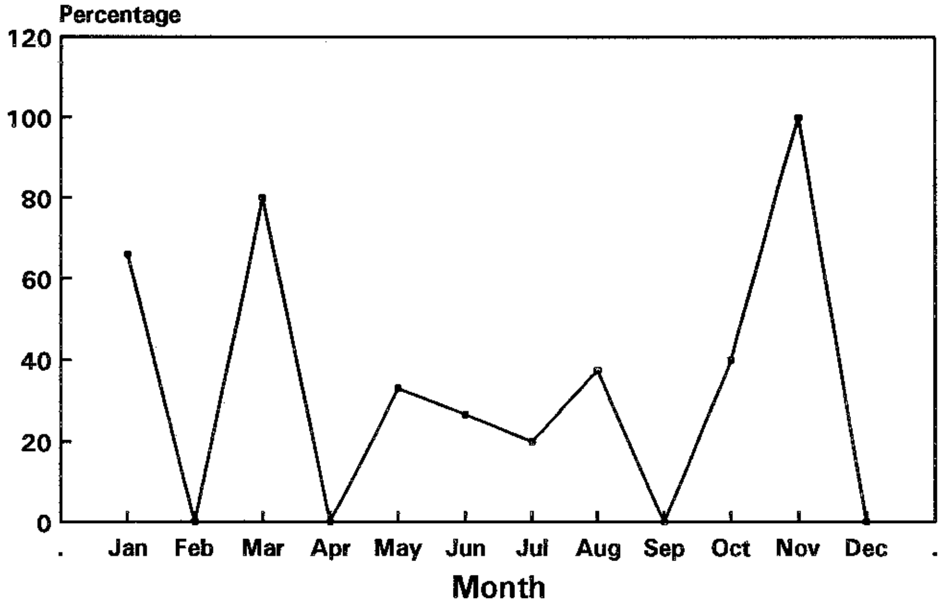
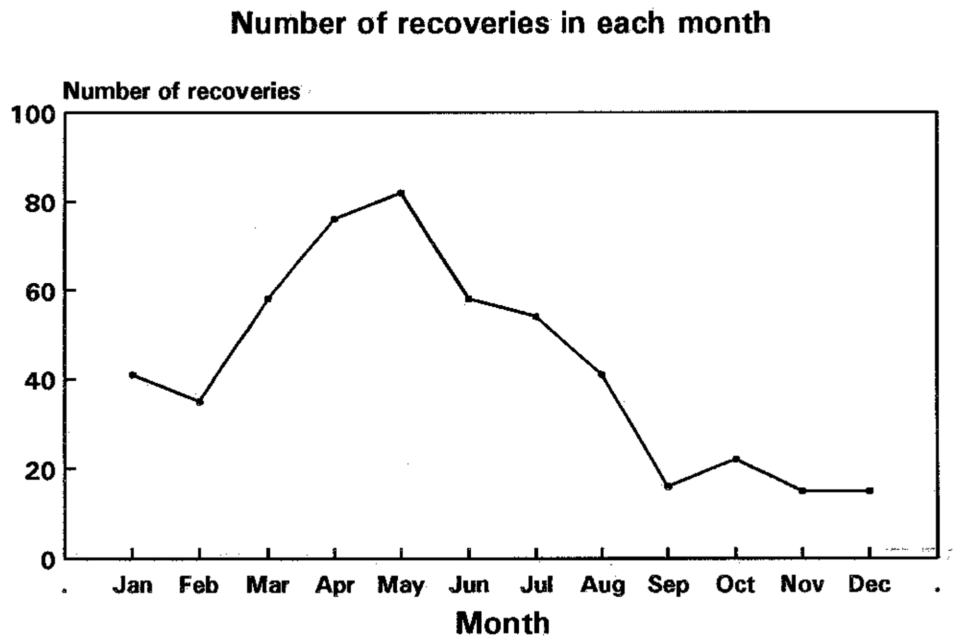


Figure 3 Seasonal distributions of all recoveries (upper) and of proportion of recoveries ascribed to non-traumatic causes (lower) for the Linnet.

YELLOWHAMMER



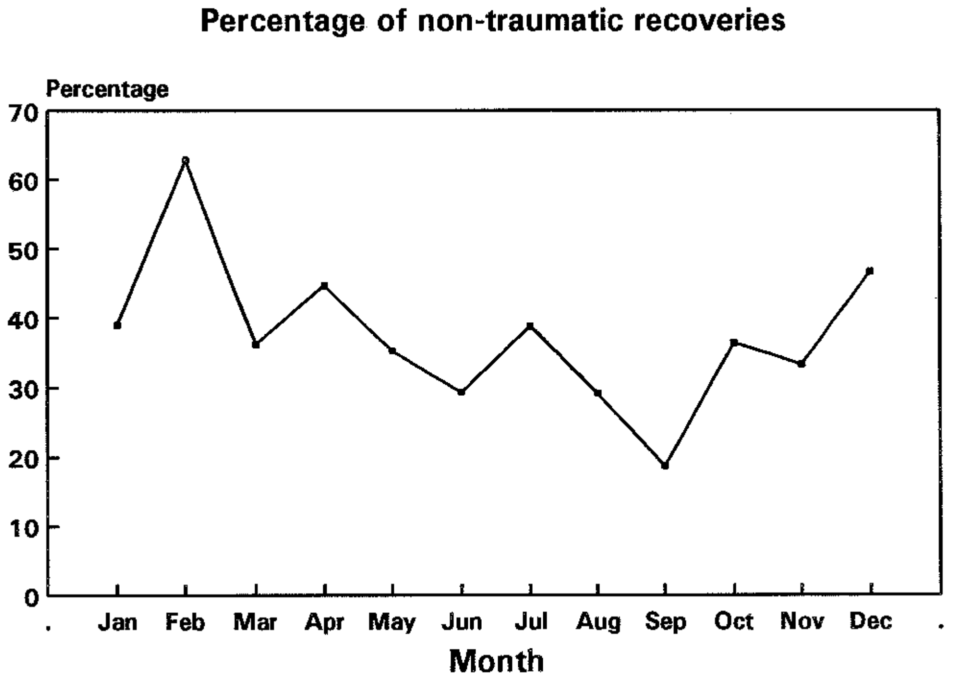
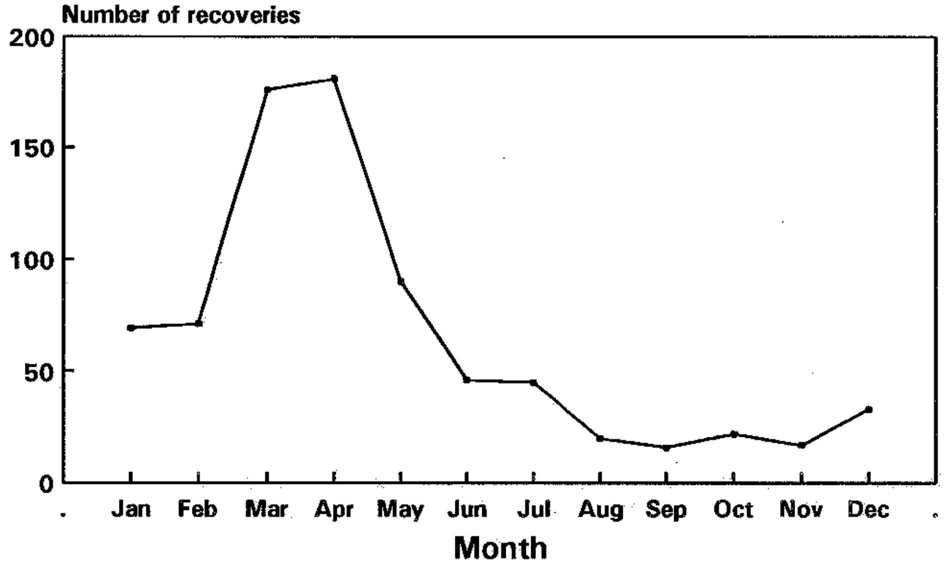


Figure 4 Seasonal distributions of all recoveries (upper) and of proportion of recoveries ascribed to non-traumatic causes (lower) for the Yellowhammer.

REED BUNTING

Number of recoveries in each month



Percentage of non-traumatic recoveries

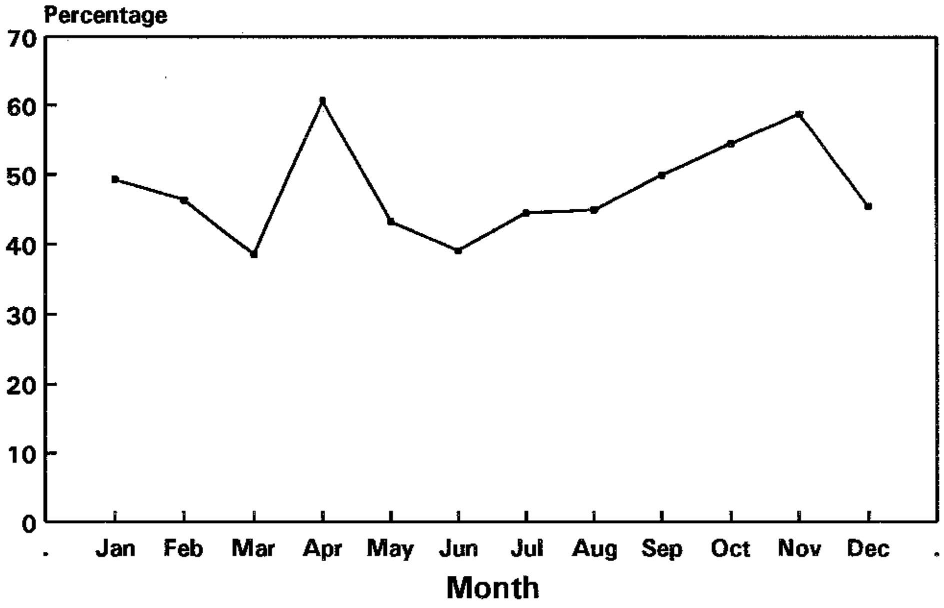
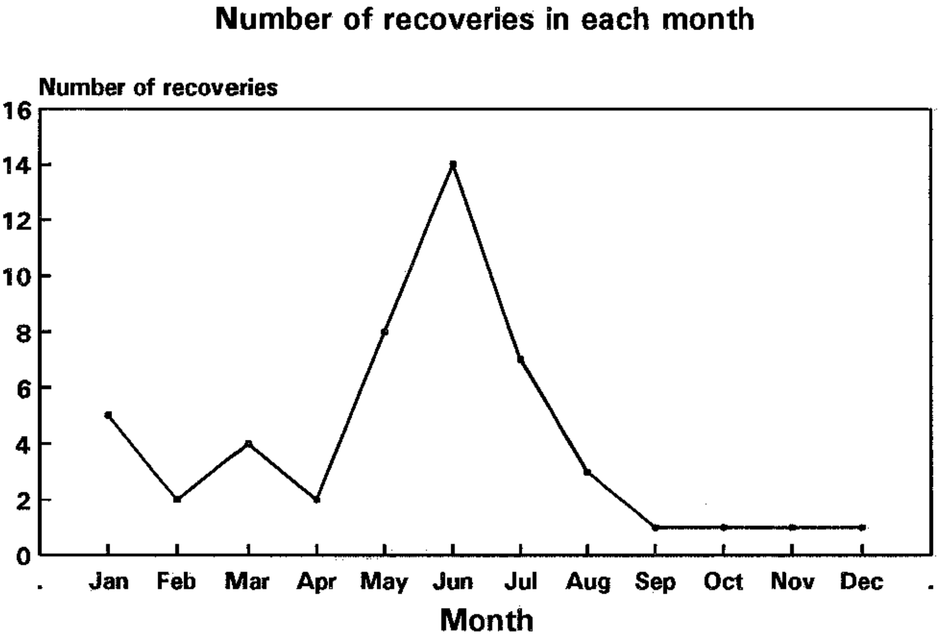


Figure 5 Seasonal distributions of all recoveries (upper) and of proportion of recoveries ascribed to non-traumatic causes (lower) for the Reed Bunting.

CORN BUNTING



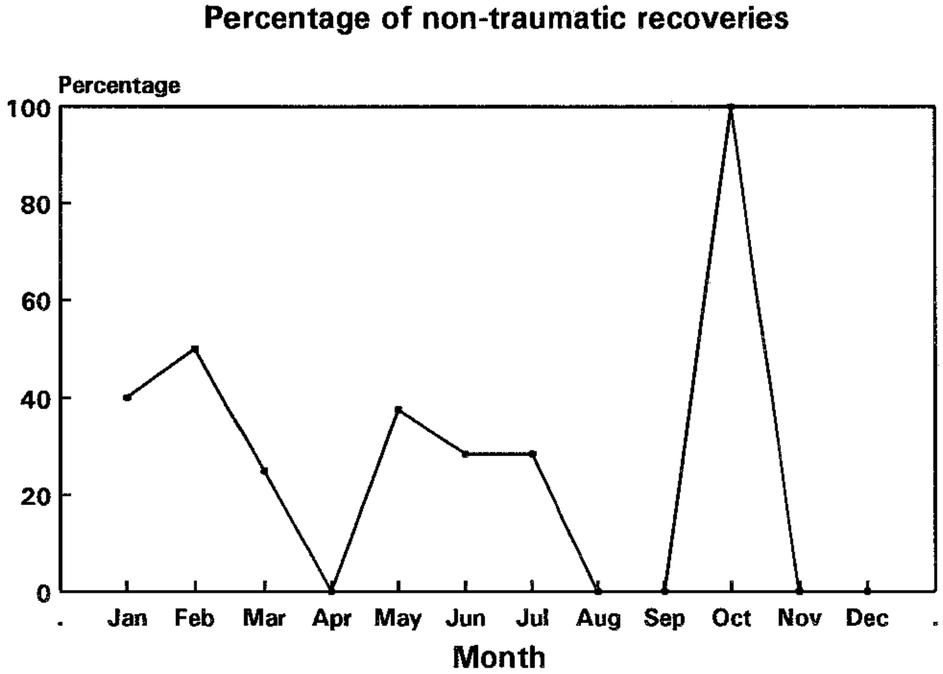


Figure 6 Seasonal distributions of all recoveries (upper) and of proportion of recoveries ascribed to non-traumatic causes (lower) for the Corn Bunting.