Long-term trends in breeding success of some British birds

Raymond J. O'Connor and David N. Pearman

April 1987

A report to the Environmental Research Fund on work under a TERF research grant.

British Trust for Ornithology
Beech Grove
Tring
Herts
HP23 5NR

ACKNOWLEDGEMENTS

Funding for the present project was provided by the Environmental Research Fund and supported the employment of D.N. Pearman through its duration. Raymond O'Connor's participation was whilst holding a post funded by the Nature Conservancy Council. The BTO's Nest Records Scheme has long received support from the Nature Conservancy Council and additional assistance with the computerisation of historical data was provided by the National Evironment Research Council and the Manpower Services Commission. We gratefully acknowledge these sources of support.

We would like to thank various colleagues at the BTO for their help. The current MSC data processing team assisted with data input, especially in the late stages of the project: we thank Miss Sara Cross, Miss P. Adams, S. Butler, Mrs. L. Dawson, Mrs. J. Drage and Miss J. Goodman. Useful advice and help was also provided by the BTO Nest Records Officer, David Glue, and his assistant Mrs. M. Tourle. Dr. M.E. Moser kindly read the report in draft and Mrs. Janet Mewis provided the typing and secretarial support needed for its production.

INTRODUCTION

During the late 1950s the use of persistent organo-chlorine compounds in agrochemicals spread throughout Britain, with their use in the form of seed dressings being particularly pronounced. Following evidence of extensive mortality amongst seed-eating birds (reviewed by Cramp & Conder (1961) and Cramp et al. (1962), a voluntary ban on the use of such compounds was introduced in 1961, with further restrictions in 1966. In parallel with these restrictions the Pesticides Safety Precautions Scheme developed as a method of screening-out adverse environmental effects of new chemicals proposed for agricultural use. This screening has largely eliminated mass poisoning of birds, and the occasional exceptions (e.g. Stanley & Bunyan 1979) reflect unusual circumstances. Research into the problem prevailing in the early 1960s showed a second effect of persistent organochlorines, in the form of eggshell thinning (Ratcliffe 1970), brought about as a side effect of the ingestion of the compounds concerned. Unusually thin eggs suffered very high mortality, as a result both of physical breakage of the thin shelled eggs during incubation and of chemically-induced physiological abnormalities (reviews in Ratcliffe 1970, 1980 and Newton 1974, 1979). Much of the evidence concerning this reduced breeding success relates to species high in food chains, notably raptors and herons but O'Connor & Mead (1982, 1984) documented similar population declines associated with reduced adult survivorship and reduced egg success for the case of the Stock Dove Columba oenas in Britain. As with the raptorial species documented by Ratcliffe (1980) and Newton (1979, 1986), a recovery in breeding success and in population levels took place following the introduction of voluntary bans on the use of persistent organochlorines in agriculture.

The present report examines trends in breeding success for the period 1950-85 in a cross-section of British passerine birds, to investigate the extent to which reduction in breeding success may have taken place in seed-eating birds in general and the extent to which any such reduction has subsequently alleviated. The analysis also permits an examination of the extent to which reductions in breeding success brought about in some species by changing agricultural practices in Britain (O'Connor & Shrubb 1986) might be apparent nationally. The species examined were chosen ahead of analysis to give a cross-section of granivorous, omnivorous and insectivorous species birds differing in their dependence on arable land, with some subsequent adjustments to avoid technical problems with certain species. The present report is essentially a preliminary account of the trends found and further work involving data outside the scope of the present project will be required to clarify their origins.

MATERIALS AND METHODS

Data were taken from the British Trust for Ornithology's Nest Record Scheme. Participants in this scheme complete a nest record card for each nest they find, recording thereon the contents of the nest on one or more visits, together with data relating to the location and habitat of the nest. With a well-timed sequence of visits to the nest it is possible to establish from such records the date of laying of the first egg, the number of eggs eventually laid, their hatching date and success, and the number of young fledged.

Where the nest fails, the card may record the cause of failure. Not all records provide such detail but it is possible to combine all cards allowing e.g. clutch size estimates, to assess the distribution of this variable amongst the population at large and to combine cards from other sub-sets to provide a population estimate of each other variable of interest e.g. of date of first egg laying for that same population. Details of the scheme are provided in Mayer-Gross (1970). The extent of habitat recording for each nest varies considerably between observers who are predominantly amateur ornithologists rather than trained ecologists. A system of coding devised by the BTO allows maximum use of what information is available. The procedure for this consists in its essentials of review of each card by a technical assistant to classify the card to one of 99 possible habitat categories and additionally to mark key-words in the observer's general description of the nest habitat and site details. These codes, and the key-words thus identified, are subsequently entered as part of the computer record for that card, allowing the extraction of the records by habitat or by key-word.

The proportions of successful and failed nests recorded in the BTO scheme are subject to bias, in that the fraction of nests initiated by birds but failing before their discovery by observers is unknown. The recorded percentage of successes is thus based on a censored sample. This problem was overcome by use of the method of Mayfield (1961, 1975). This essentially consists of summing the number of days for which each nest in the sample was under observation (with separate recording for egg stages and for chick stages where mortality may differ between these stages) and assigning the number of observed failures in the sample to this observation period, on the assumption that mortality rate is constant throughout the stage concerned. These assumptions have been checked by a number of authors e.g. Johnson (1979) and proved to be fairly robust for small passerines. Appropriate programs to implement these algorithms have been written at the BTO.

For the present study nest records for the period 1950-85 were reviewed. As far as possible all available cards were considered but in the later stages of the project, time constraints necessitated basing analyses on samples of the available cards. Such samples were drawn randomly, except that they were taken as far as possible from cards with three or more visits; cards with two visits or, exceptionally, with only one (which can yield useful information if chick ages are estimated precisely) were included only where necessary. Such sampling has previously been used extensively in nest record analyses e.g. by O'Connor & Shrubb (1986a) and the procedure appears to be robust against potential biases.

Selection of cards took place in one of two ways. For the years 1950-61 and 1982-85 the available cards were inspected manually and those relating to farmland were extracted for subsequent coding. The cards were coded by a single person, to ensure consistency of habitat coding, and the information input to computer by one of a number of data inputters. For the years 1962-80, approximately 2,000 nest record cards from a variety of habitats had already been computerised for other purposes and were not re-input. These 1962-80 cards comprised for the main part samples of the available nest record cards but for some species constituted all available records for the species concerned. An abstraction program was written to extract from such multi-habitat files all those cards relating to agricultural habitats. Where additional cards not previously input to the computer were available for these years, they were inspected manually in line with the procedure adopted for the early or later years i.e. cards relating to agricultural habitats were extracted manually and coded in the usual way. The two samples were then combined to make a year-file based on all available nest records cards for agricultural habitats. Finally, for some species the volume of cards had previously permitted input of the entire holdings available to the early 1980s and hence required only extraction of the agricultural habitat cards before analysis. For one species analysed, the Blackcap *Sylvia atricapilla*, the sample sizes for farmland cards alone for individual years were too small to permit analysis. As this species was intended to serve as a control for the more typically agricultural Whitethroat *S. communis* an all-habitats analysis was performed on the total BTO holdings for this species (but still confined to 1950-85).

Table 1 summarises the species considered for the present project and indicates the total sample sizes eventually considered. Two entries appear here for the Woodpigeon *Columbus palumba* since the cards for this species were processed in two separate groups of "early" (first visit before 1 July) and "late" (first visit on or after 1 July) nests. Murton *et al.* (1963) have shown that the breeding season of this species is bimodal, with a peak of early breeding by birds using spring sowings for food and a larger peak of late breeding centred on the autumn harvests. The latter birds are more successful and their young grow more rapidly and fledge sooner than do spring young. The different exposure of the two groups to organochlorine compounds indicated that separate analyses would be appropriate here.

The cards thus extracted for analysis were subjected to a series of standard analytical programs. Ricklefs (1969) considered two types of nest mortality, that pertaining to total loss of the nest and that pertaining to partial losses (where some but not all of the eggs or chicks in the nest were lost). Total loss is often due to predation, nest destruction, or loss of the adults. Partial losses are predominantly due to starvation in the case of chicks and to infertility in the case of egg losses. For the present study partial losses of eggs were potentially of interest, since eggshell thinning could result either in infertility or in eggs being lost to accidental damage by the parent's movements on the nest during incubation. Separate programs were therefore run to compute overall mortality rates of nests (computed separately for egg stage and chick stage) and overall mortality of eggs or chicks on an individual basis. The difference between the two mortality rates represents, according to Ricklefs (1969), the partial loss rates. However, it was found in the course of the present analysis that this equation does not hold where mortality varies differentially across clutch sizes: where small clutches or small broods suffer disproportionately heavy mortality, negative values of partial losses (biologically an impossible result) were estimated. Analysis of partial loss data was therefore dropped. The results presented here were thus based finally on overall individual mortalities of eggs and chicks, though the results from the additional analyses are drawn upon where particularly revealing.

Analysis of the full set of data yielded 36 annual estimates of breeding success for eggs and for chicks respectively for most species. However, the sample sizes and variance of the individual annual estimates varied substantially. The problem faced in analysis, therefore, was to detect a decrease in breeding success (or, equivalently, a rise in mortality) of unknown form but whose timing coincided with the period of intensive use of persistent organochlorine chemicals in the face of sample-dependent variability. This problem was resolved by use of a complex non-linear filter to estimate a smooth fit to the data in an objective manner. The filter chosen was the 4253H of Tukey (1977), as implemented by Velleman and Hoaglin (1981). This filter has the merit of removing outliers in the sequence at an early stage, thus minimising their effect on the resultant smooth curve. This feature was particularly desirable in the present work where sample sizes varied considerably from year to year. These smooth curves were then-replotted over the original data to allow visual inspection of long-term trends against a background of original data scatter. For two species, the Great Tit _Parus major_ and the Rook _Corvus frugilegus_ the data were badly fragmented by years in which few or no farmland cards were received at all. For these two species, therefore, adjacent years were grouped together and analysed on a cruder time step, without subjection to filter smoothing.

Trends in the mean size of clutch laid by the various species over the period of study were also examined. _A priori_, some reduction in clutch size might be expected in the face of organochlorine usage, either because the physiological malfunctioning that led to thin eggshells also interfered with the total volume of egg material produced over the full clutch of eggs or because poisoning of experienced adults allowed less experienced birds (prone to laying smaller clutches) enter the breeding population at an earlier age than might otherwise be the case. This latter is relatively unlikely to ocur with short-lived passerines, where most individuals breed in their first summer. The clutch size data were smoothed in the manner described above.

The restrictions on the use of persistent organochlorines introduced in 1961 and 1966 coincided with a period of low population levels amongst resident species, brought about by the severe winters of 1961-62 and 1962-63. In these species numbers subsequently increased steadily for some years as they returned to equilibrium or quasi-equilibrium levels. Populations at low levels are often concentrated into the best available habitats and their subsequent expansion may bring them into successively poorer habitats (Brown 1969, Fretwell & Lucas 1969). Such a process could result in an apparent decrease in overall breeding success or in clutch size that was quite unassociated with the use of organochlorines. However, O'Connor & Mead (1982, 1984) showed that when the Stock Dove population in Britain reached its lowest in 1961 the birds occupied a wider range of habitats than was usually the case, due to the deterioration of their preferred and most extensive habitat, arable farmland. These possibilities were checked here by computing two indices of nest habitat diversity, based on the distribution of the proportion p of the population that was in the _ith_ habitat. The first index of nest habitat diversity (NHD) was

$$NHD = 1/\Sigma p_i^2$$

as recommended by May (1976). The second was simply the maximum value of p_i prevailing over all habitats in that year, again as suggested by May (1976). The data were again smoothed as above before being plotted over the raw data. In the event, the original data for both indices proved well correlated for most species, so that only the former index is discussed below.

As a further check against changes in habitat, the individual proportions of the population present in each agricultural habitat included in the sample was tabulated by year, thus allowing the source of changes in habitat distribution to be identified.

All data were tested for time trends by evaluating their correlation with year, using non-parametric Spearman rank correlation coefficients to avoid the difficulties otherwise inherent in non-normally distributed data. The inter-correlations of the different variables were also computed and are discussed where appropriate.

RESULTS

1. Woodpigeon

Woodpigeons are par excellence a granivorous bird on farmland and might be expected to be particularly vulnerable to pesticide poisoning. Analysis of the breeding trends here is complicated by two factors, however. First, the biology of the early April-June nesting attempts, based on exploitation of the spring sowings, differ significantly from the autumn breeding peak exploiting the grain harvest (Murton et al. 1963). Secondly, as a result of the shift by farmers from spring-sown to autumn-sown cereals, the breeding season of woodpigeons in Britain has advanced significantly, with concomitant changes in average breeding success and productivity (O'Connor & Shrubb 1986a).

Figures 1.1 and 1.2 present the egg mortality data for early and late nest respectively. The results are similar for the early part of the study period, indicating some improvement in egg success through the 1950s, perhaps slightly later in the late season nests. This is followed by a period of worsening egg mortality until the mid-60s since when egg success recovered, stabilising in the case of the early season nests but more erraticly leading to a steady increase in success in late season nests. The worsening during the 1960s is compatible with organochlorine poisoning until the 1966 ban came in and there is a slight suggestion that this affected the spring nests more in early years than was the case for the autumn nests. The differences in patterns in recent years may be attributable to autumn nests (but not the spring nests) being affected by the advancement of the harvest with the greater planting of winter cereals, as already mentioned. The patterns of chick mortality (Figure 1.3, 1.4) again suggest that the early season nests were more adversely affected than late season nests but it is difficult to identify clear patterns in the most recent data.

Clutch size data (not presented) varied little because of the relative constancy of clutch size (two eggs per nest) in this species, with only ocasional clutches of one or of three eggs. However, there is a slight indication that the early season nests especially may have had a greater frequency of one egg clutches between 1960 and 1969, again coinciding with the period of organochlorine use.

The data on nest habitat diversity show an extremely pronounced pattern (Figure 1.5, 1.6). Habitat diversity for early season nests decreased sharply from the mid-1950s to about 1962, thereafter

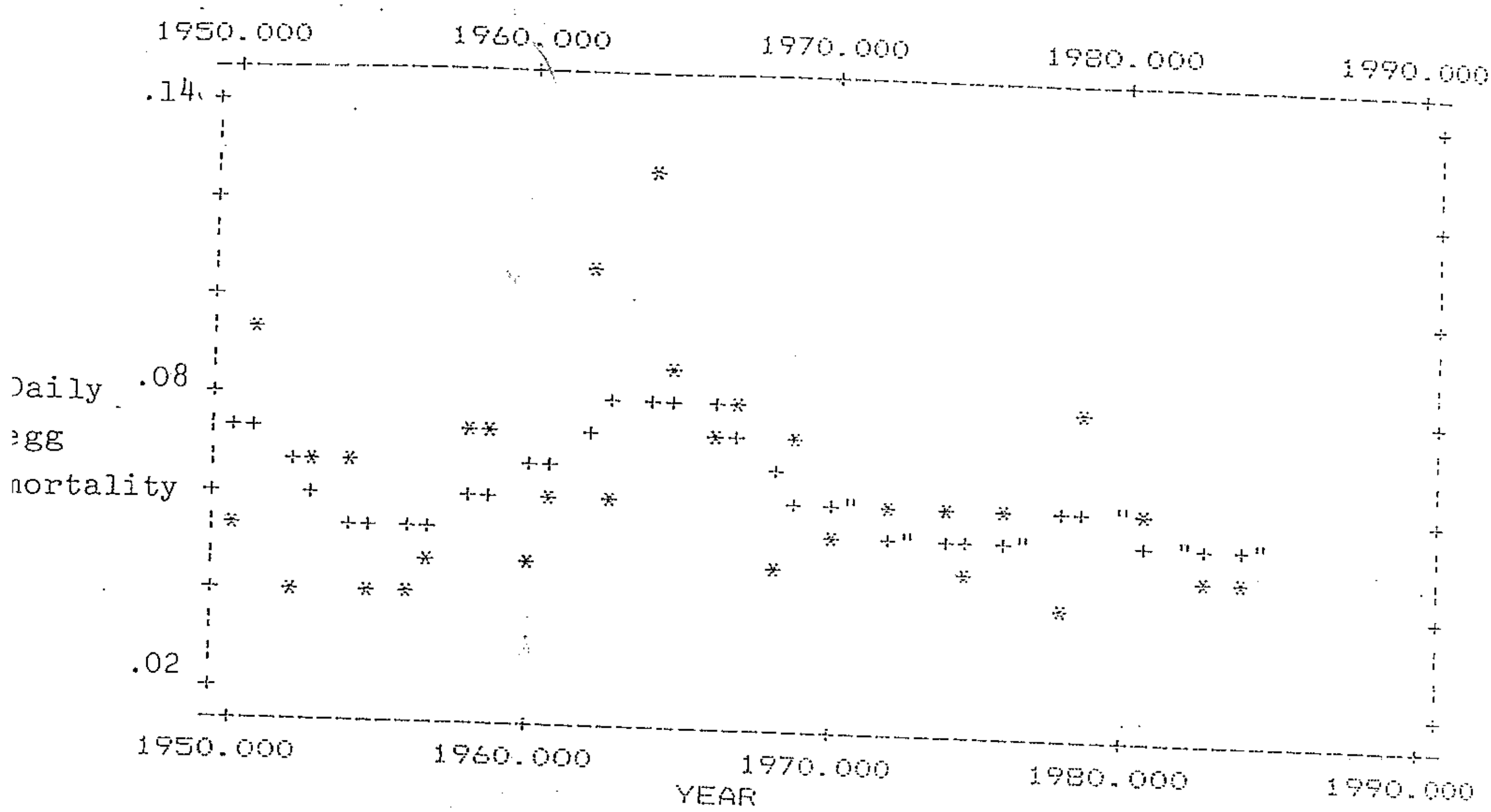

Figure 1.1 Temporal trends in egg mortality (Proportion lost per day) in early-nesting Woodpigeons. The plus (+) symbols indicate the location of the best fit trend line (see text for details), the asterisks (*) indicate data points (average value for that annual sample) and the quotes (") indicate where data point and best fit line overlap on the plot.

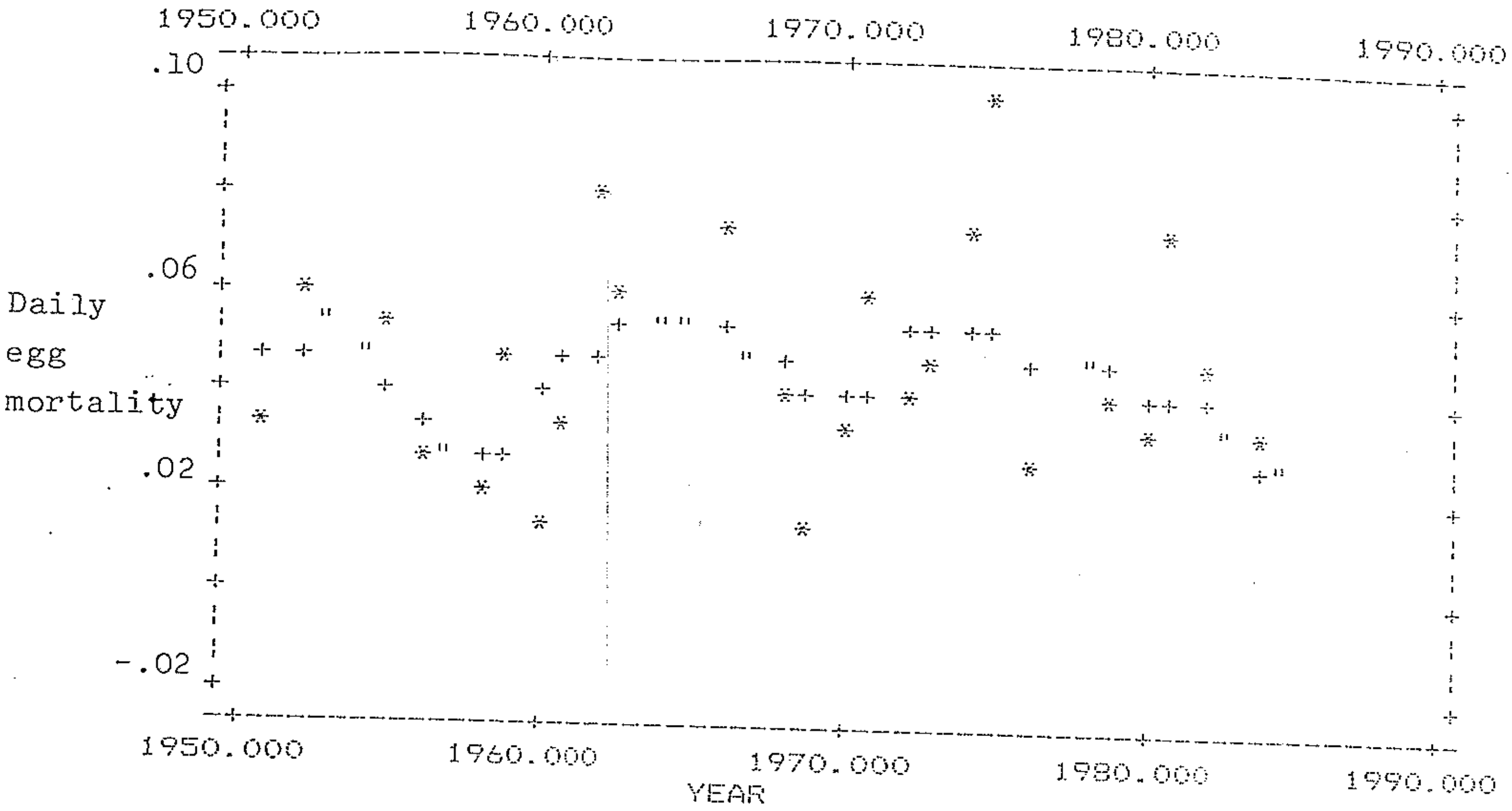

Figure 1.2 Temporal trends in egg mortality in late-nesting Woodpigeons, 1950-85. For symbols see Figure 1.1

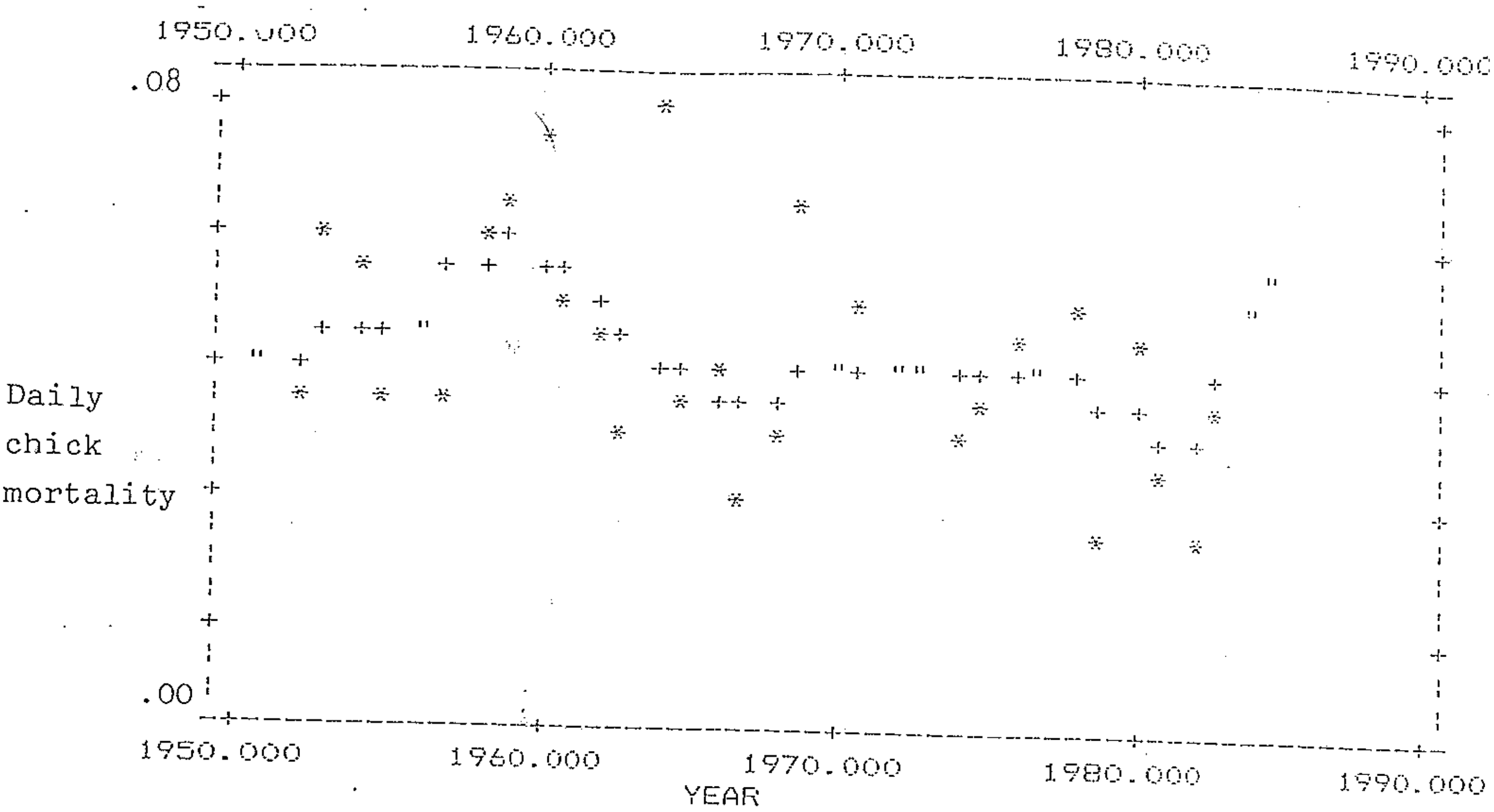

Figure 1.3 Temporal trends in chick mortality (proportion lost per day) in early-nesting Woodpigeons.

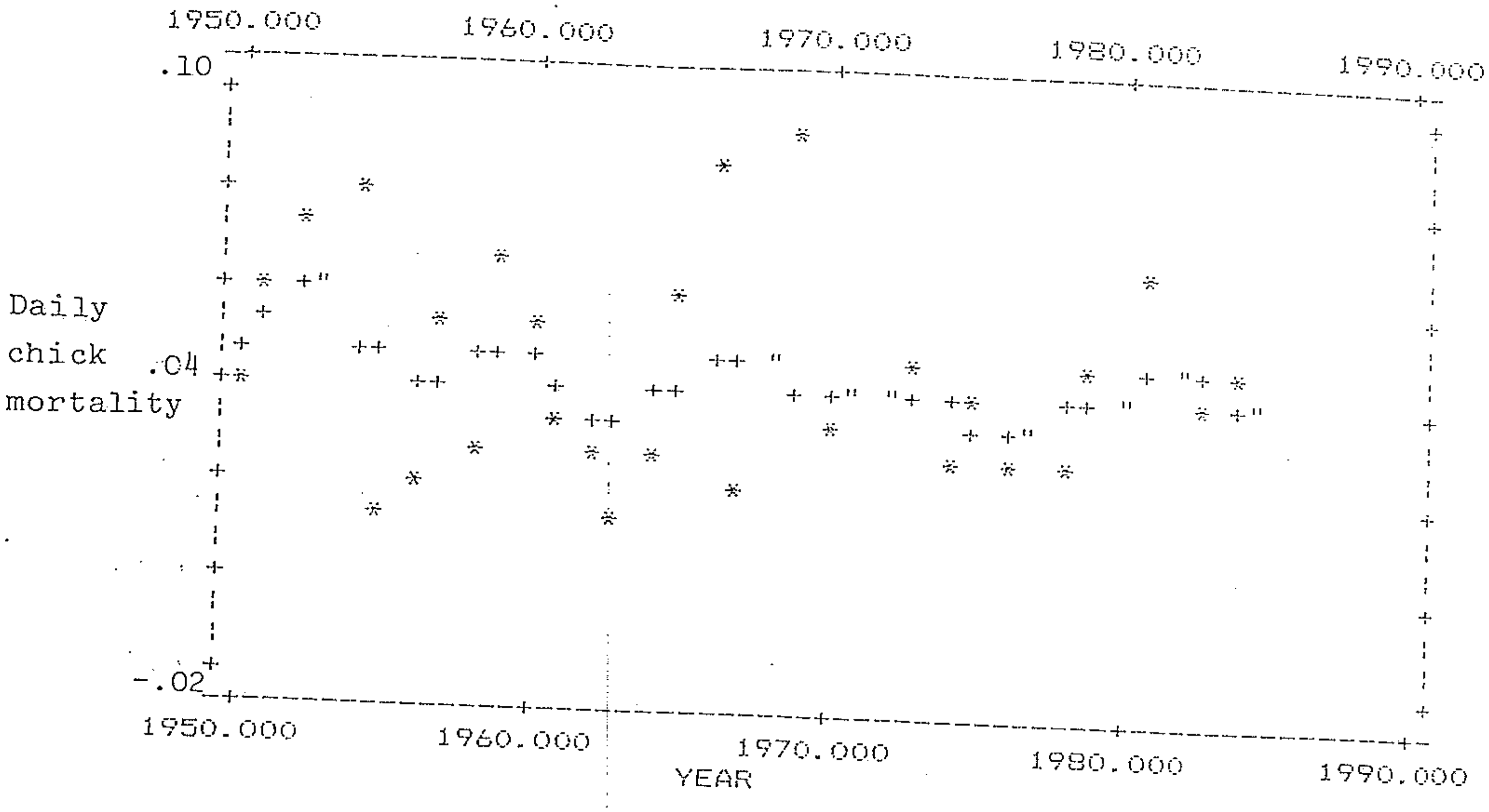

Figure 1.4 Temporal trends in chick mortality (proportion lost per day) in late-nesting Woodpigeons.

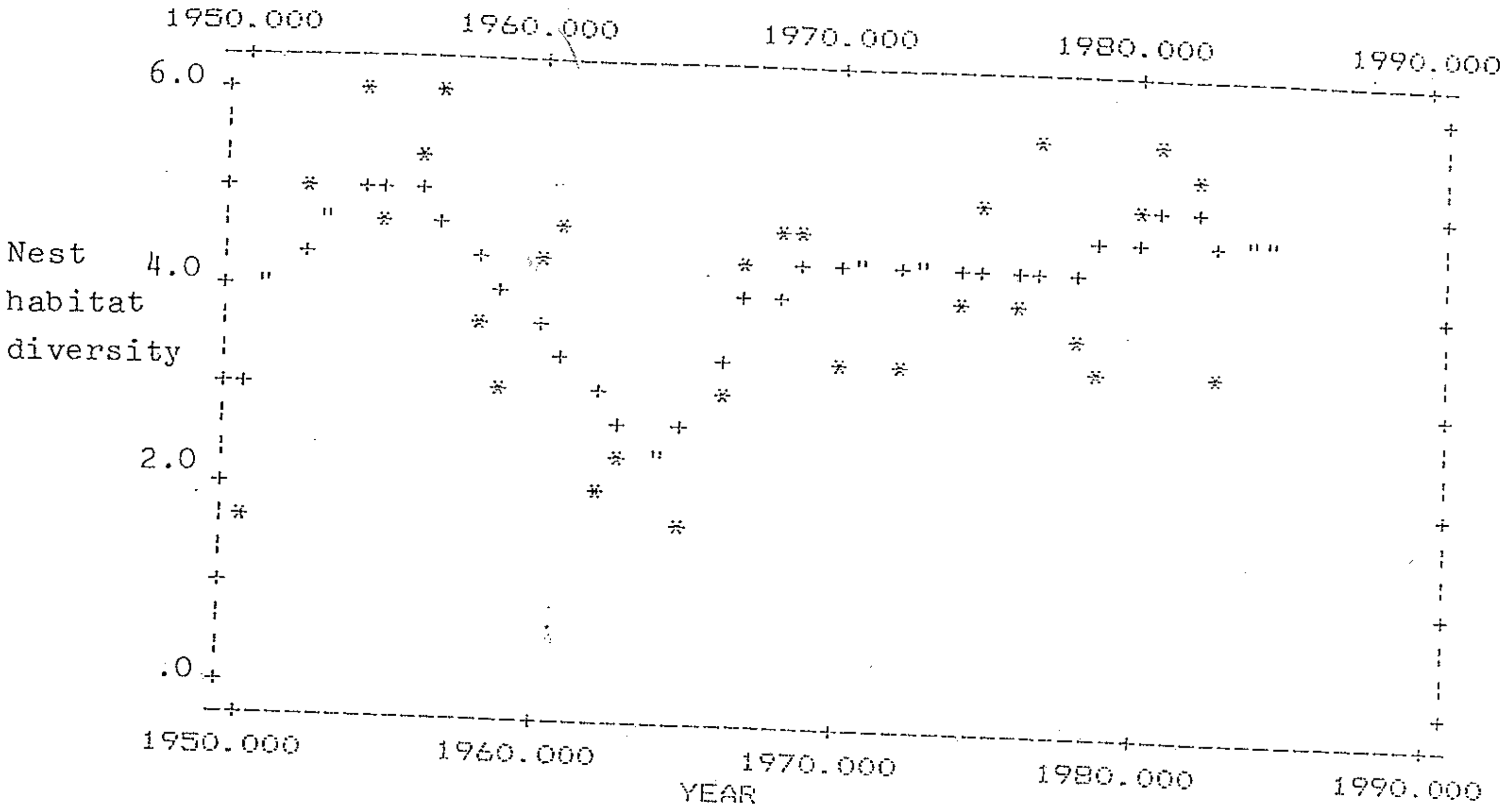

Figure 1.5 Nest habitat diversity of early-nesting Woodpigeons over 1950-85.

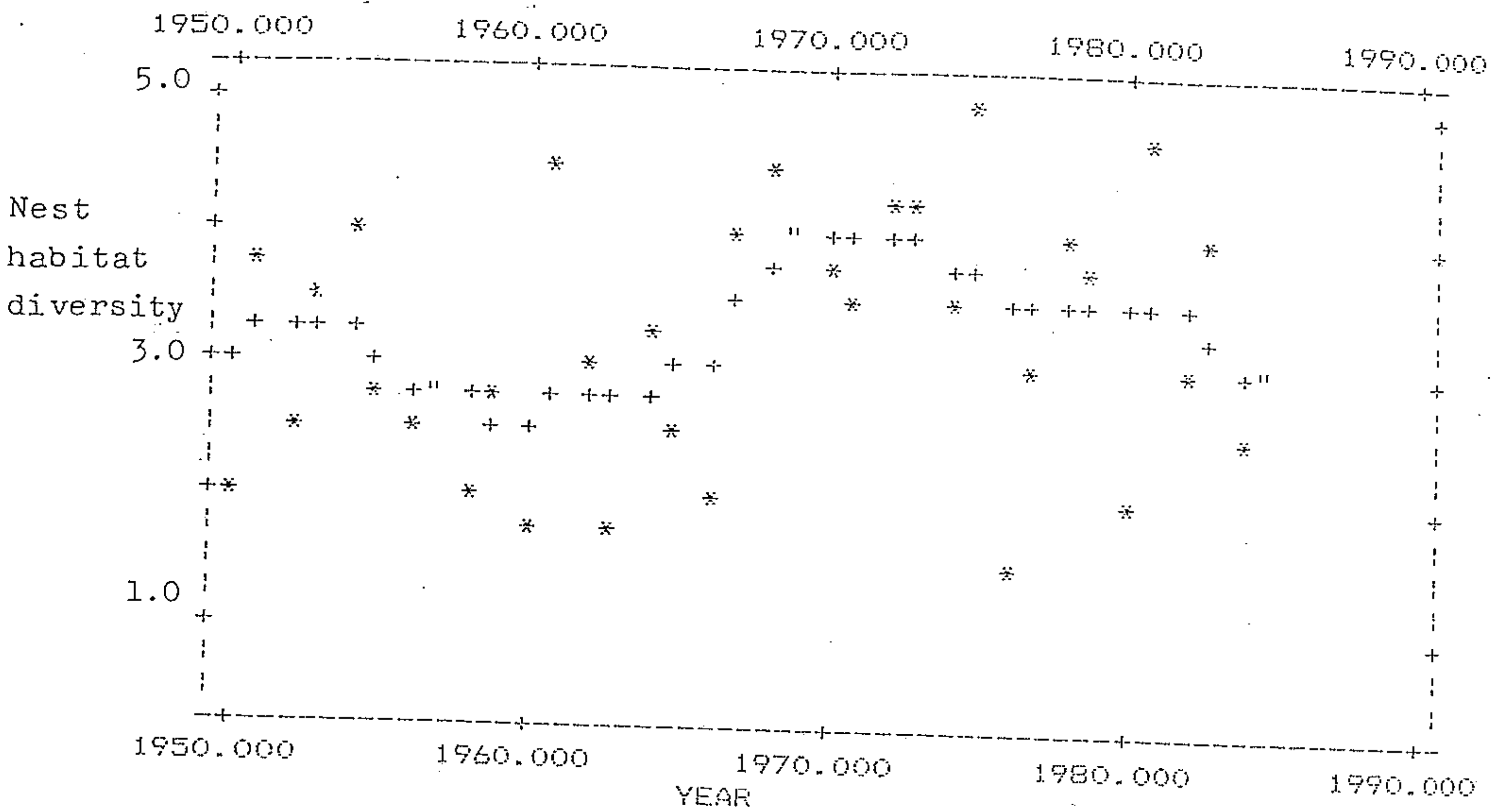

Figure 1.6 Nest habitat diversity of late-nesting Woodpigeons over 1950-85.

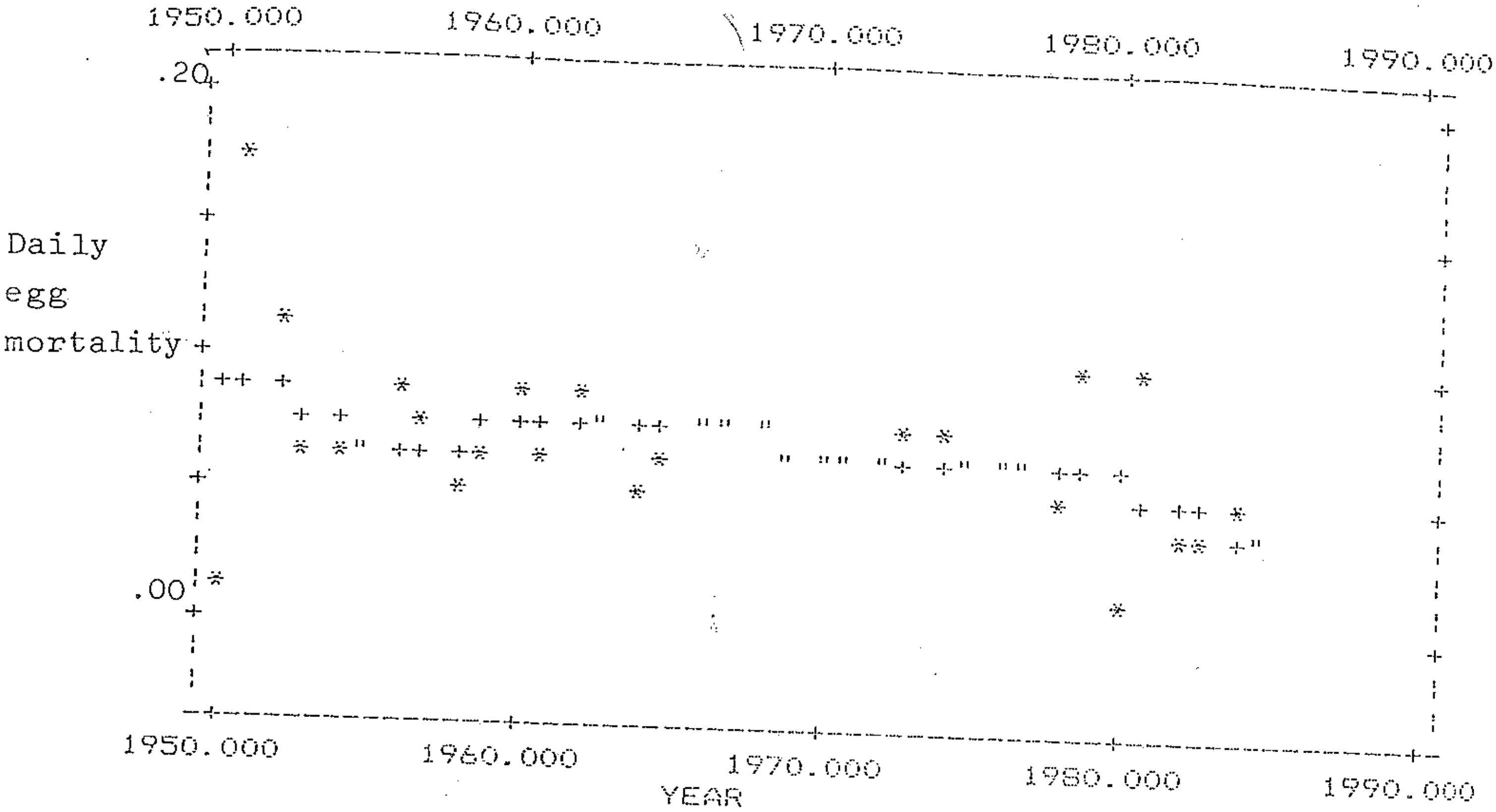

Figure 2.1 Temporal trends in egg mortality in the Skylark, 1950-85. Symbols as Figure 1.1

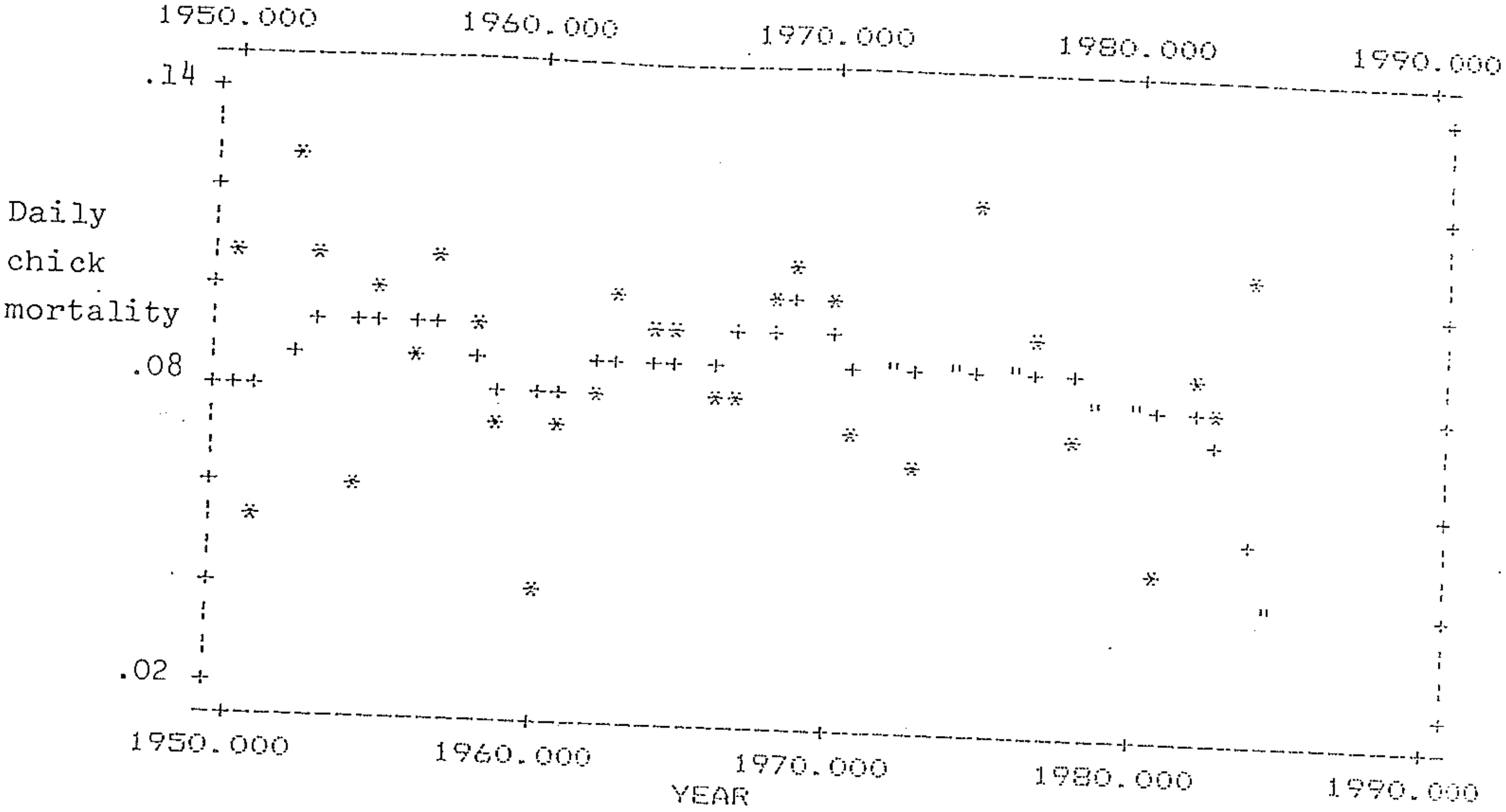

Figure 2.2 Temporal trends in chick mortality in the Skylark, 1950-85. Symbols as Figure 1.1

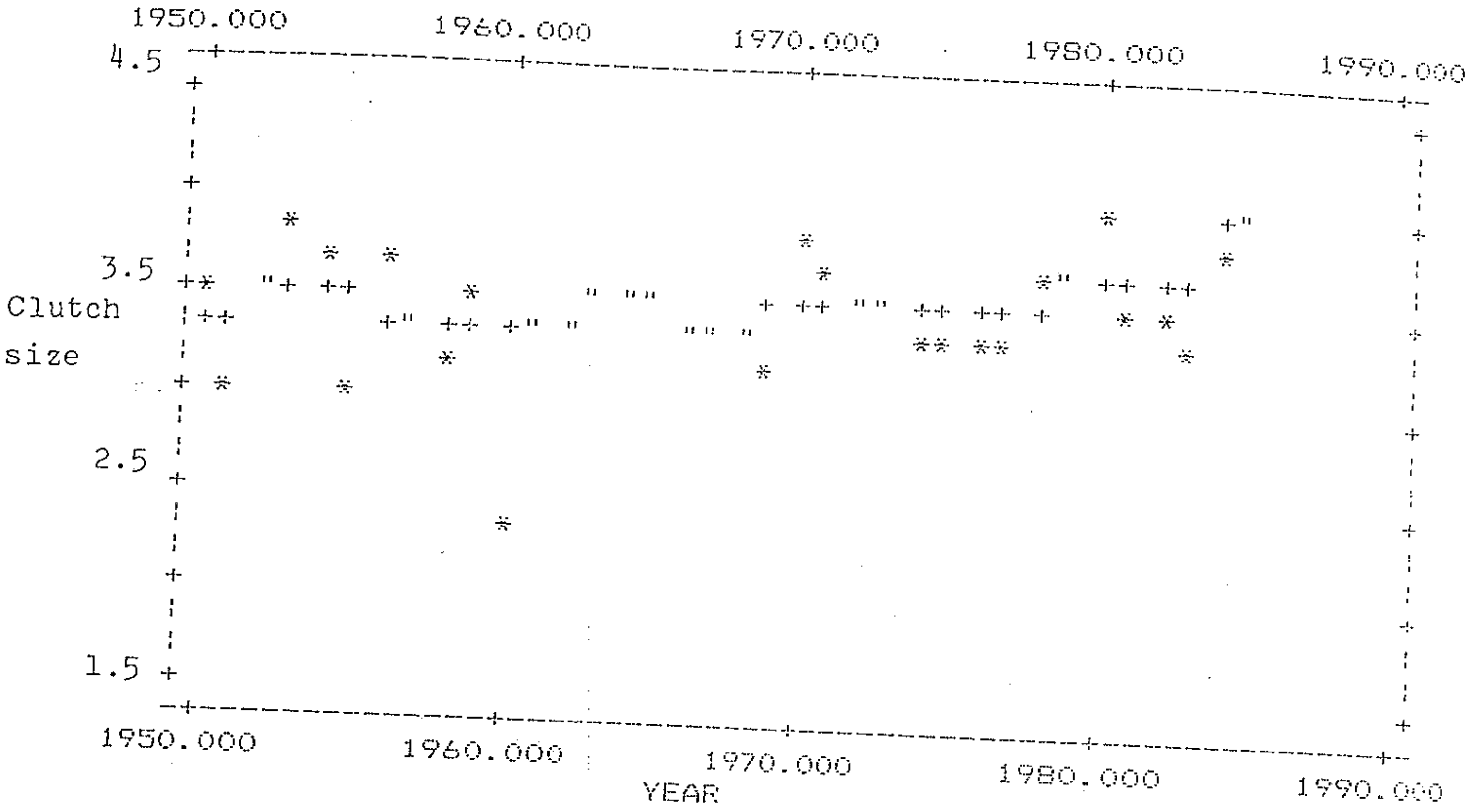

Figure 2.3 Temporal trends in mean annual clutch size in the Skylark, 1950-85. Symbols as Figure 1.1

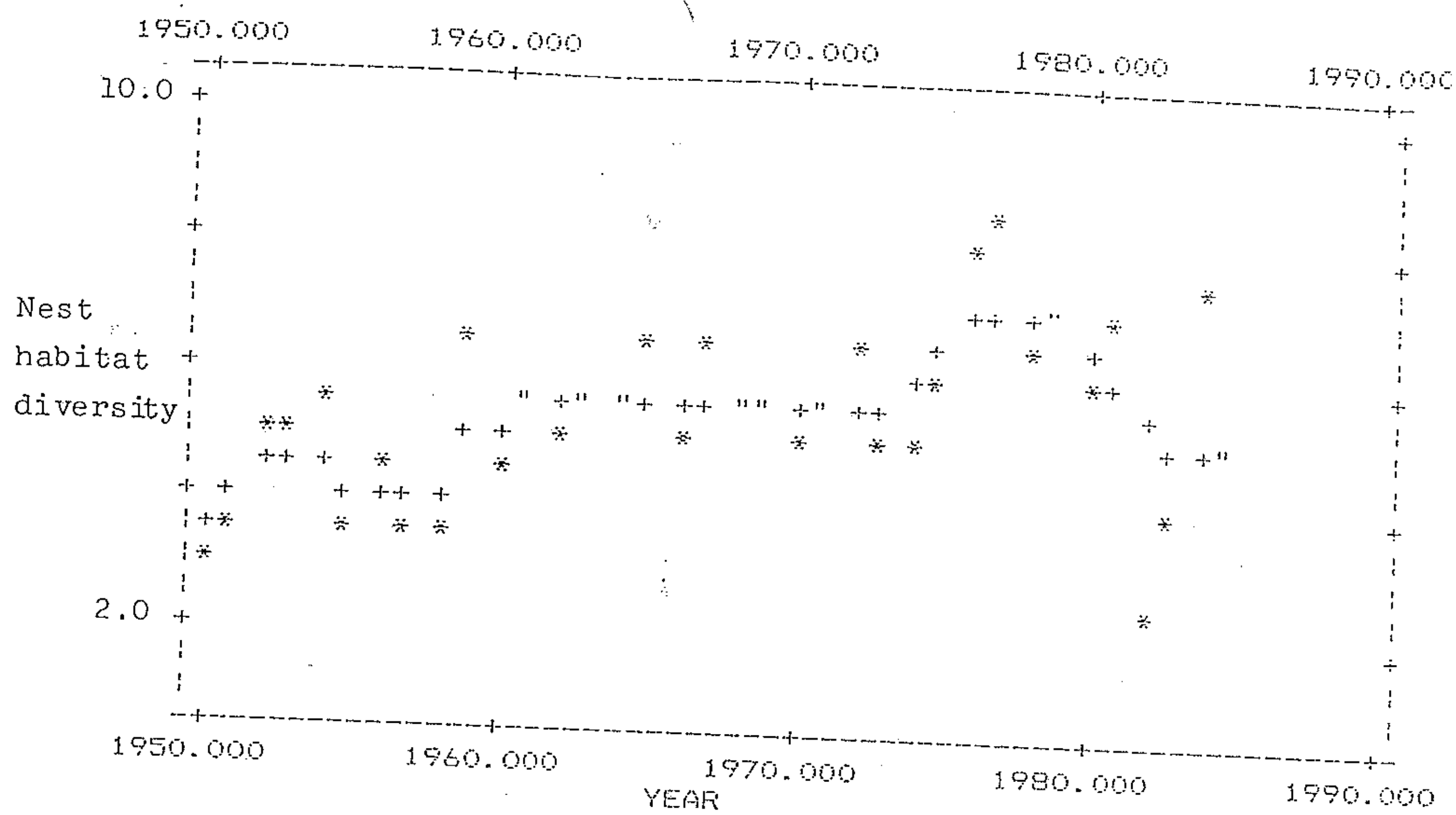

Figure 2.4 Temporal trends in the diversity of nesting habitat used by Skylarks 1950-85

increasing to the end of the decade; since then diversity has been relatively stable, though possibly increasing in very recent years. For late season nests a similar but less pronounced decrease in diversity began somewhat earlier but was not as deep; since 1970 late nests have tended to occur in progressively fewer habitats. Examination of the distribution of individual habitats on agricultural land in use over this period showed that Woodpigeon nests on arable land constituted a very small proportion of the nest records received for the early to mid-1960s, as compared to periods before and after. This is consistent with birds there being poisoned. The position for Woodpigeons in this respect was different from that found by O'Connor & Mead (1982, 1984) for the Stock Dove. They found that arable habitats were poorly represented in the nest record samples during the period of pesticide-induced decline. However, overall nest habitat diversity increased at that time because the smaller population was then spread over proportionately more habitats, including a number of new ones not normally used such as coastal stacks and islands. For the more numerous Woodpigeon, however, the component of the population breeding on arable land appears to have been largely lost, without a relative increase elsewhere. Presumably this reflects the greater dependence of the Woodpigeon on grain supplies, the Stock Dove being able to exploit weed seeds in other physically suitable habitats.

2. Skylark

Although widely regarded as a bird characteristic of arable farming, the Skylark in fact uses a wide range of habitats both during and outside the breeding season. O'Connor & Shrubb (1986a) in fact showed a close correlation between the national Common Birds Census index for this species and the proportion of young leys in England and Wales. Hence, although Skylarks are potentially vulnerable to poisoning by organochlorine compounds, only a proportion of the population was likely to be affected in any one year.

Overall egg mortality has tended to reduce systematically through the study period (Figure 2.1) whilst chick mortality has oscillated slightly about a more or less equilibrium level (Figure 2.2). Interestingly, it seems that slightly lower than normal egg and chick mortalities were experienced in the late 1950s. In recent years chick mortality may have improved still further, a trend in parallel with that in clutch size (Figure 2.3). Over the study period as a whole nest habitat diversity has increased within farmland, except that in recent years (since about 1976) some decline seems to have set in (Figure 2.4).

3. Dunnock

The Dunnock is a ground-feeding, gleaning and insectivorous bird taking rather few grains. It is common on agricultural land and therefore provides an example of a species not liable to poisoning by seed-dressing usage.

The results for egg mortality (Figure 3.1) indicate relatively stable egg success but with two periods of reduced mortality, from about 1959-65 and again from about 1975-85. The only correlate of these two time periods that we know of is the level of total passerine numbers in the country, reduced in the early period both by

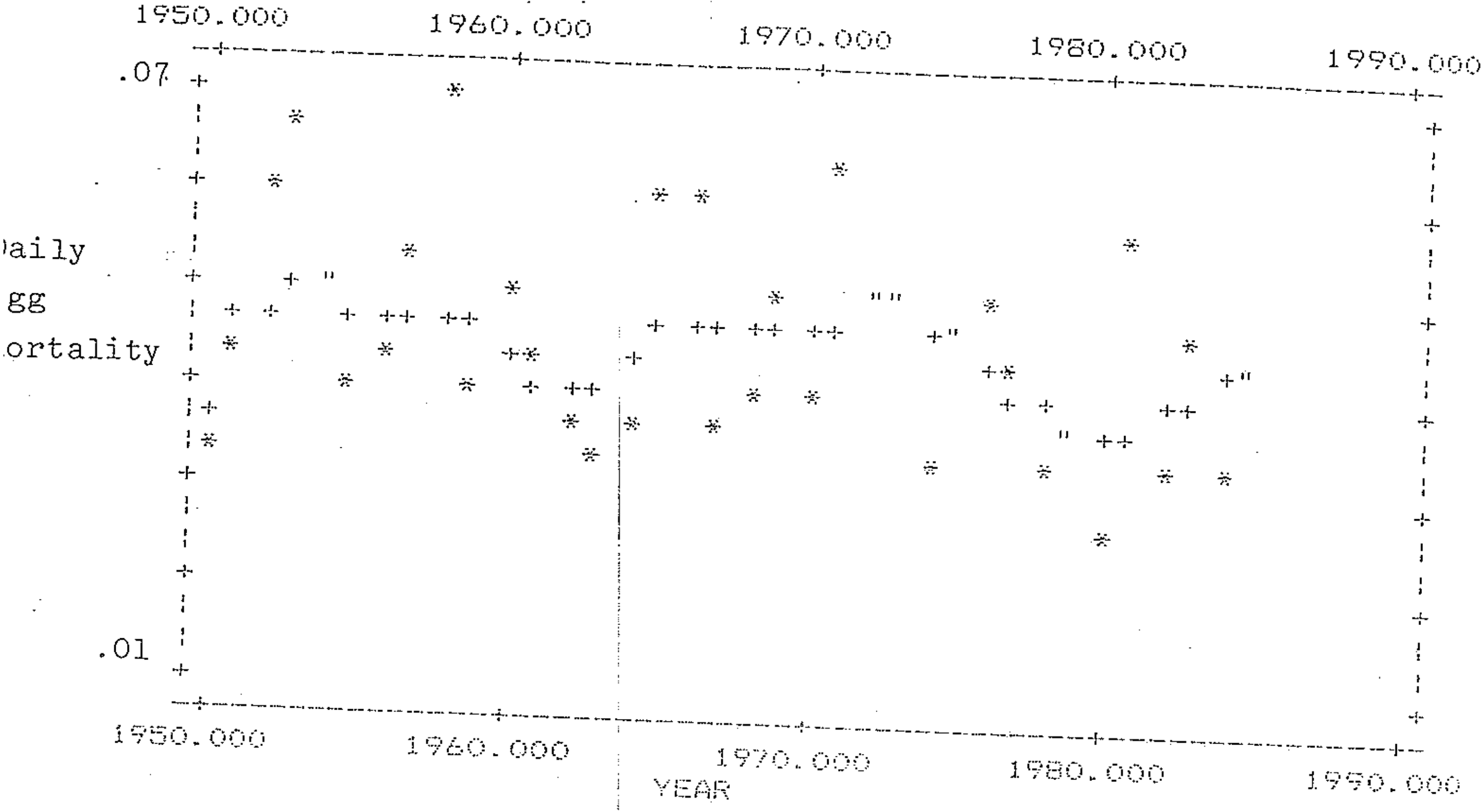

Figure 3.1 Temporal trends in egg mortality in the Dunnock, 1950-85. Symbols as Figure 1.1

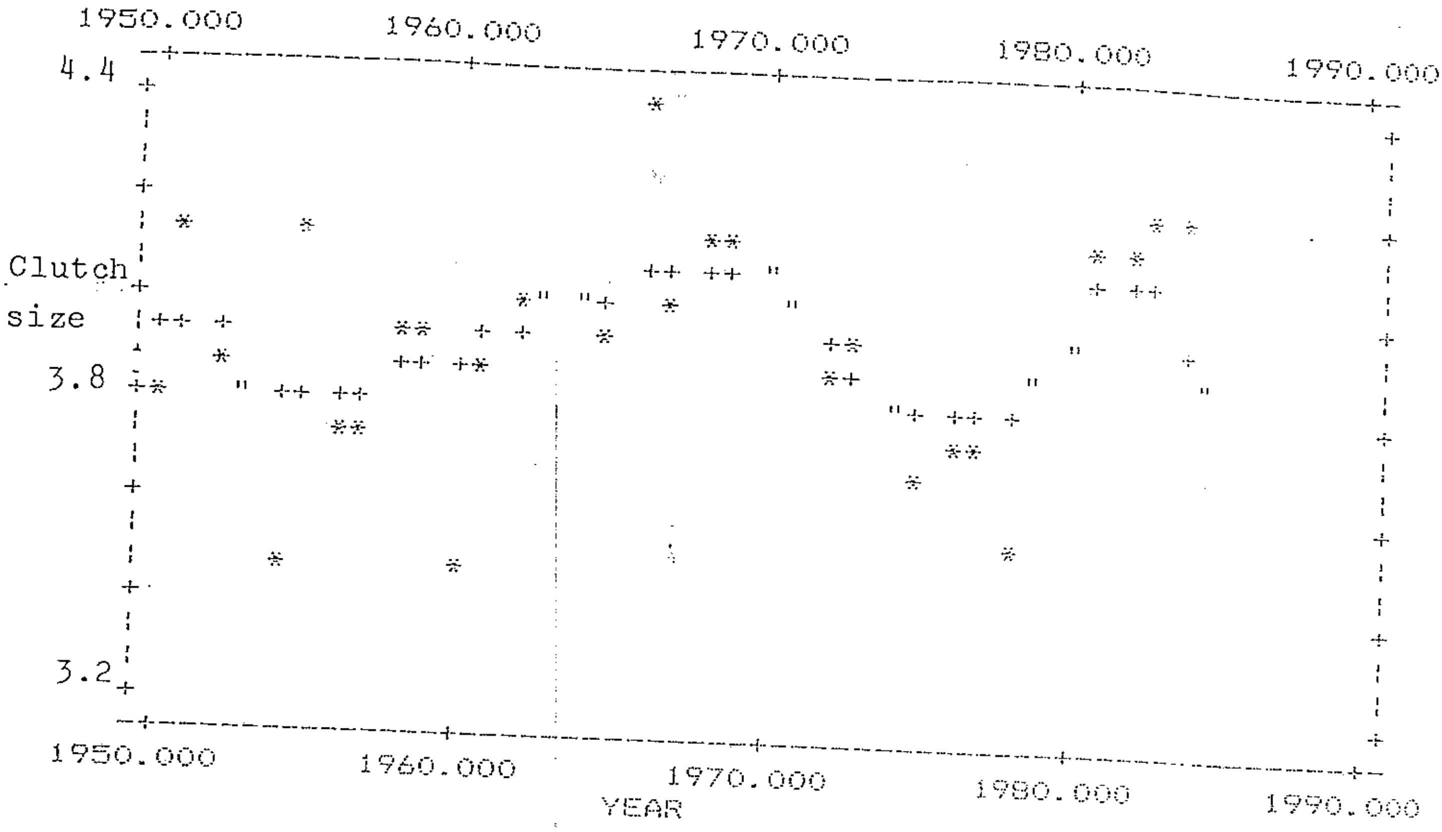

Figure 3.2 Temporal trends in mean annual clutch size in the Dunnock, 1950-85

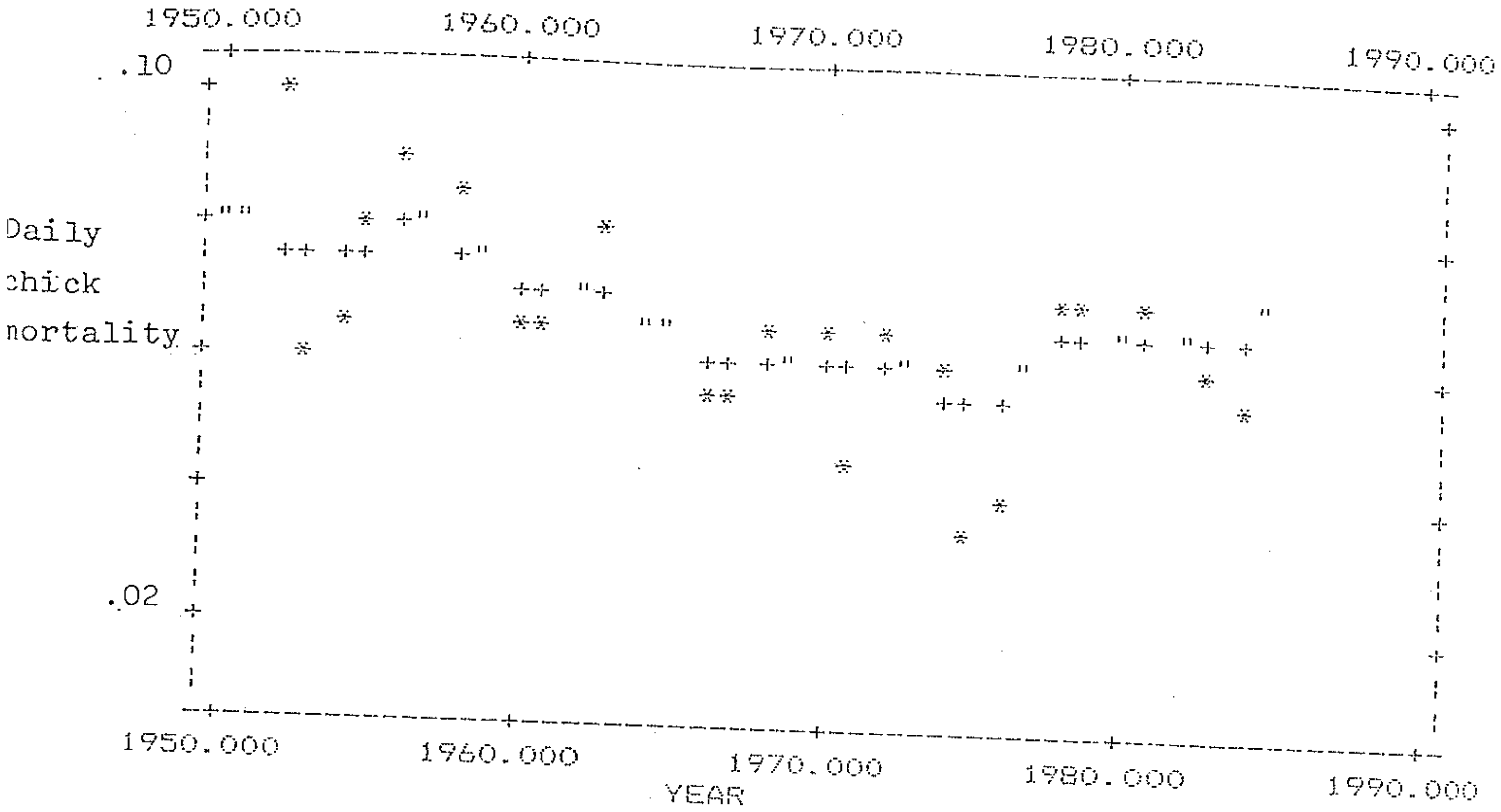

Figure 3.3 Temporal trends in chick mortality in the Dunnock, 1950-85.

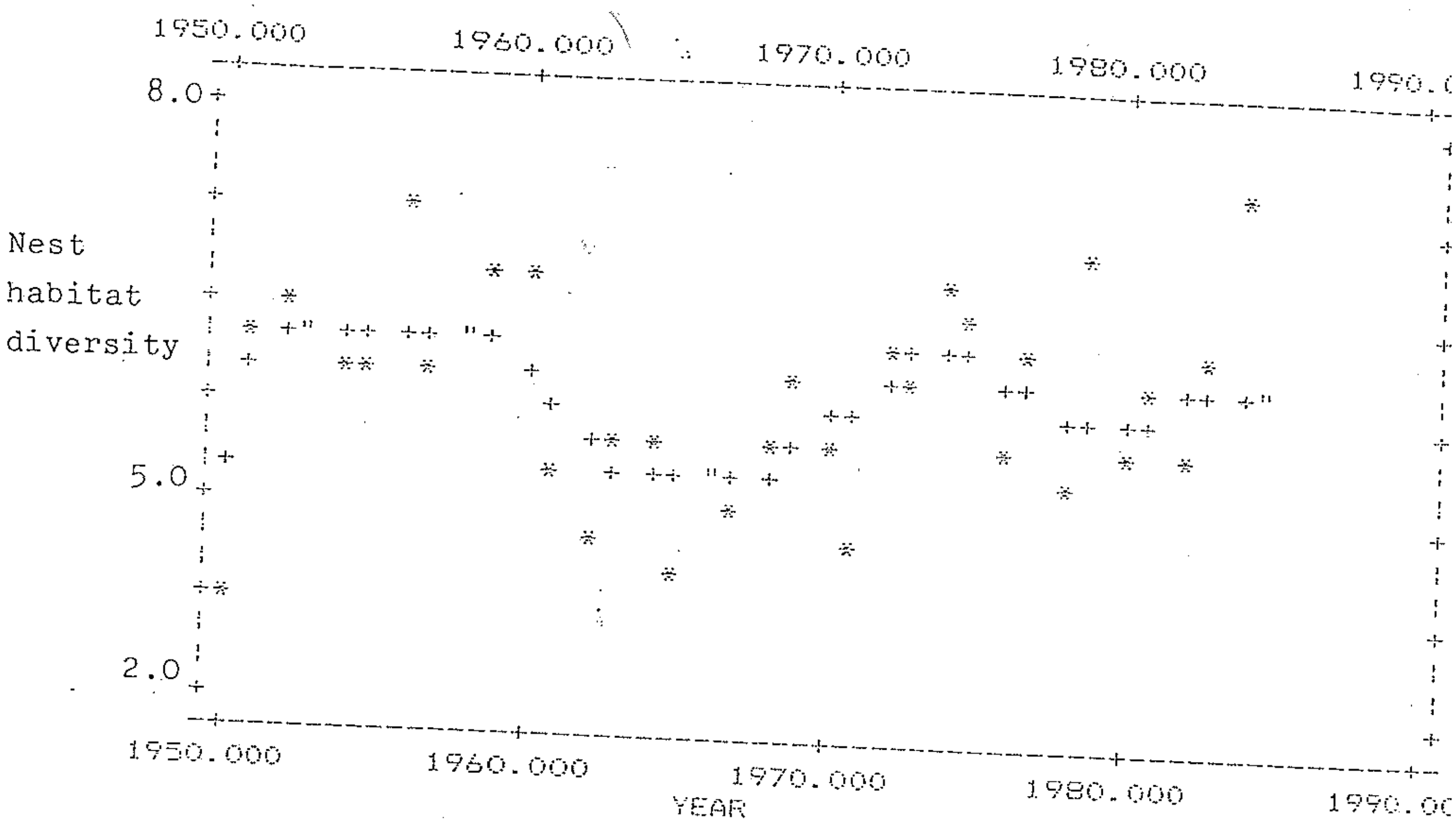

Figure 3.4 Temporal trends in nest habitat diversity for Dunnock, 1950-85.

organochlorine use and by severe winter weather and in the latter period by changes in agricultural practice that reduced the numbers of many resident species in the late 1970s (O'Connor in press). If the Dunnock were subject to considerable "diffuse competition" (MacArthur 1972), its breeding success might well rise at these periods of reduced competitor numbers. Clutch size data (Figure 3.2) rose throughout the period of improved egg success but continued until about 1969 before a decrease began which lasted until about 1978. Chick mortality (Figure 3.3) may also be consistent with the clutch size pattern, with steady improvement from about 1959 to 1968, then remaining relatively stable until the late 1970s when chick mortality again increased slightly.

Data on nest habitat diversity (Figure 3.4) may be closely related to these results, although not statistically correlated with any of the variables concerned. A reduction in diversity of habitats used is suggested from the late 1950s until 1961 or 1962, around which time an increase in diversity began, this lasting until about 1975 or 1976. This pattern would be consistent with interspecific competition with other passerines, with the Dunnock pushed out into marginal habitats when other species are numerous but being able to move into the best available habitats in years of low competitor numbers. Overall, therefore, these results may indicate that Dunnocks have been affected by changes in farming practice only indirectly, through the effects of these changes on other species.

4. Song Thrush

This is a ground-feeding species taking considerable numbers of invertebrates, especially earthworms and snails, year-round, to a lesser extent also taking berries in winter.

The egg mortality data (Figure 4.1) indicate a general improvement in the egg success of this species over the period, except that in recent years egg mortality may have risen again. There may be a slight suggestion in the data of increased mortality in the late 1950s and early 1960s. Chick mortality has also improved fairly steadily over the period as a whole, without evidence of any recent increase (Figure 4.2). Examination of the data on clutch size (Figure 4.3) suggests that clutch sizes in the late 1960s and early 1970s were higher than either previously or since. The habitat diversity data (Figure 4.4) indicate a general increase in diversity over the period 1961-80, possibly with lower values in recent years. It is noteworthy that particularly low values are associated with the immediate aftermath of severe winters (1962-63 and 1982-83). This is not surprising in a species which is known as a partial migrant, with additional birds moving out of Britain in severe weather. The data suggest a slight decline in diversity of habitat during the 1950s (a trend even more apparent in the data for the portion of the population in the dominant habitat - data not shown) but population levels are not known for this period which is prior to the inception of the Common Birds Census. O'Connor & Shrubb (1986a) have drawn attention to regional declines in population size of this bird in recent years, attributed to changing agricultural practices, and the time pattern of the diversity changes shown here tends to reinforce this conclusion, as does the data on increased egg mortality.

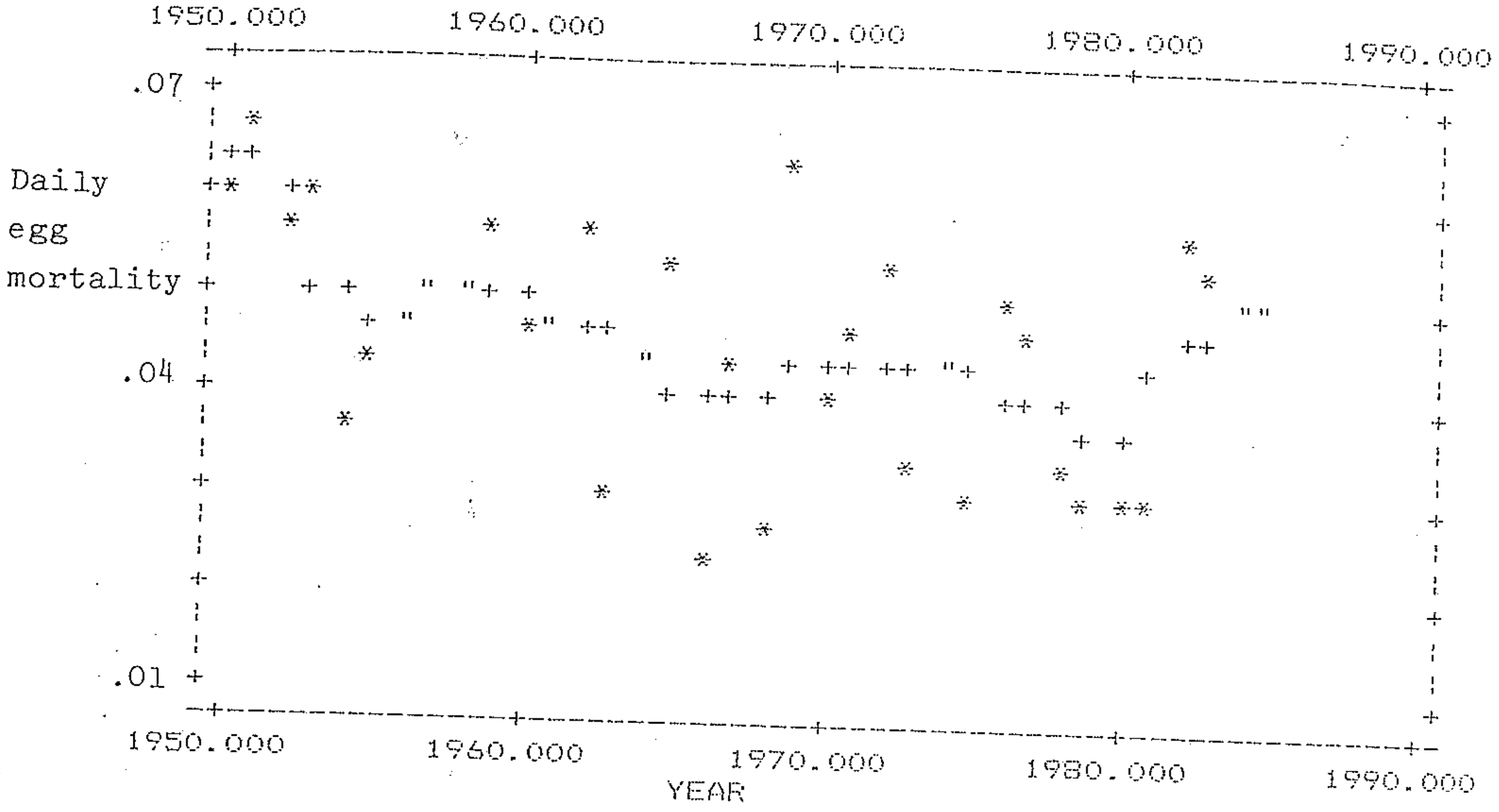

Figure 4.1 Temporal trends in egg mortality in the Song Thrush, 1950-85. Symbols as Figure 1.1

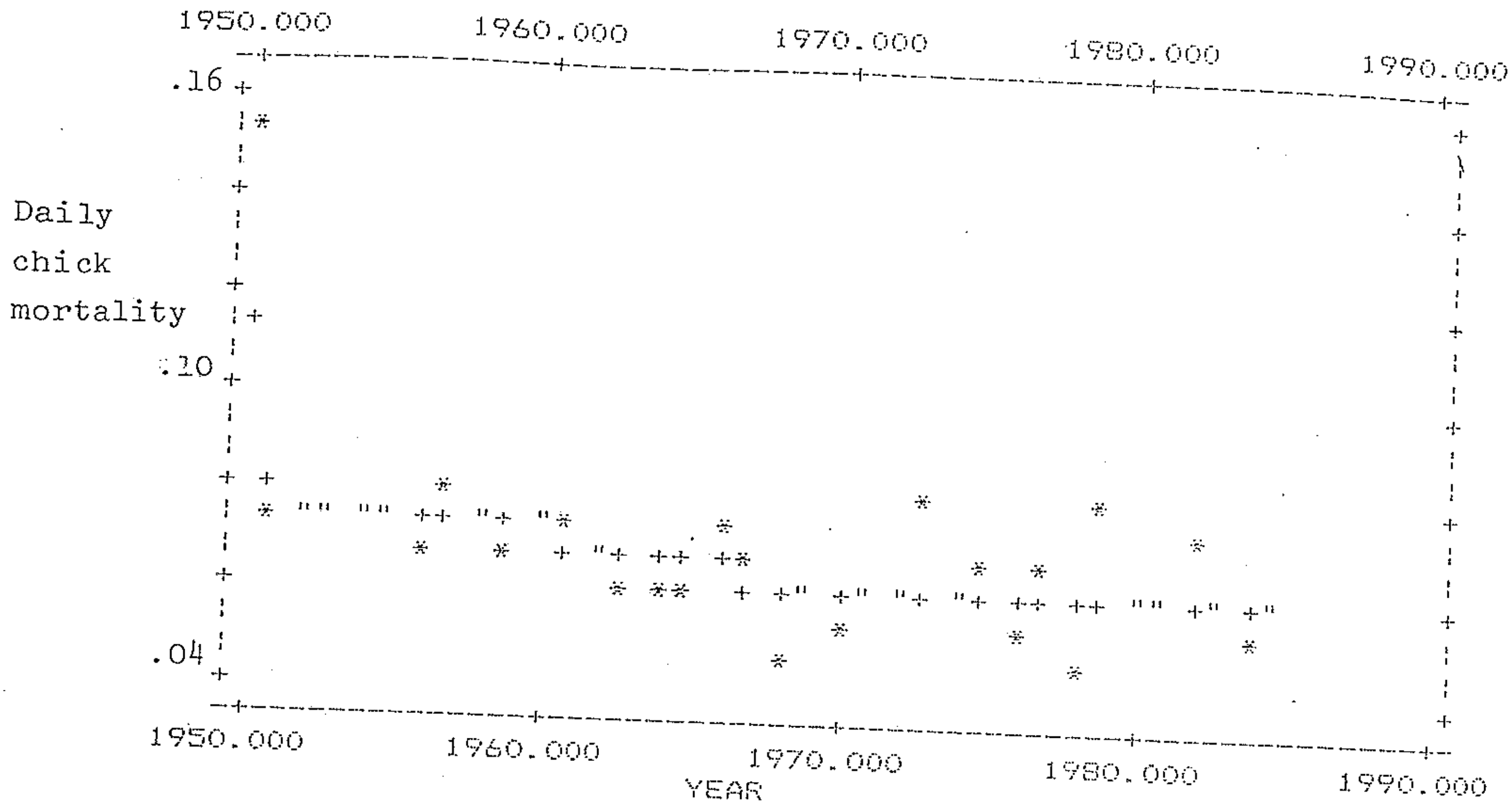

Figure 4.2 Temporal trends in chick mortality in the Song Thrush, 1950-85.

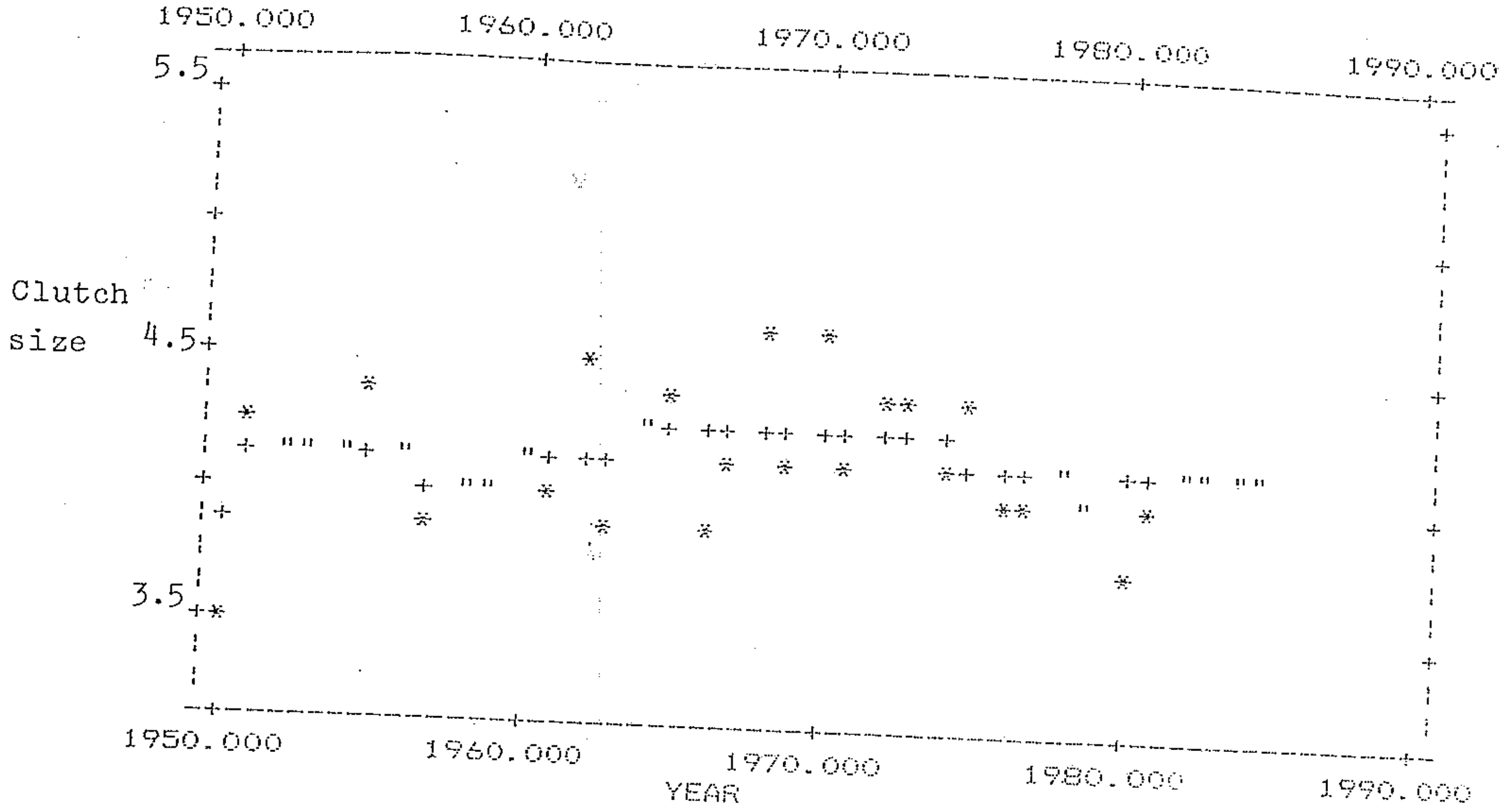

Figure 4.3 Temporal trends in mean annual clutch size in the Song Thrush, 1950-85

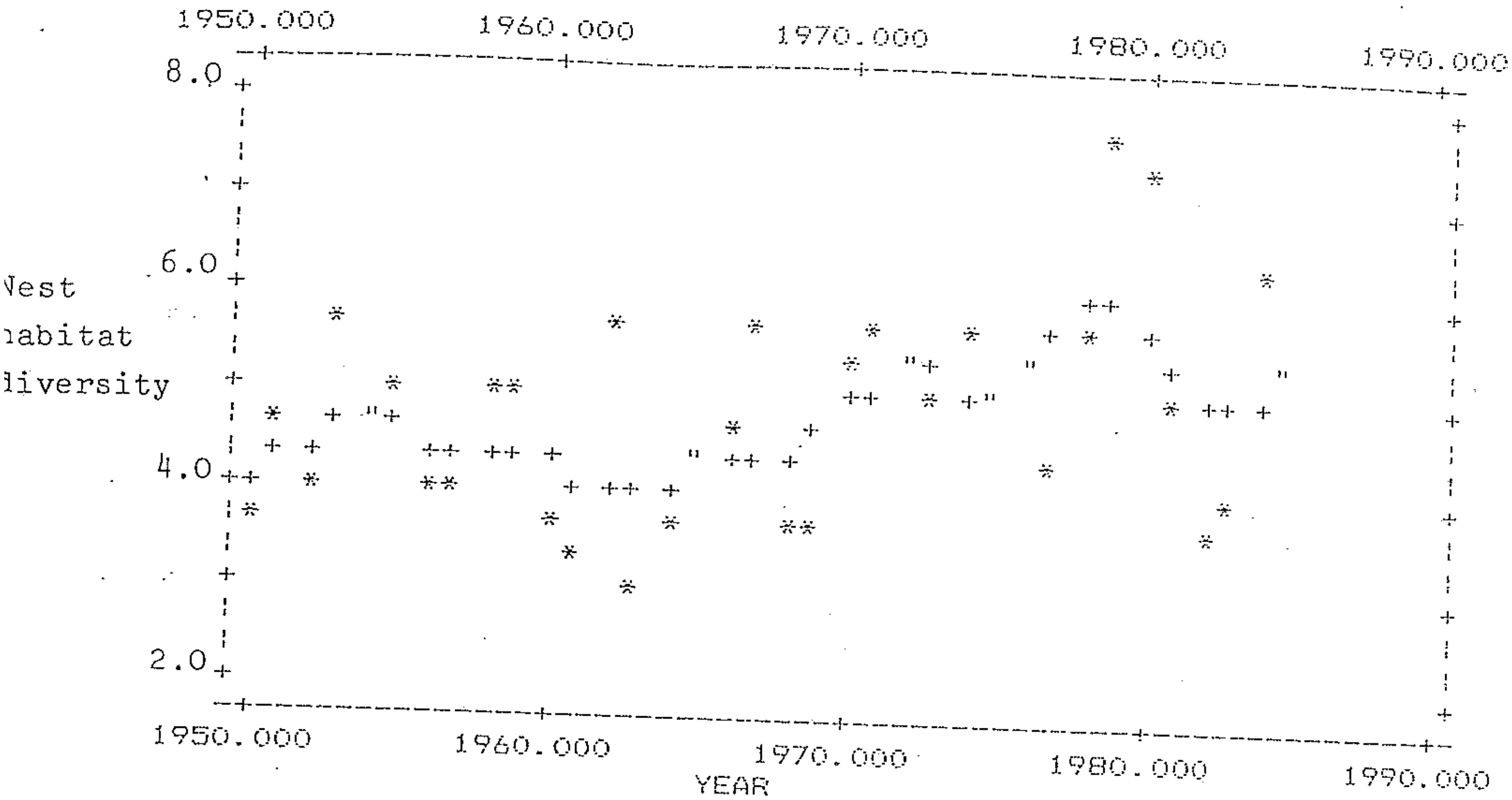

Figure 4.4 Temporal trends in nest habitat diversity for Song Thrush, 1950-85

5. Mistle Thrush

Mistle Thrushes are primarily invertebrate feeders during the breeding season and are invertebrate and berry feeders in winter. Consequently they would be expected to be little affected by the use of organochlorine seed dressings in the early part of the study period. They have, however, been shown to have benefitted in recent years from the advancement of mowing with the switch from haymaking to forage harvesting, with clutch size and fledging success both increasing in areas where mowing is most prevalent (O'Connor & Shrubb 1986a).

Figure 5.1 shows that egg success has varied rather little over the study period, though possibly with a reduction in success in the very late 1960s. Such a reduction is also apparent in the data on chick success (Figure 5.2). Although there is substantial variation in the individual years' estimates, the trend figures suggest a sharp increase in mortality in the very early 1950s, continuing slowly to about 1965. Fledging success appears to have increased through the latter 1960s, stabilising (or possibly slightly worsening) until the very late 1970s, since when success has risen. Data on clutch size (Figure 5.3) suggest a slight drop in the late 1950s, followed by steady improvement through to the mid-seventies, when a decrease began which lasted until about 1980; since then clutch size has tended to increase. None of these changes were statistically correlated on an annual basis with species diversity but it is worth noting that the diversity of nesting habitats in use was low in the late 1950s and early 1960s, with this followed by an increase to more or less plateau levels from about 1967 to 1980 (Figure 5.4). Habitat diversity may have decreased slightly during the 1980s. The increase in habitat diversity through the 1960s has been considered by O'Connor (1986) who noted that this was correlated with the increase in population size that developed as the birds recovered from the effects of the severe 1962-63 winter.

6. Whitethroat

Whitethroats suffered a severe population crash in the late 1960s due to drought in the Sahel zone of South Africa (Winstanley et al. 1974). As a result, no useful estimates of egg mortality could be obtained for five of the years in the study period, and the filtering used in data processing here is thus subject to some perturbation. Nevertheless, the results for egg mortality (Figure 6.1) show an improvement in the early 1950s, followed by a worsening until the mid-1960s, then by a reversion to steady improvement in success. Data on chick mortality suggest that chick success was slightly better during the 1960s and again around 1980 than at other times, though the variation is small (Figure 6.2). It is difficult to account for these patterns, in that the Whitethroat is an insectivorous migrant which should be largely immune from the effects of organochlorine chemicals, yet its egg success fell at this time. The general improvement in egg success in the 1970s could be attributed to the lower densities then present on the breeding grounds, leading to reduced intraspecific competition. If organochlorines were not responsible for the worsening conditions experienced earlier, possible explanations might be steadily worsening conditions on the wintering grounds, even before the onset of full drought, with spring migrants returning to Britain in poor condition. Clutch size data (Figure 6.3) show a fall in the early

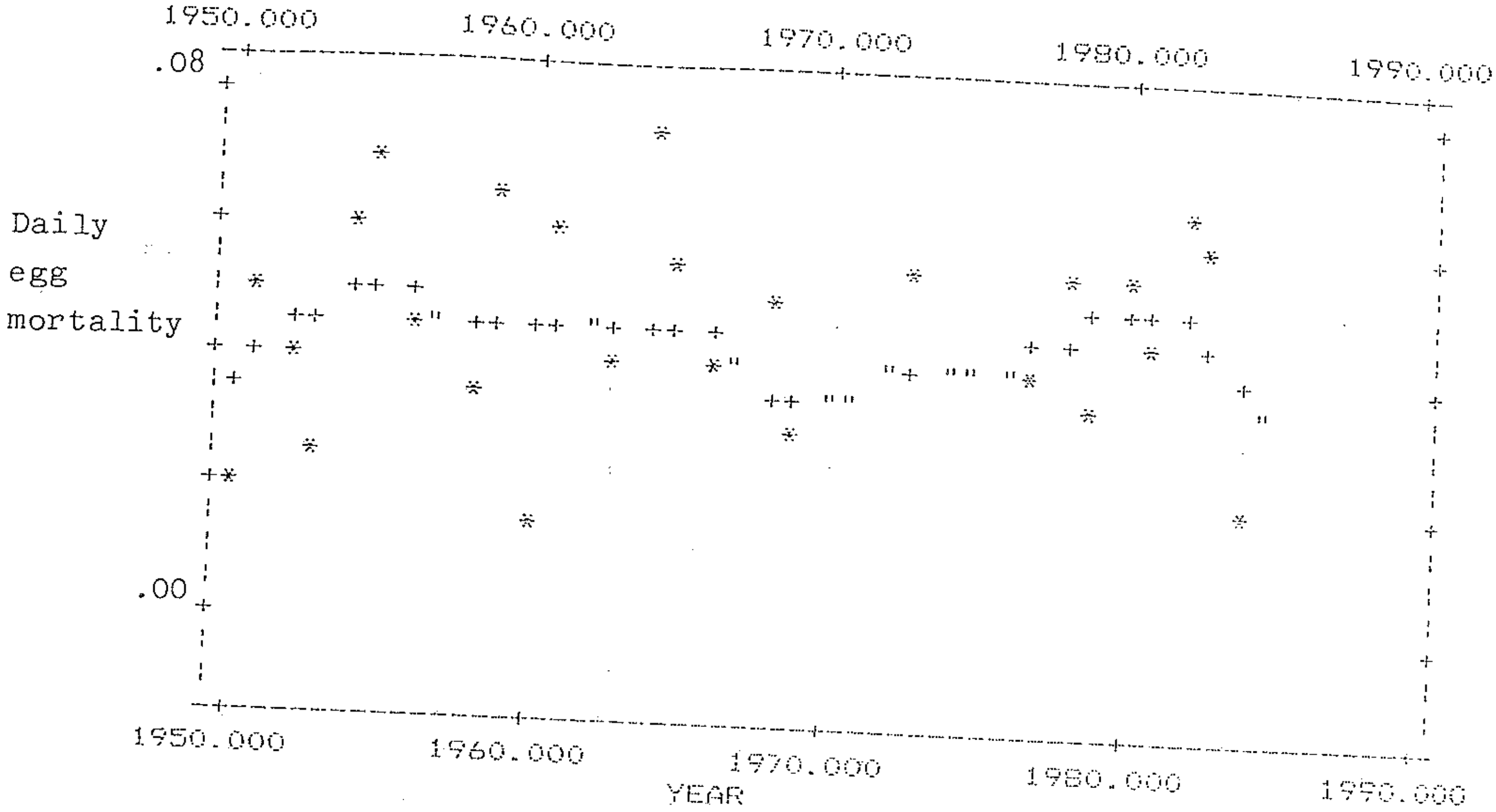

Figure 5.1 Temporal trends in egg mortality in the Mistle Thrush, 1950-85. Symbols as Figure 1.1

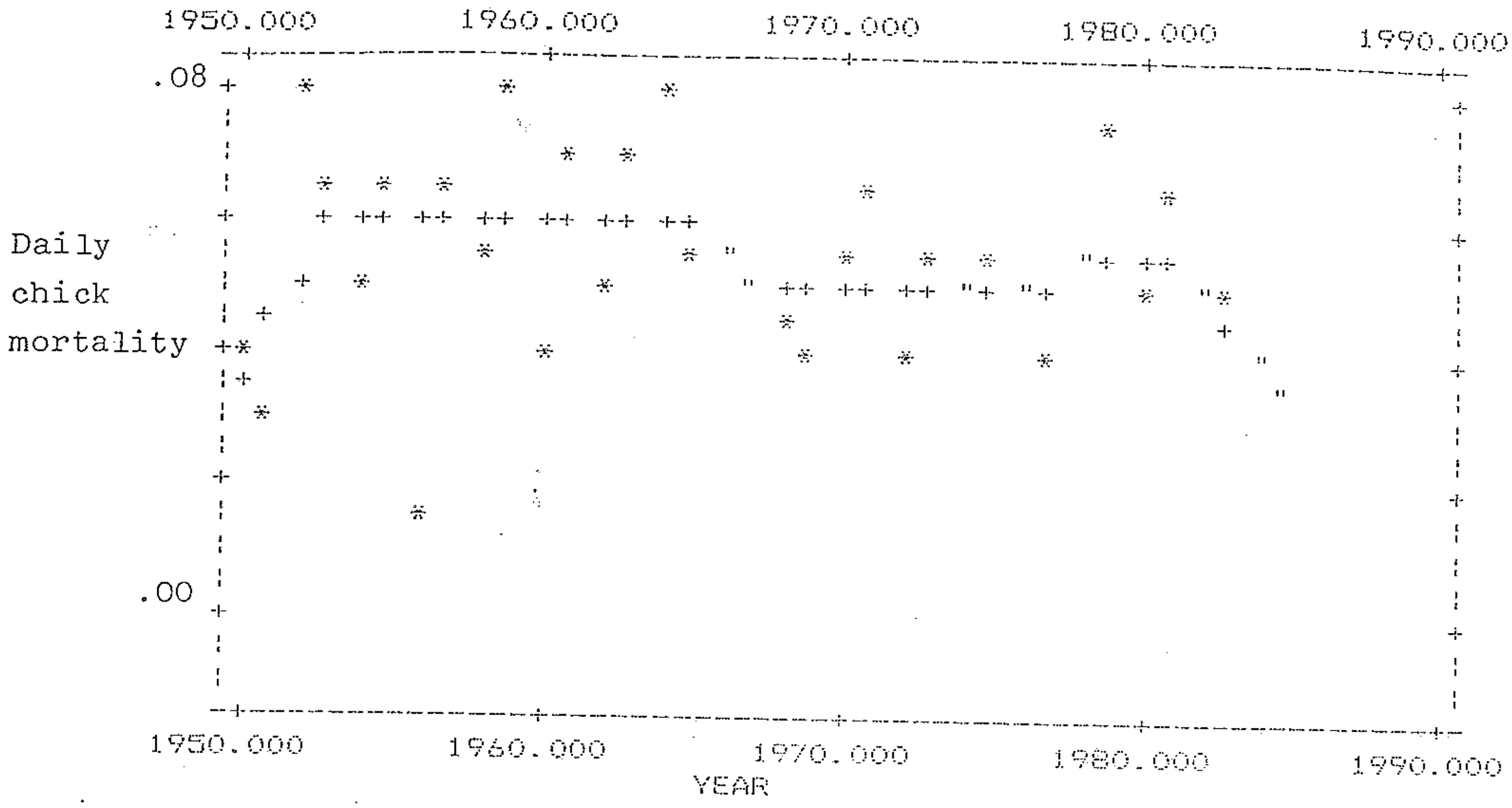

Figure 5.2 Temporal trends in chick mortality in the Mistle Thrush, 1950-85.

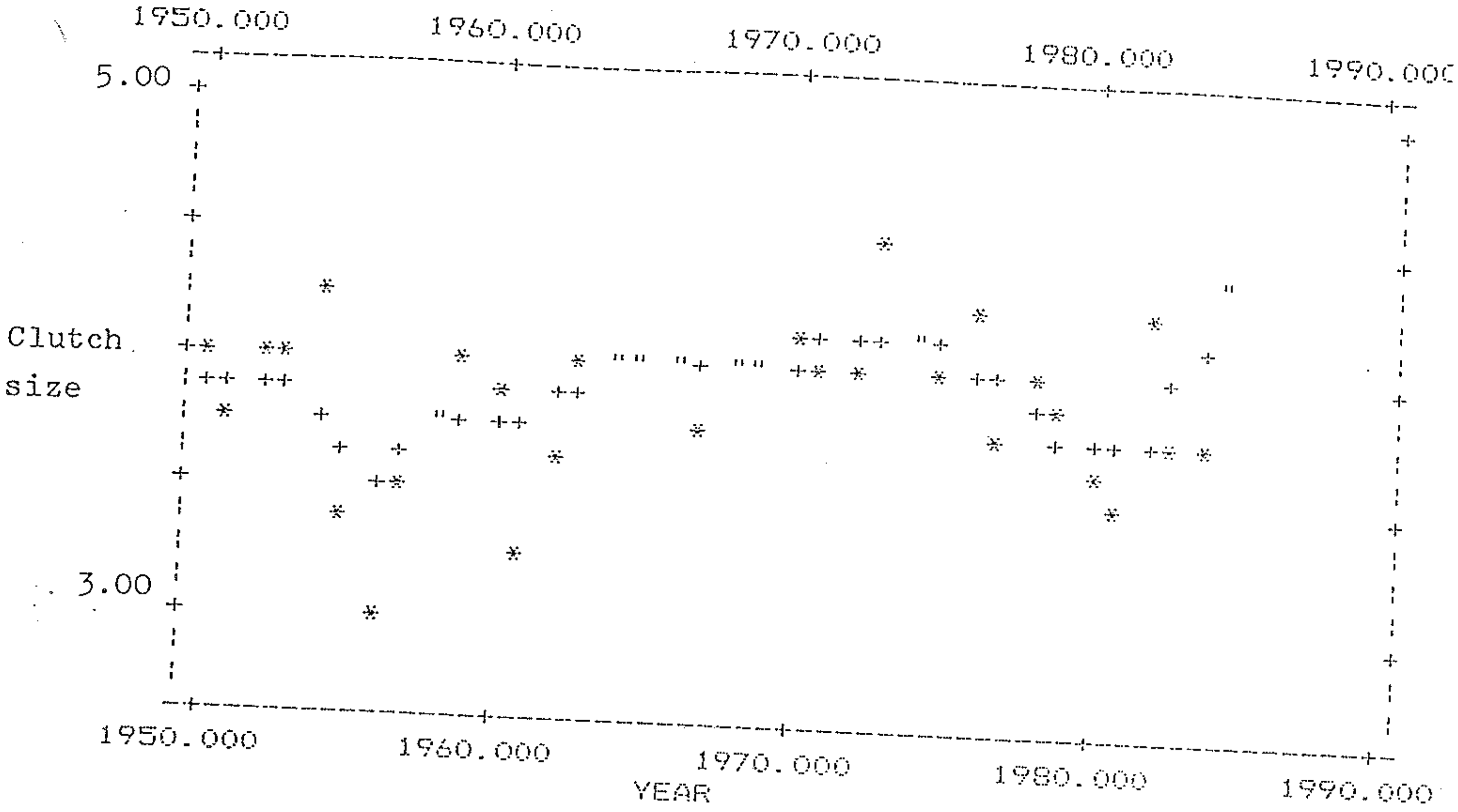

Figure 5.3 Temporal trends in mean clutch size in the Mistle Thrush, 1950-85.

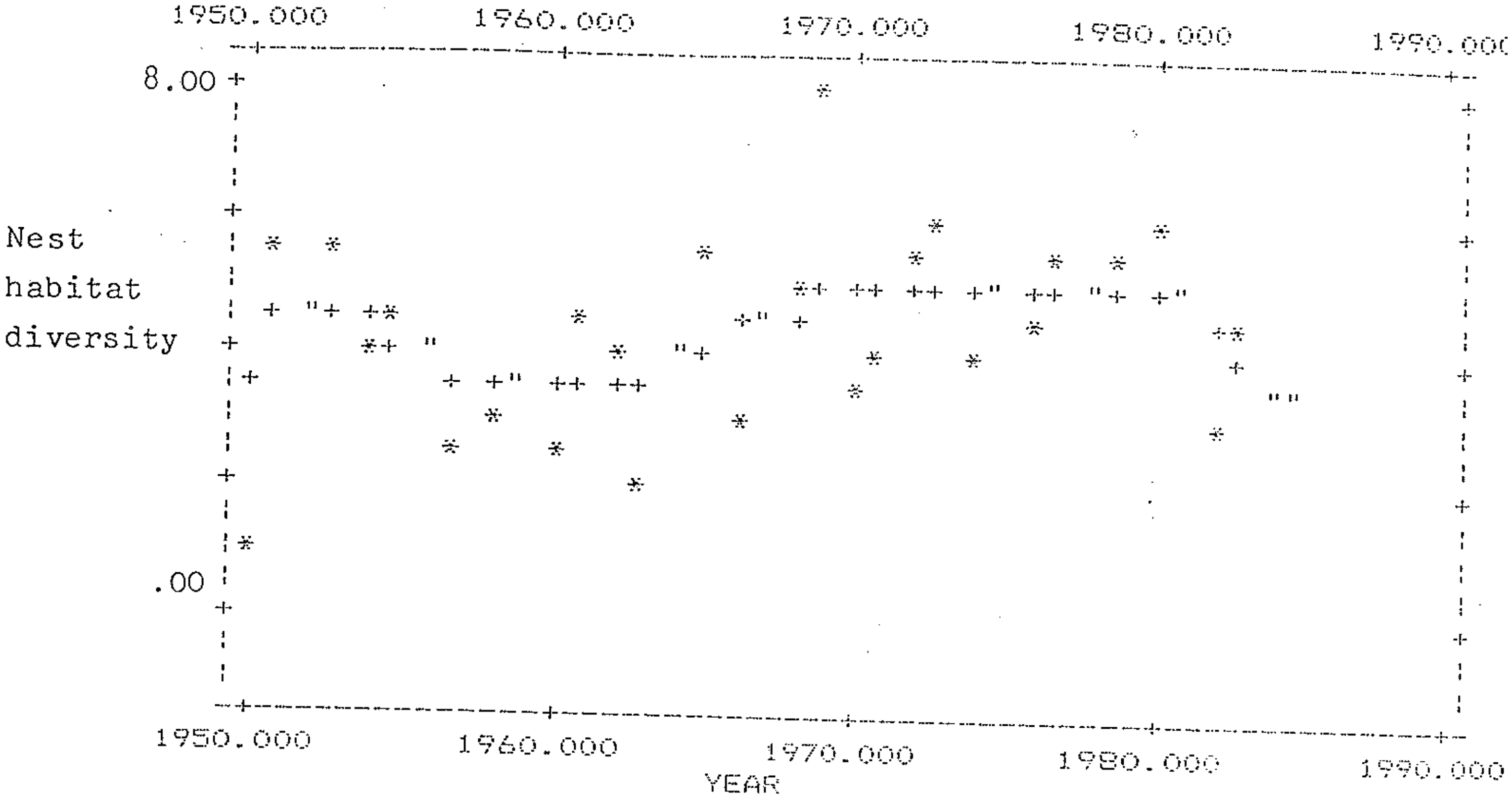

Figure 5.4 Temporal trends in nest habitat diversity for Mistle Thrush, 1950-85

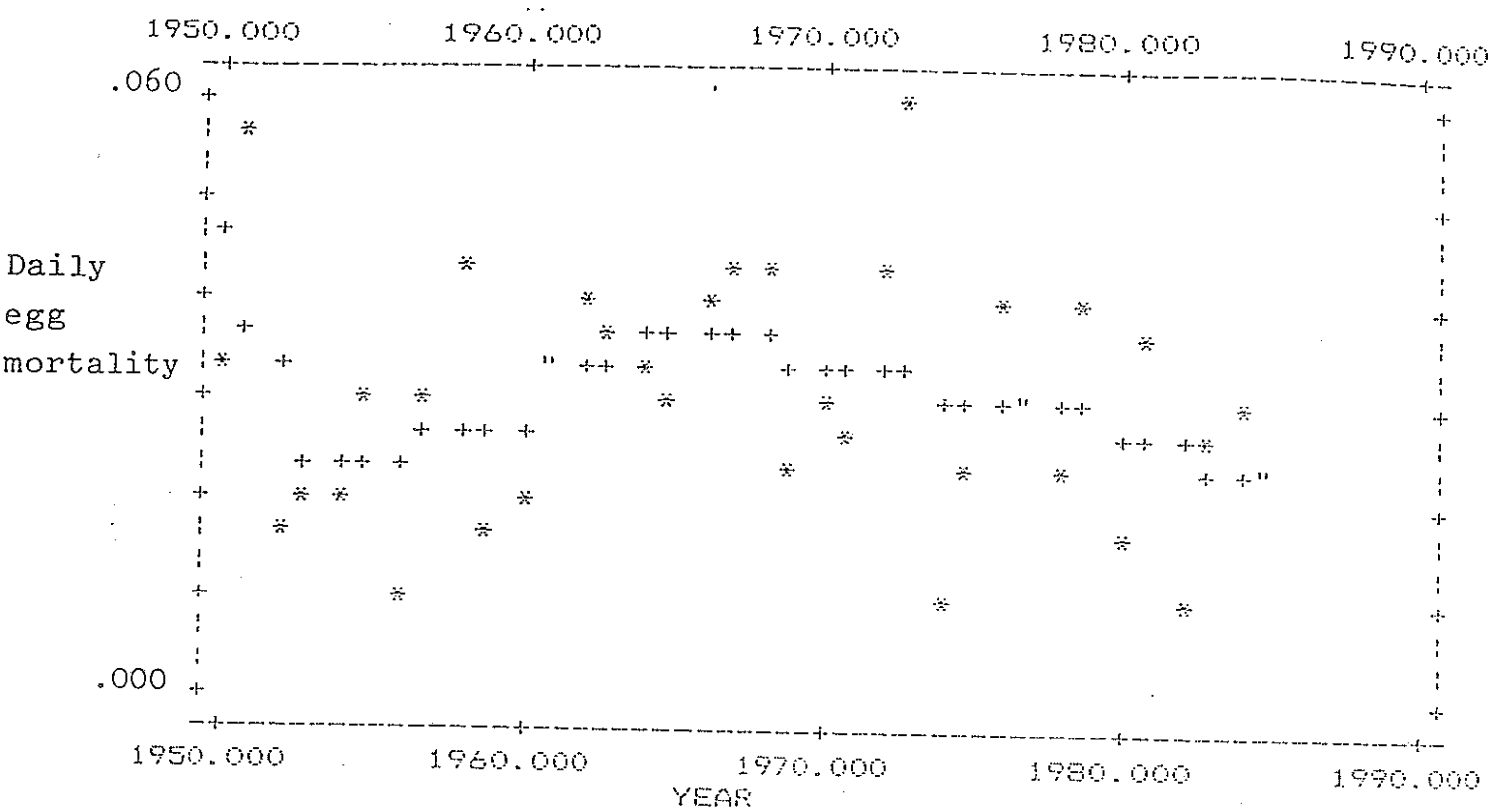

Figure 6.1 Temporal trends in egg mortality (proportion lost per day) in the Whitethroat, 1950-85. Symbols as Figure 1.1

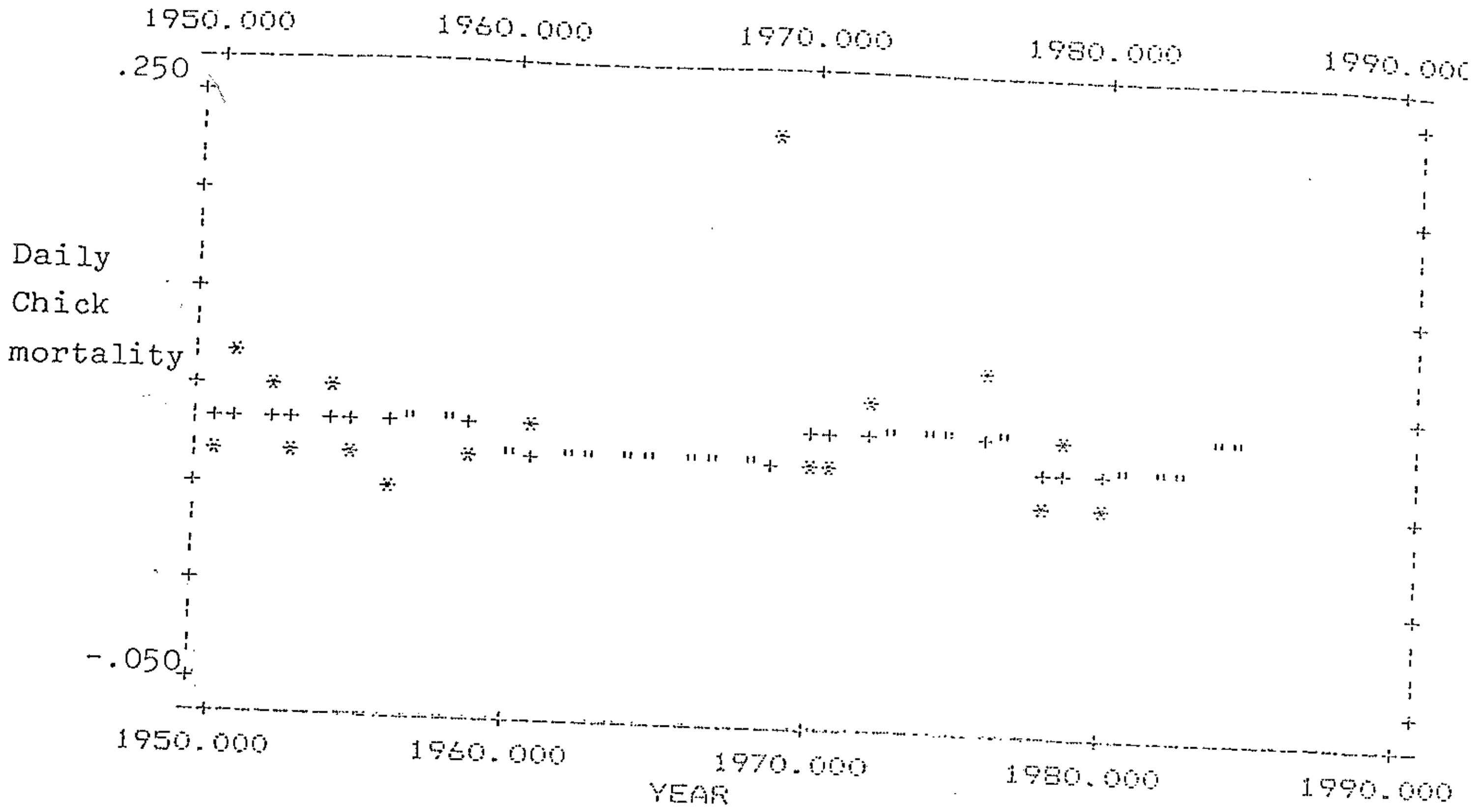

Figure 6.2 Temporal trends in chick mortality (proportion lost per day) in the Whitethroat, 1950-85.

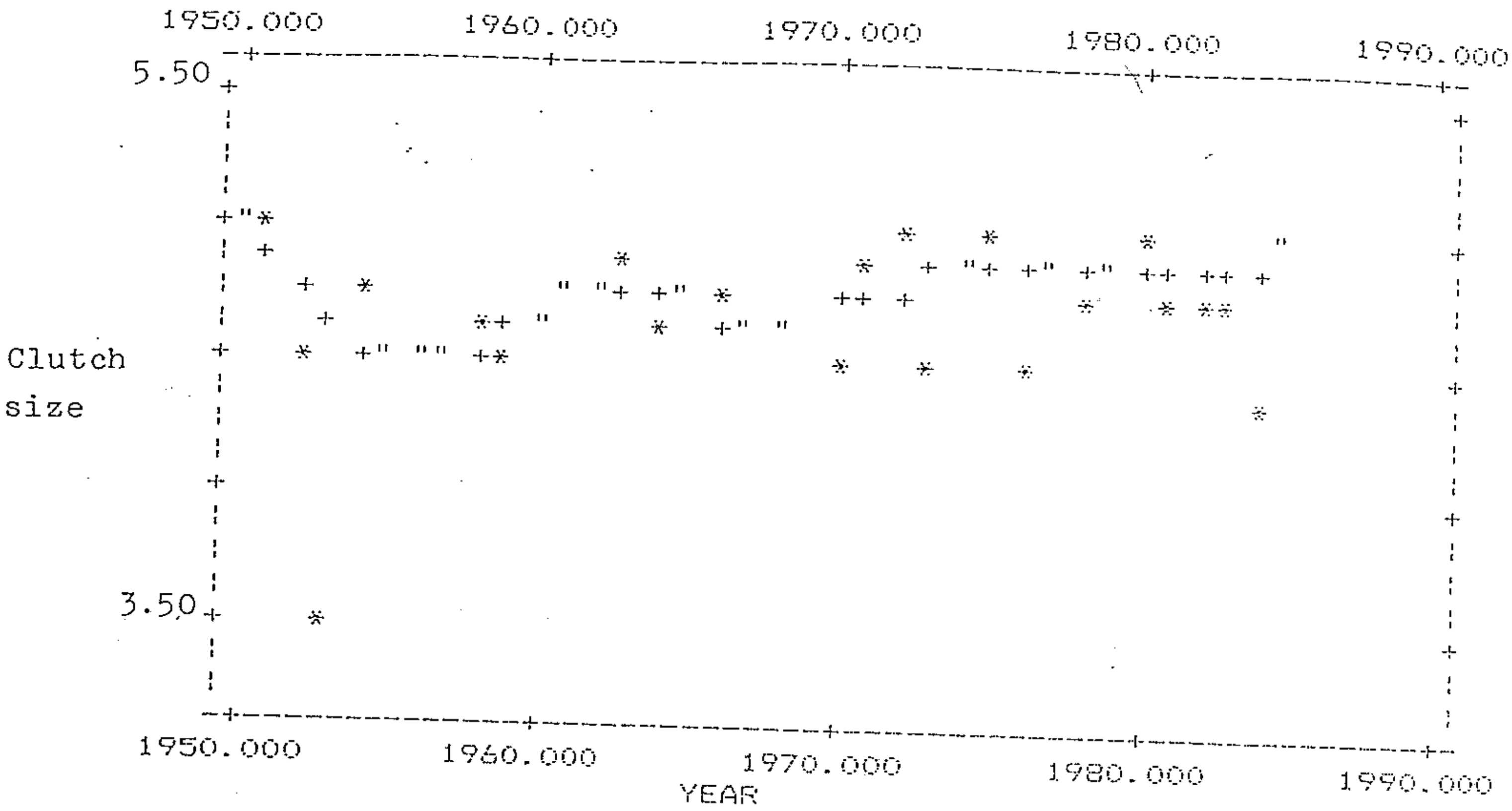

Figure 6.3 Temporal trends in clutch size in the Whitethroat, 1950-85.

1950s followed by a generally steady increase in clutch size ($r = 0.312$, $P<0.05$). The pattern of habitat diversity on farmland likewise shows a weak increase over the period as a whole, though with some oscillations ($r = 0.260$, n.s.). One would normally expect this type of diversification of nesting habitat to be associated with a population increase and a worsening of clutch size and nesting success (Fretwell and Lucas 1969, O'Connor 1985) but here this trend was superimposed on a major population crash and was weakly associated with improved clutch size.

7. Blackcap

This species is a migrant insectivore that occurs predominantly in woodland, unlike the more agricultural and congenic Whitethroat. As noted above, the present analysis is based on records from all available habitats since the number of farmland Blackcap nest record cards proved small. As an insectivorous species, the Blackcap was expected to be little affected by organochlorine pesticides and its inclusion here was primarily as a control for trends in the Whitethroat.

The Blackcap shared with the Whitethroat a tendency towards increased diversity of nesting habitat with time ($r = 0.607$, $P<0.01$), a trend which became particularly pronounced in the early 1960s (Figure 7.1). Habitat diversity may have decreased slightly in the late 1970s but has increased once more in recent years. This enlarged diversity of habitat is associated with a systematic decrease in average clutch size (Figure 7.2), a statistically significant trend ($r = -0.435$, $P<0.01$). This would be expected if increased diversity involved using successively poorer habitats at times of population expansion. Clutch size is itself negatively correlated with habitat diversity across years ($r = -0.384$, $P<0.05$).

Figure 7.3 shows that egg mortality also increased sharply in the early 1960s before stabilising, but has decreased again in recent years. The overall trend is therefore not statistically significant ($r = 0.131$, n.s.). The chick mortality data (Figure 7.4) fluctuates much more, worsening in the mid-1950s, improving through the late 1950s to 1961 or 1962 and worsening again until about 1968. Since then a steady improvement has prevailed until about 1980, since when things may have worsened. Chick productivity was therefore greatest about the time when many resident species were reduced in numbers, either due to pesticide use or to the severe winters of 1961-62 and 1962-63. These changes may be linked to changes in the densities of resident competing species, for over the CBC period as a whole (1962-85) a clear negative relationship prevails between the pooled densities of residents and the pooled densities of migrants, both on farmland and on woodland plots (O'Connor unpublished). This global pattern suggests that competition between migrant and resident species may be quite prevalent even on agricultural land. If this explanation is correct, the habitat diversification shown by the Blackcap may well be in response to the increasing abundance of resident species recovering from the mortality of the 1962-63 winter. O'Connor (1985) records that several migrant species increased their nest habitat diversity in the aftermath of the 1962-63 winter whilst resident species simultaneously contracted in habitat diversity, evidence which he suggested showed that migrants were normally kept out of certain habitats by the abundance of residents therein.

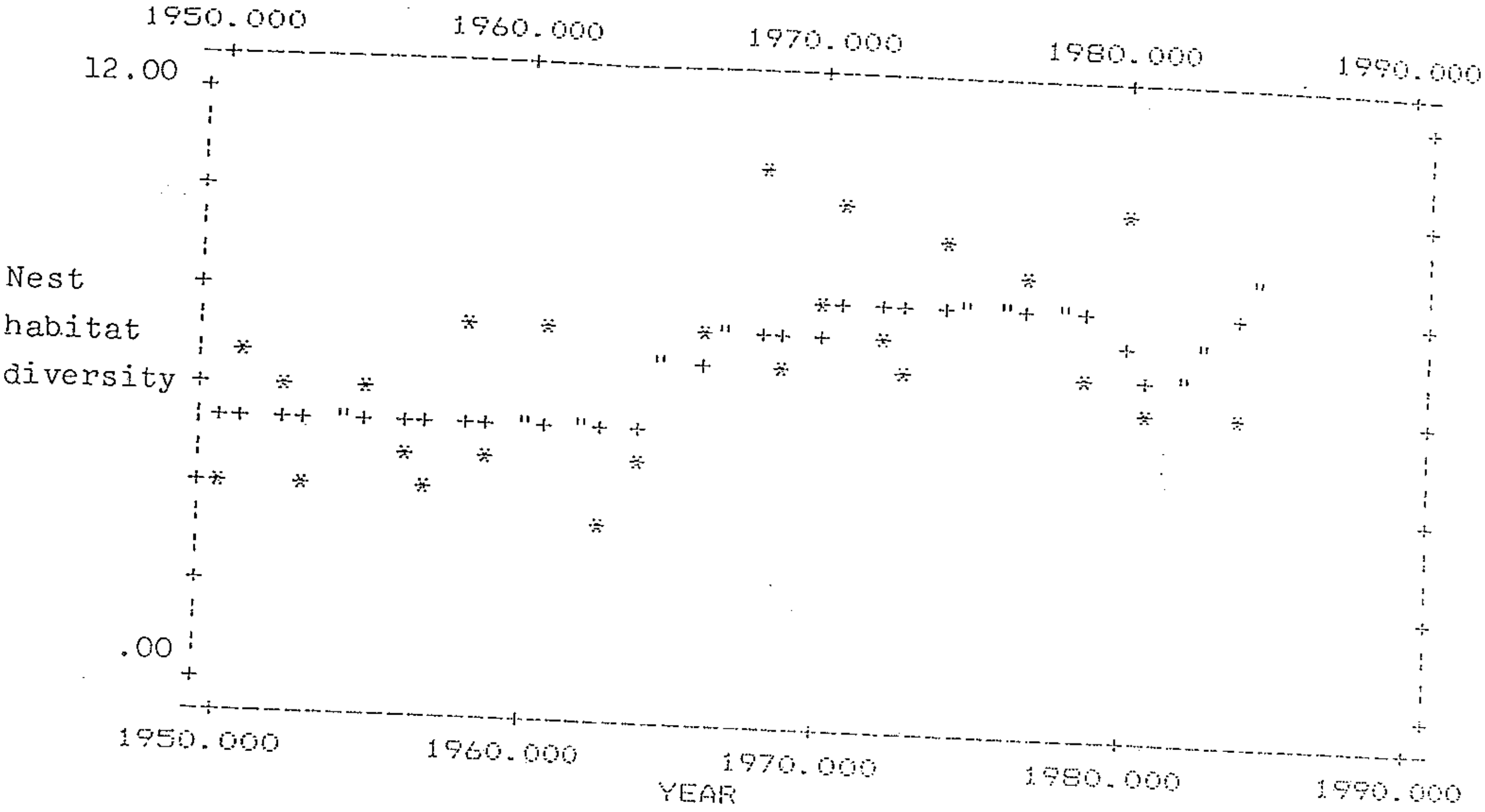

Figure 7.1 Temporal changes in the overall diversity of nesting habitats recorded for the Blackcap, 1950-85. These data are based on cards from all habitats, agricultural and non-agricultural. Symbols as Figure 1.1

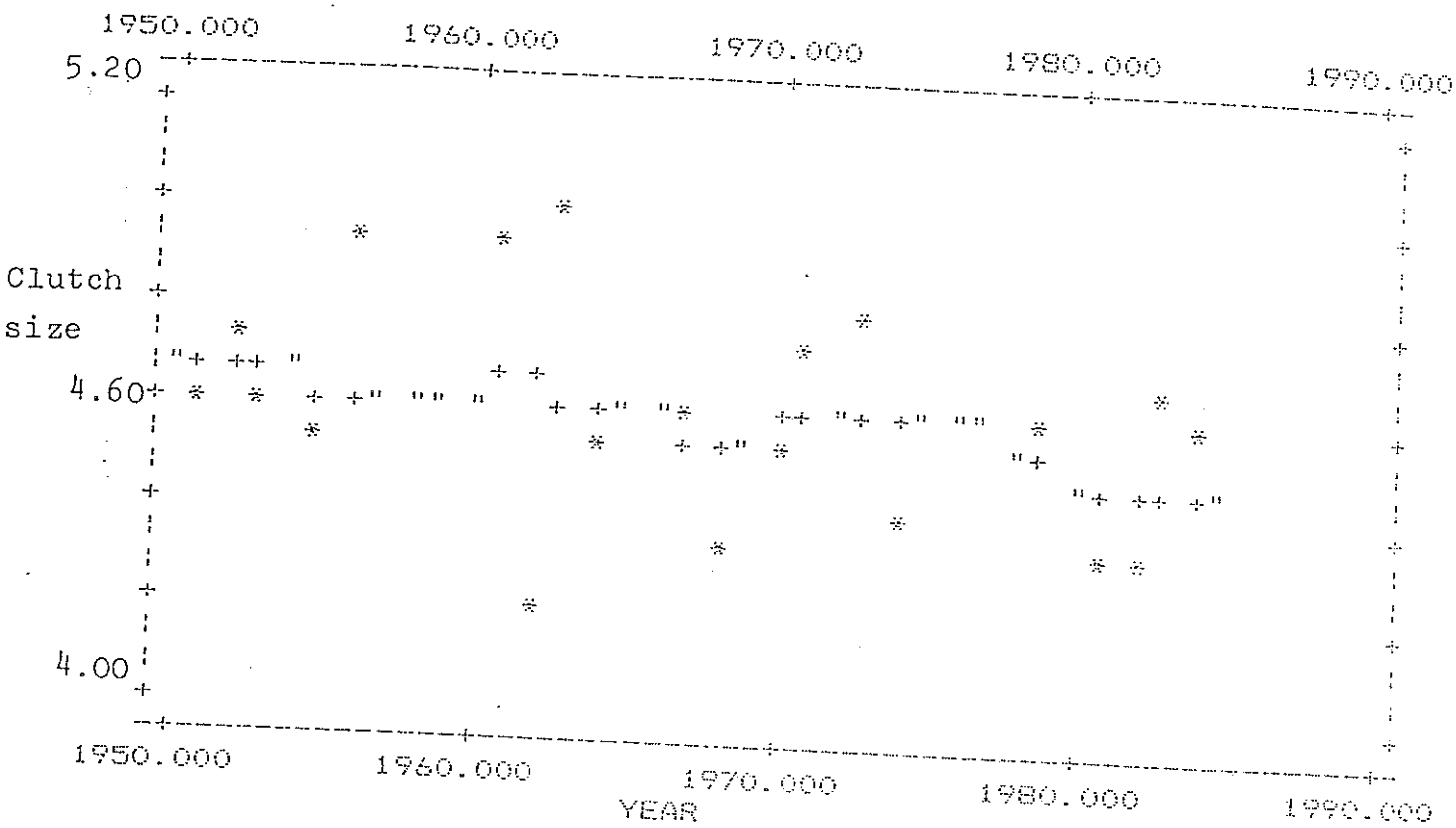

Figure 7.2 Temporal trends in mean clutch size in the Blackcap, 1950-85.

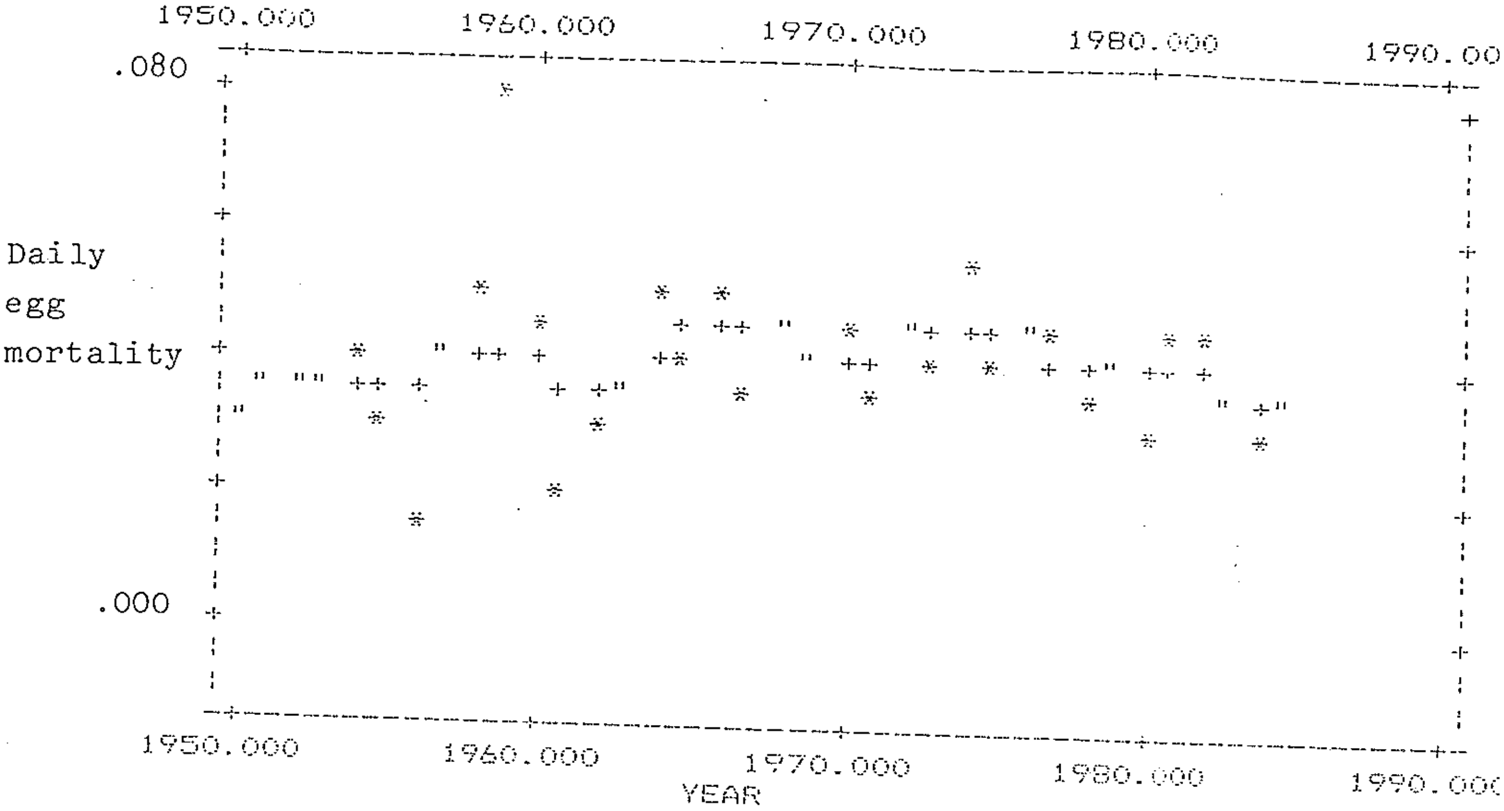

Figure 7.3 Temporal trends in egg mortality in the Blackcap, 1950-85.

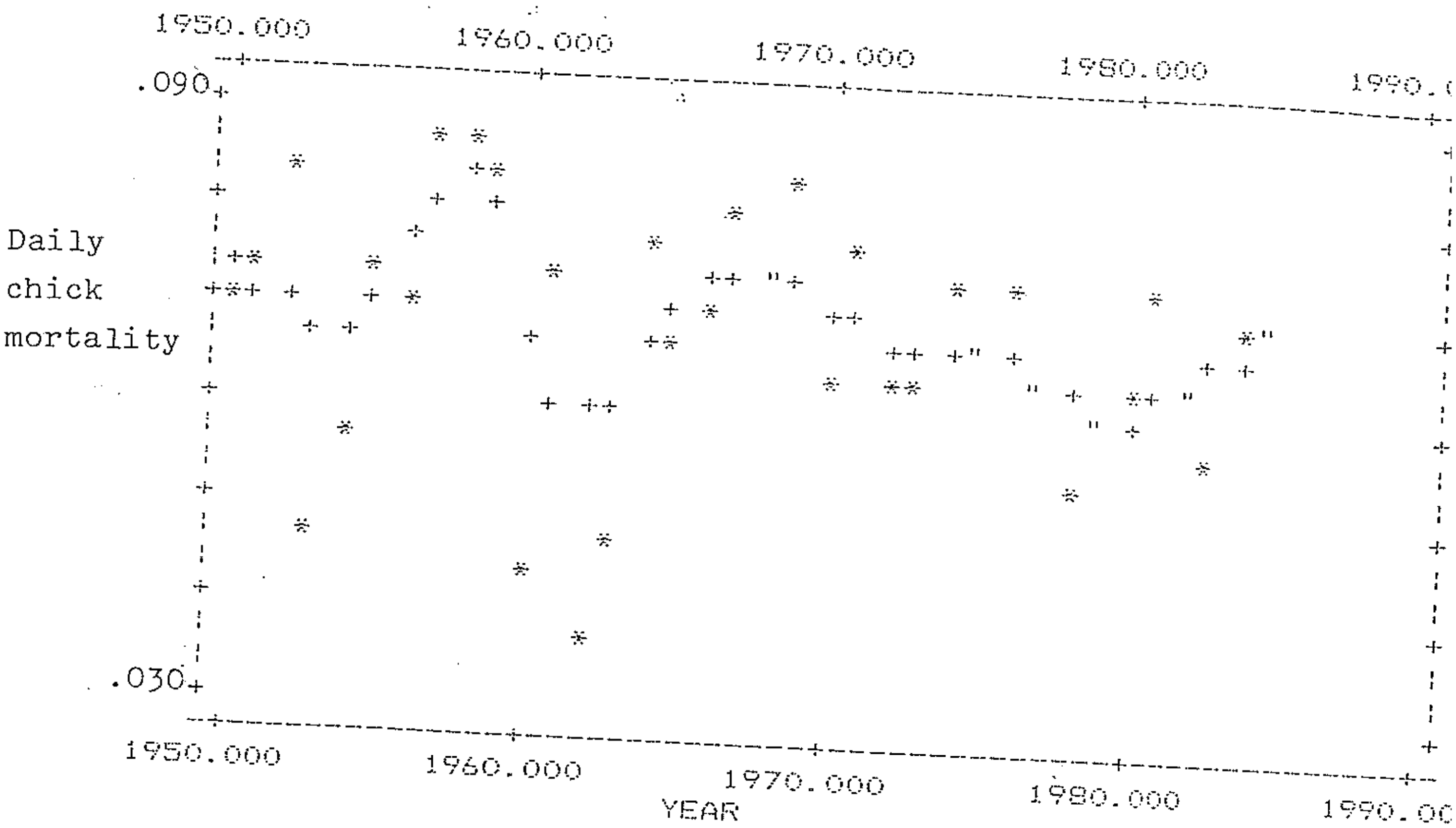

Figure 7.4 Temporal trends in chick mortality in the Blackcap, 1950-85

8. Great Tit

The Great Tit is primarily a woodland species, breeding in holes and feeding its young almost exclusively on caterpillers. At high population densities, some individuals overflow into farmland, this principally affecting first-year breeders that are sub-dominant to adults (Perrins 1979). Although farmland is probably a poorer habitat for Great Tits than is woodland, both in terms of clutch size and breeding success (Perrins 1979), clutch size is nevertheless strongly density-dependent on farmland (O'Connor 1980b), indicating considerable scope for ecological influences. For the present study, therefore, the insectivorous Great Tit was considered potentially a useful control for other species.

In the event, the number of farmland Great Tit nests for some early years proved extremely small, so that annual trend analyses proved impossible. The data were therefore lumped by four-year periods (1950-53, 1954-57, etc.), providing three periods before the 1961 restrictions and six subsequently. These data were not smoothed, in view of the smaller sequence available and analyses were based on these four-year period averages.

Many of the Great Tit nests considered here came from nestboxes and the positioning of these may have determined to a large extent the habitats in which the nest was recorded. There were in fact no trends in nest habitat diversity over time (r = 0.167 n.s.). Similarly, clutch size may be affected by the choice of nestboxes, for Karlsson & Nilsson (1977) showed that in a variety of species the size of clutch laid in nestboxes was greatest in boxes with largest floor area. Changes in clutch size recorded in the present study might, therefore, have been affected by changes in the design of nestbox used over time. Analysis of the data recorded showed that clutch size was only weakly correlated with time (r = 0.250, n.s.), and inspection of data plots showed no features worthy of comment.

Figures 8.1 and 8.2 show the data for egg and chick mortality respectively. The former appears to have increased somewhat between 1950 and 1961, with mortality being substantially lower after that date. The trend for mortality decline over the period as a whole is almost significant (r = -0.633, P<0.10). Chick mortality similarly declined but even more steeply over the period as a whole (r = -0.746, P<0.05), though the highest value here occurred in the period 1954-57. These data suggest that breeding conditions for Great Tits steadily improved on farmland over the period as a whole.

These patterns are difficult to interpret. Great Tit numbers fell sharply during the cold winters of 1961-62 and 1962-63, stabilising subsequently, and this would be expected to lead, if anything, to a reduction in egg and chick success, as found for clutch size by O'Connor (1980b). The opposite pattern found here suggests, therefore, that Great Tits were instead more influenced by conditions in farmland. The fact that high mortalities were prominent in the 1950-61 period is intriguing, given that the bird feeds little on grain. One possibility is that other organochlorine compounds, such as DDT sprays, affected the invertebrates taken by this bird, such that either food shortages or poisoning were present in the early period, but with the sparse data more detailed analysis in pursuit of this point is impossible.

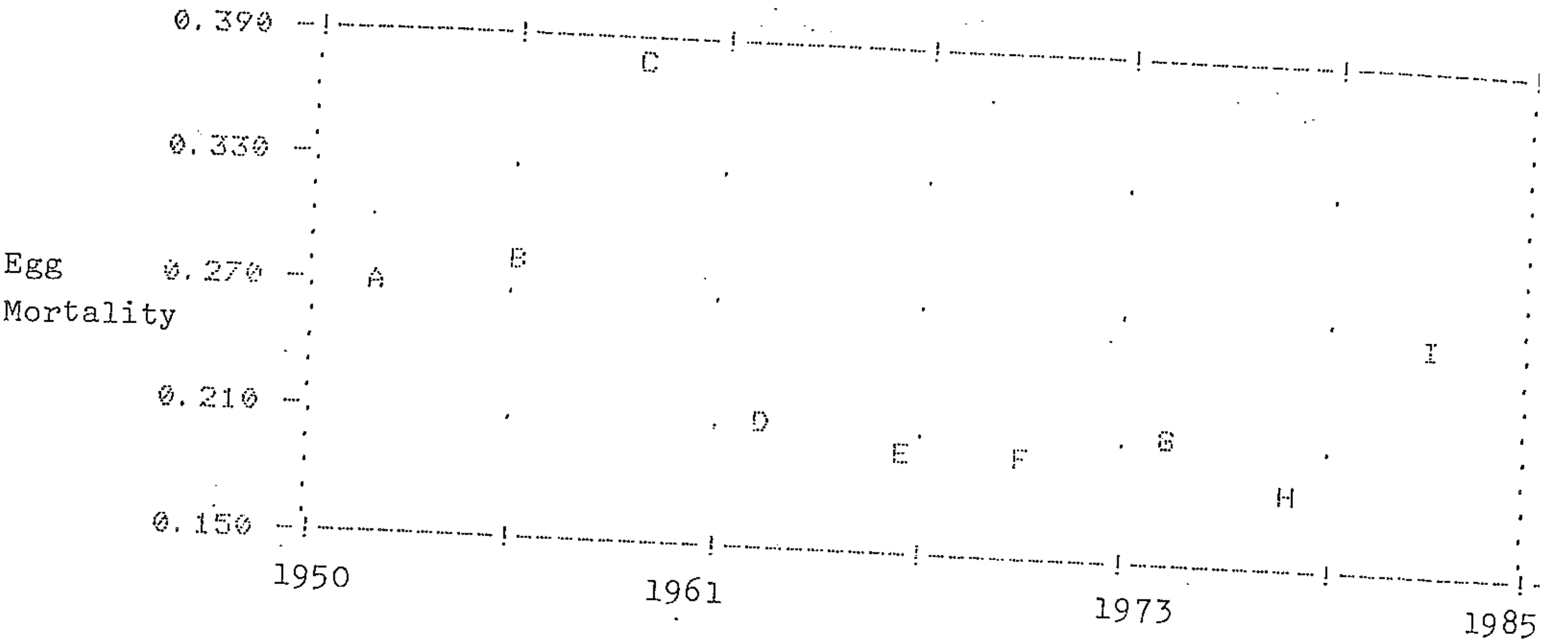

Figure 8.1 Temporal trends in egg mortality in Great Tits for the period 1950-85. Data are grouped by four-year periods.

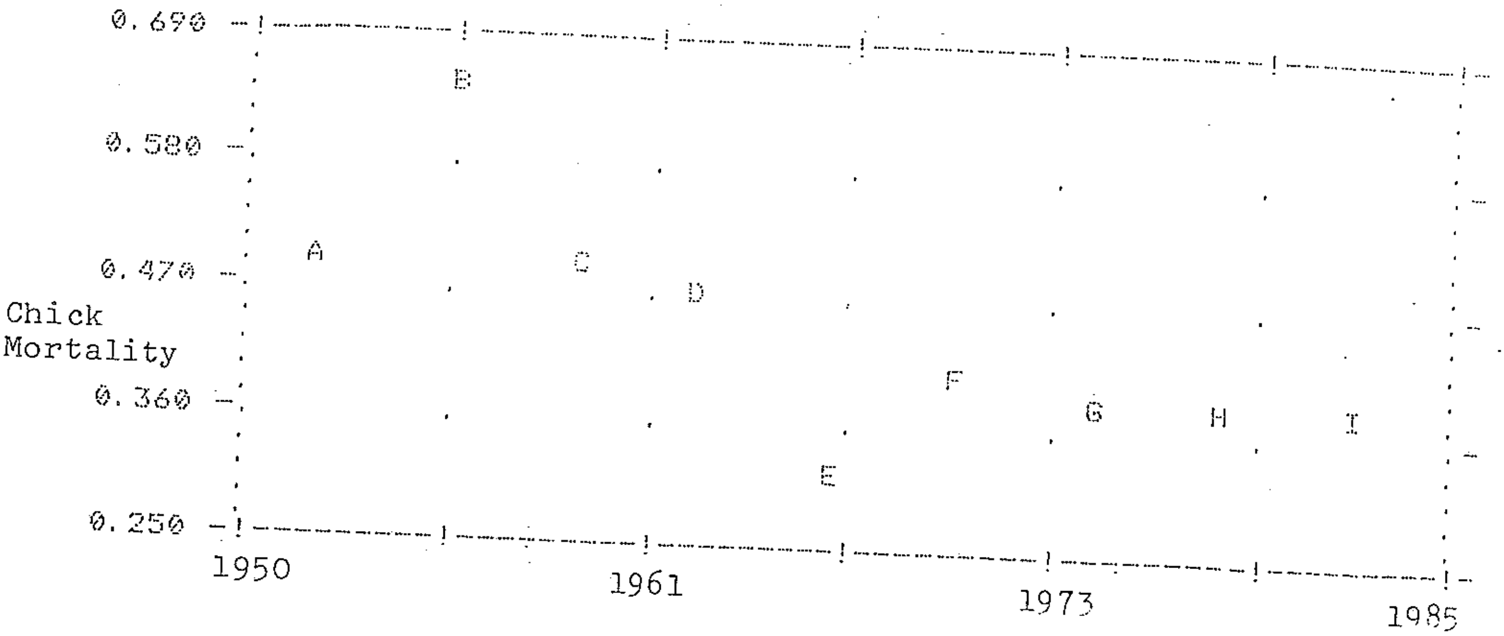

Figure 8.2 Temporal trends in chick mortality in Great Tits for the period 1950-85. Data are grouped by four-year periods.

9. Magpie

This widespread species has increased considerably in numbers in recent years, colonising many new habitats, including suburban and urban areas. This is reflected in the pattern for its nest habitat diversity (Figure 9.1), which increased steadily from 1950 through to about 1974, since when some contraction has occurred. Note, though, the slight reduction in the rate of increase apparent in the late 1950s.

Data on egg mortality rates (Figure 9.2) show that conditions for Magpies improved slowly from the mid-1950s to early 1960s, after which a short-lived increase in mortality occurred; the net increase in egg success then resumed ($r = 0.400$, $P<0.01$). The chick mortality data (Figure 9.3) are not dissimilar, with a steady increase in chick success since the late 1970s preceded by a 12-14 year period of improving, then deteriorating, conditions. The clutch size data (Figure 9.4) also suggest an initial transitory period, with clutch size dropping, then recovering ,between 1950 and 1965-66, continuing at this level until the late 1970s when clutch sizes may have dropped slightly but temporarily around 1979. Over the period as a whole clutch sizes show slight (but statistically not significant) drift upwards in size.

Little is known about the factors responsible for these changes, nor for the concomitant increase in Magpie densities in Britain as a whole. However, it seems clear that an early decrease in clutch size was accompanied by improvements in egg and chick success (correlated with clutch size at $r = -0.201$, n.s., and $r = 0.421$, $P<0.01$ respectively) in the early period, since when productivity of individual nests has increased steadily from a relatively constant clutch size. Again, it is worth noting that the improvements in egg and chick mortality coincided with some contraction in habitat use, suggesting that birds may have vacated the less satisfactory habitats initially colonised in their early expansion. This phenomenon has been discussed for other species by O'Connor (1986, in press). Possible causes of the Magpie expansion have been discussed by O'Connor & Shrubb (1986) who considered that improved sheep stocking on hill farms may have led to greater availability of sheep carrion which in turn promoted breeding success; the surplus young of this highly territorial species had then to migrate to new areas and habitats. On this interpretation it would be possible to regard the slightly higher egg and chick mortalities apparent in the mid-1950s as being due to an effect of organochlorine sheep dips, heavily used in these areas at that time, though subsequently withdrawn from use.

In summary, therefore, trends in Magpie breeding success appear to be associated directly with changing patterns of habitat use brought about by a farming-induced population expansion, with agrochemical affects confined to a short period in the 1950s.

10. Rook

Rooks consume much grain at certain times of the year, particularly during the harvest, and in some areas are additionally a problem during the spring sowings. As a result, significant mortality was recorded during the organochlorine era and in some areas regional declines were attributed to the use of dressed seed

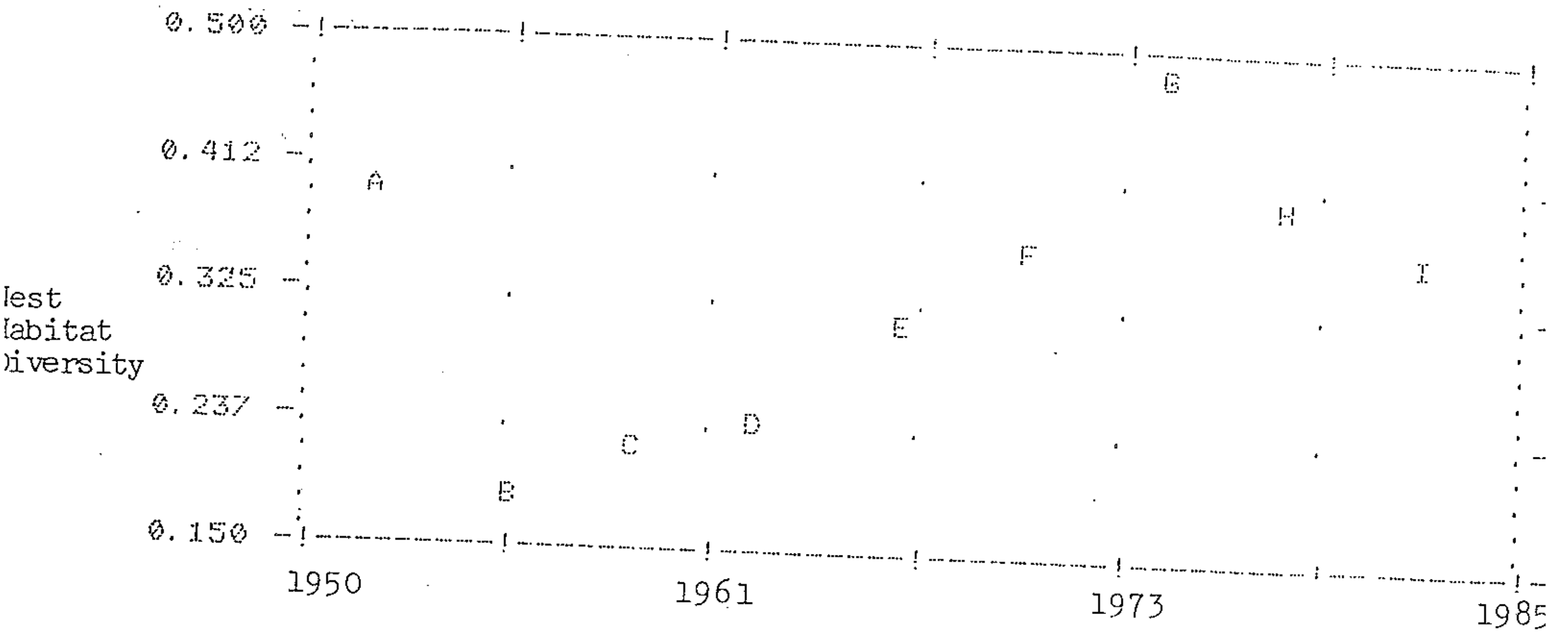

Figure 10.1 Temporal trends in nest habitat diversity for Rook, 1950-85. Data are grouped by four-year periods.

(e.g. Lomas 1968). However, the bird takes a very mixed diet, being dependent on pasture feeding at certain times of year and in fact is most numerous in areas where pastoral and arable farming are closely in balance (Brenchley 1984).

The sample of nest record cards for this species differed from those for the other species in that a significant fraction of the cards were obtained from colony record sheets, a form used by the BTO to allow easy recording of many nests sharing location and date of observation data in common. This feature of the data, however, generated greater heterogeneity of sampling over space and time than is the case with individually recorded cards. For this reason, therefore, their cards were pooled by four year periods and analysed as grouped data, without being subject to filtering.

Figure 10.1 shows the pattern of nest habitat diversity over time. This suggests that diversity of nesting habitat increased systematically from about 1955 through to about 1975, decreasing slightly since. Examination of the sample in detail showed that records from arable habitats were extremely scarce in the 1950s and 1960s but became more prominent in the following fifteen years. This pattern of use of arable land is similar to that documented for the Stock Dove by O'Connor & Mead (1982), and goes a long way to explaining the pattern of diversity with time shown.

Despite this trend there is little evidence of significant links between breeding parameters and time, plots of all three variables showing essentially random scatter (data not presented). Calculations of the correlation coefficients with time gave values of r = -0.446 for clutch size, r = 0.233 for egg mortality and r = -0.333 for chick mortality, in all cases not statistically significant.

In summary, therefore, the data suggest that the relative distribution of Rooks among the available agricultural habitats may have altered over time, with arable habitats coming into favour in recent years. The considerable scatter in the data, probably partly the result of heterogeneity associated with the use of colony-based records, preclude direct linking of these changes to an associated change in nesting mortality.

11. Starling

This species is a ground-feeding invertebrate feeder which is capable of taking a wide variety of foods, including grains, where available.

The egg data (Figure 11.1) suggest that after an initial fall mortality rose fairly steeply between about 1956 and 1966, an increase which coincides well with the increased use of persistent organochlorines. Since then egg success has improved slowly, except for some high values in very recent years. Chick mortality data (Figure 11.2) formed a very similar pattern initially but chick success then improved quite markedly until about 1974 or 1975 since which time it fell sharply to 1982 or 1983; the last couple of years have been years of low mortality. This timing suggests a similar organochlorine-affected pattern in the early part of the study period, with the improvement consequent on the 1966 ban being interrupted by changes to agricultural practice in the mid-1970s. Starling numbers have fallen sharply in several regions of the

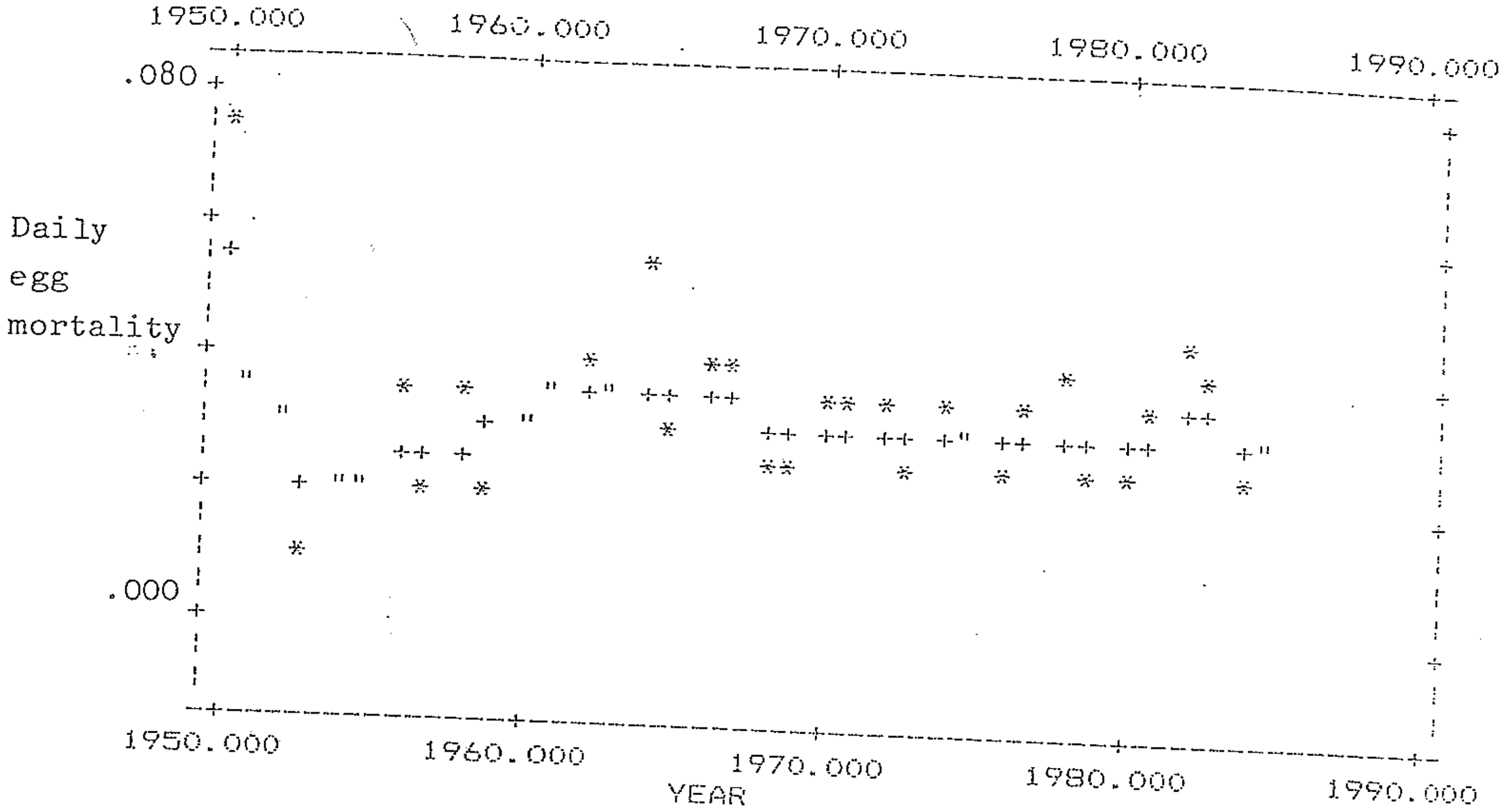

Figure 11.1 Temporal trends in egg mortality in the Starling, 1950-85. Symbols as Figure 1.1

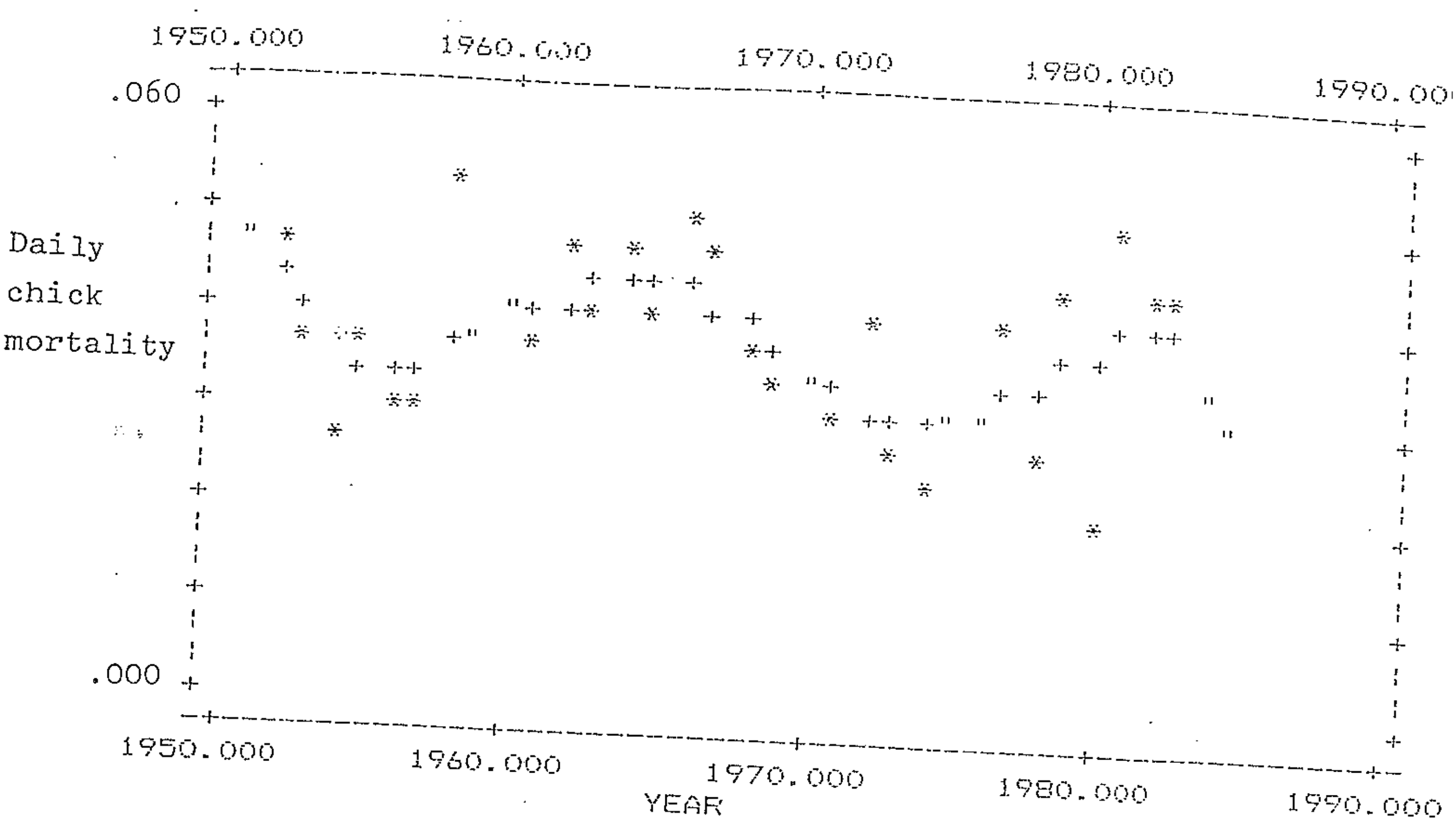

Figure 11.2 Temporal trends in chick mortality in the Starling, 1950-85.

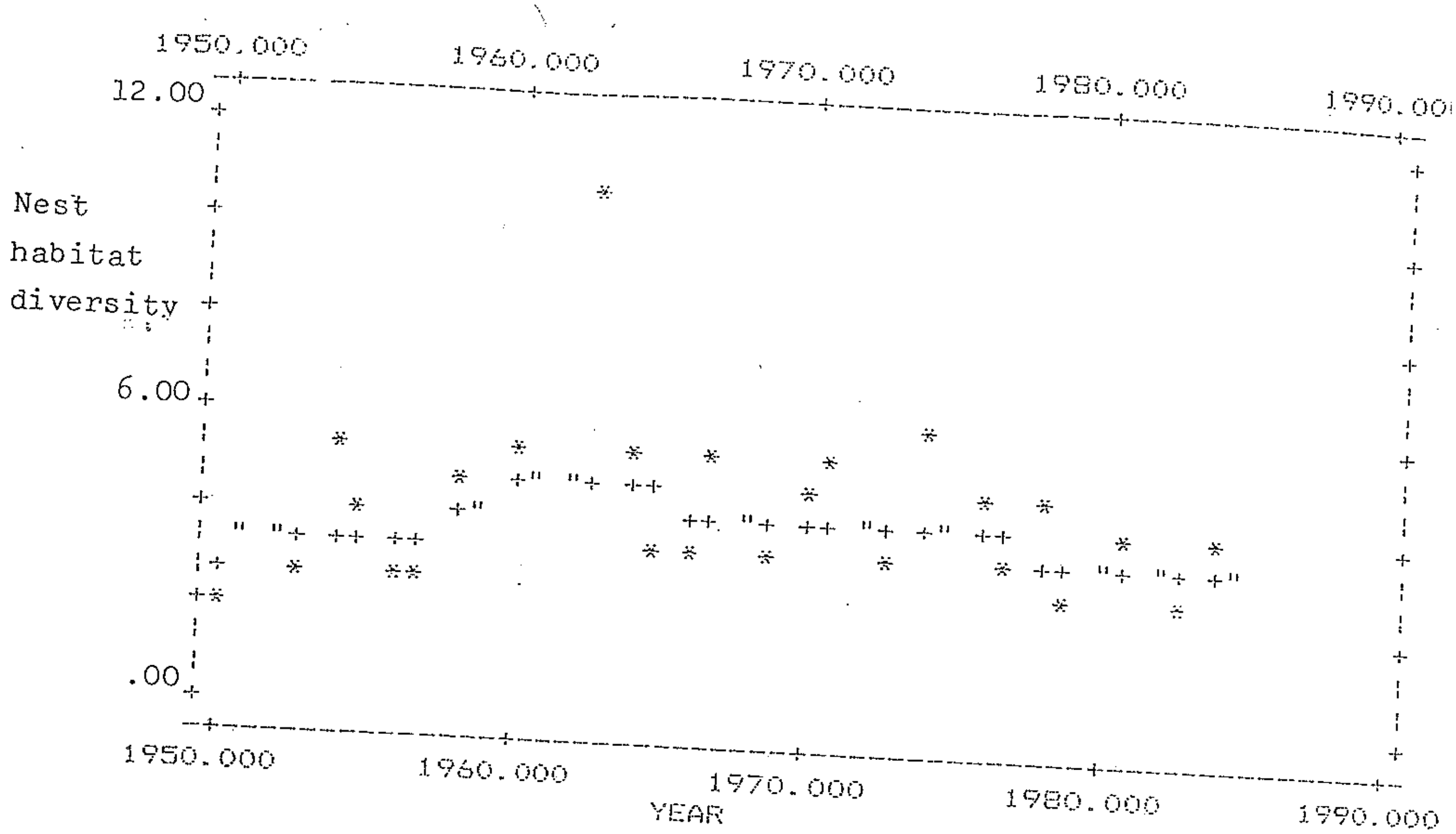

Figure 11.3 Temporal trends in nest habitat diversity for the Starling, 1950-85.

country from about this time (O'Connor & Shrubb 1986a), a trend which these authors attributed to the loss of spring tillage with the greater use of winter-sown cereals. An alternative explanation might be a reduction in earthworm populations brought about as a side effect of certain modern chemicals (C. Whittles pers. comm).

Clutch size data suggest a small increase through the early 1950s was checked by 1960 when a shallow decline began but later gave way to continued increase. A decrease which set in in the mid-1970s appears to have reversed by 1983 and might be due to shortage of spring foods, as suggested above.

Habitat diversity data (Figure 11.3) indicate a general increase in diversity of habitats used between 1950 and 1963, with a subsequent slow decline until about 1980. The rate of decrease seems to have intensified about 1975 or 1976, in step with the population decrease already noted, and may represent a contraction of a reduced population into preferred habitats. Unusually, however, these habitats seem to be the ones that were deteriorating most rapidly, as judged by breeding success (Figure 11.2). Starling populations do seem to show this type of lag effect, whereby birds persist in areas that are not the best currently available (O'Connor & Fuller 1985).

12. Chaffinch

Neither egg mortality (Figure 12.1) or chick mortality (Figure 12.2) showed evidence of systematic trends in breeding success with time. There is a suggestion of slight reduction in both egg and chick success in the late fifties but there is an even more marked reduction in both in the mid- to late-seventies, so this is unlikely to be a major effect of organochlorine use. No major changes in habitat use took place over the period ($r = 0.020$) and clutch size similarly remained constant with the time.

This general absence of trend is consistent with a species that breeds late and takes only a proportion of agricultural grains in the diet. It is more omnivorous than many of the other seed-eating species considered here and takes rather a small proportion of grain in its breeding season diet (Newton 1972).

13. Greenfinch

This is a species that makes use of agricultural grains quite extensively and recent analyses (O'Connor & Shrubb 1986a) indicate that its fortunes have been closely linked to changes in agricultural activity.

Figure 13.1 shows that egg mortality in this species had tended to decrease from 1950 until the late 1960s, rising again between about 1976 and 1983. Chick mortality (Figure 13.2) has also undergone major changes, dropping sharply through the 1950s, then rising slightly to a plateau through the 1960s and improving again to the mid-seventies; since then chick mortality has tended to increase, though the data have much scatter. The long term trend towards improved chick success is therefore not significant ($r = 0.238$, n.s.). The chick mortality figures may be associated with changes in habitat use, for habitat diversity fell during the late sixties and early seventies, though rising again in the late 1970s. The net

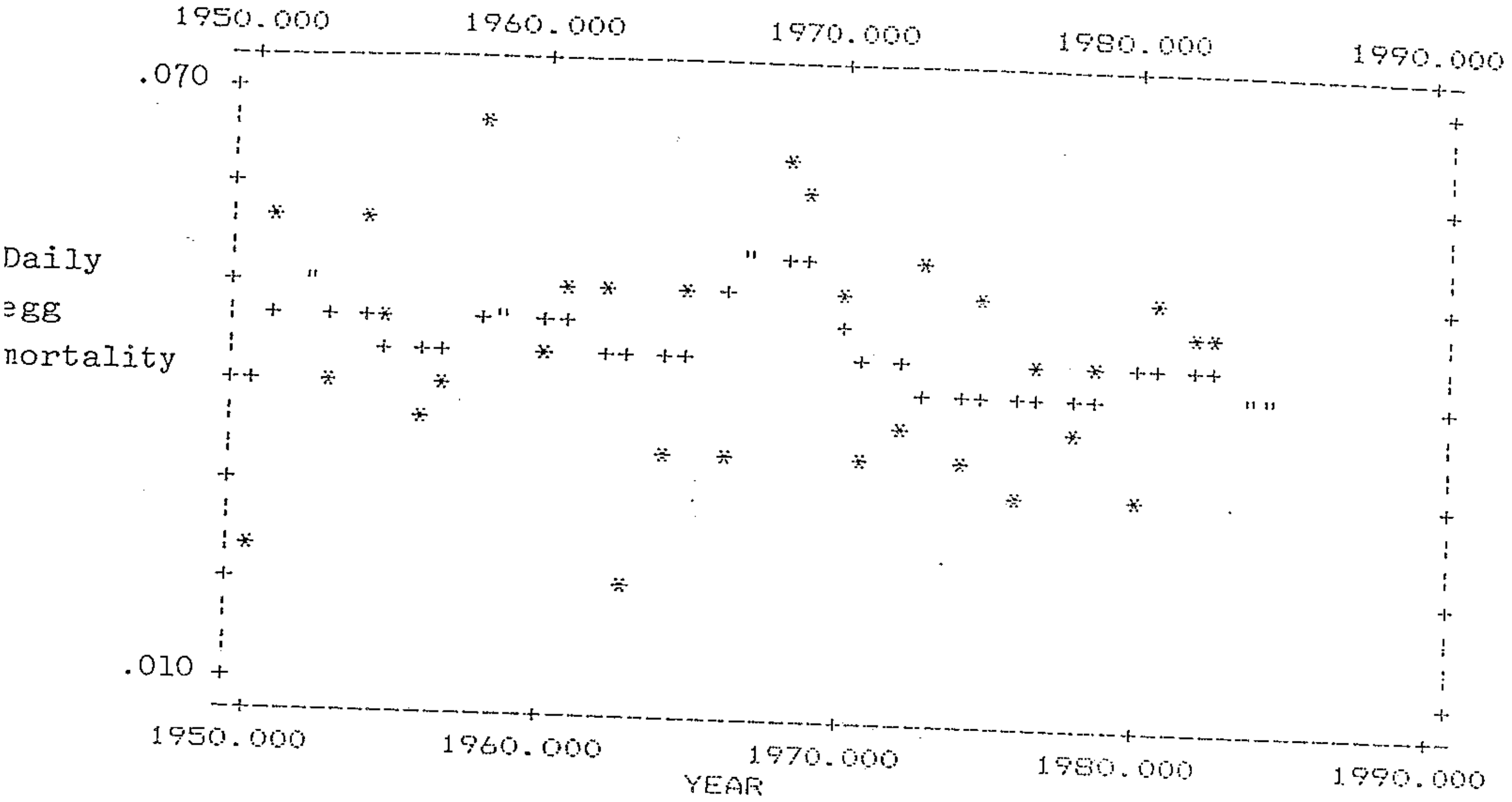

Figure 12.1 Temporal trends in egg mortality in the Chaffinch, 1950-85. Symbols as Figure 1.1

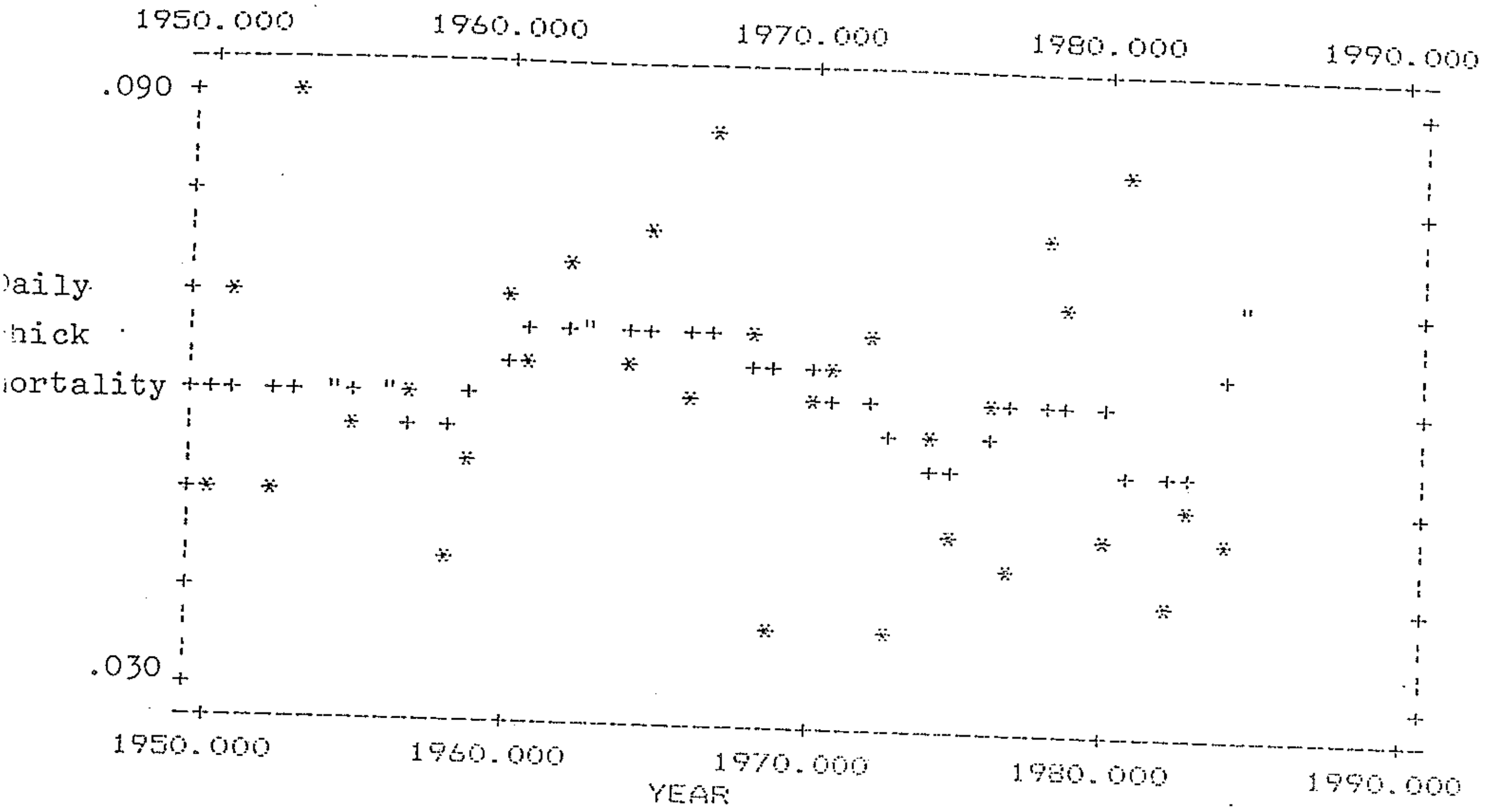

Figure 12.2 Temporal trends in chick mortality in the Chaffinch, 1950-85.

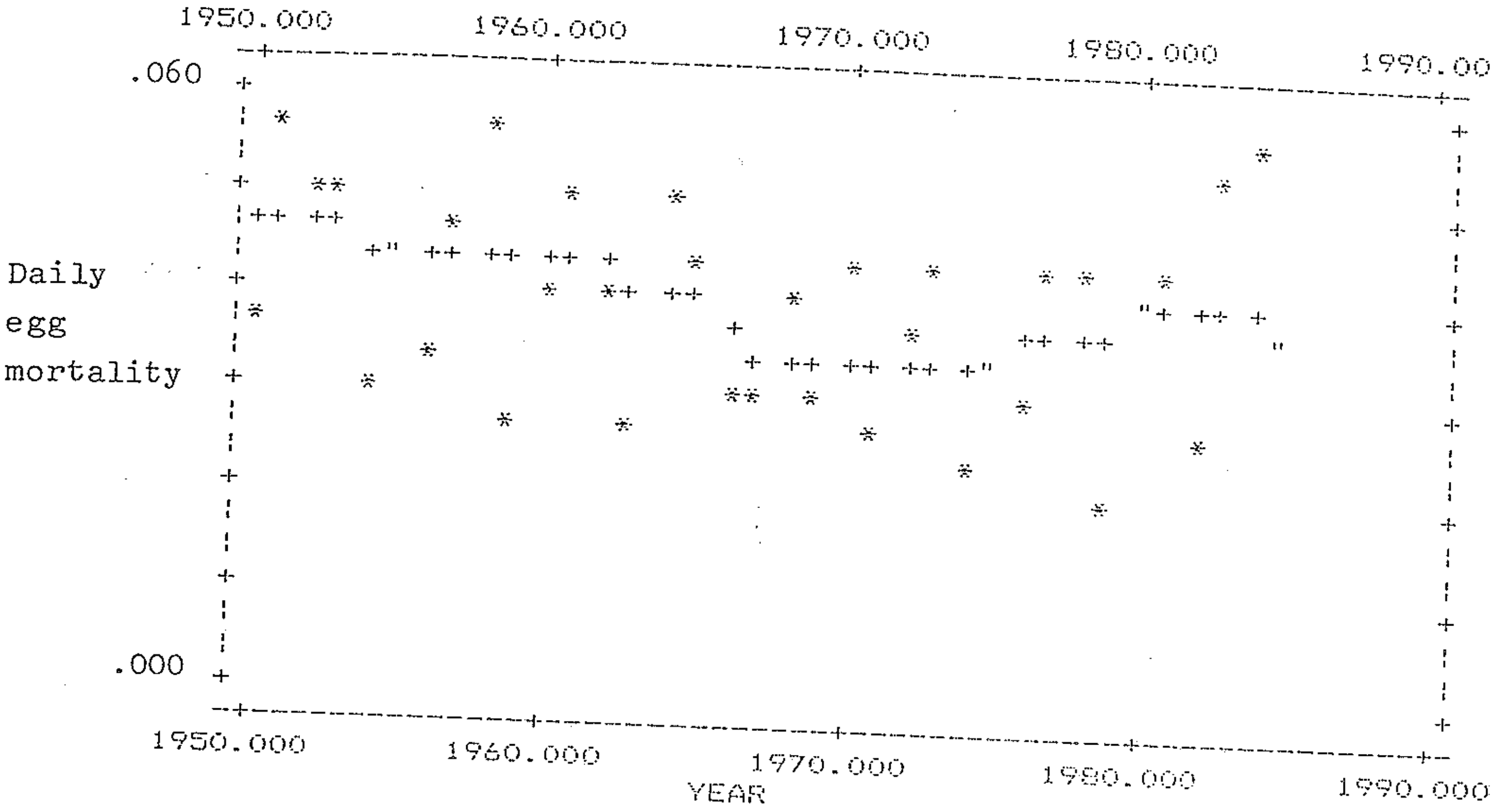

Figure 13.1 Temporal trends in egg mortality in the Greenfinch, 1950-85. Symbols as Figure 1.1

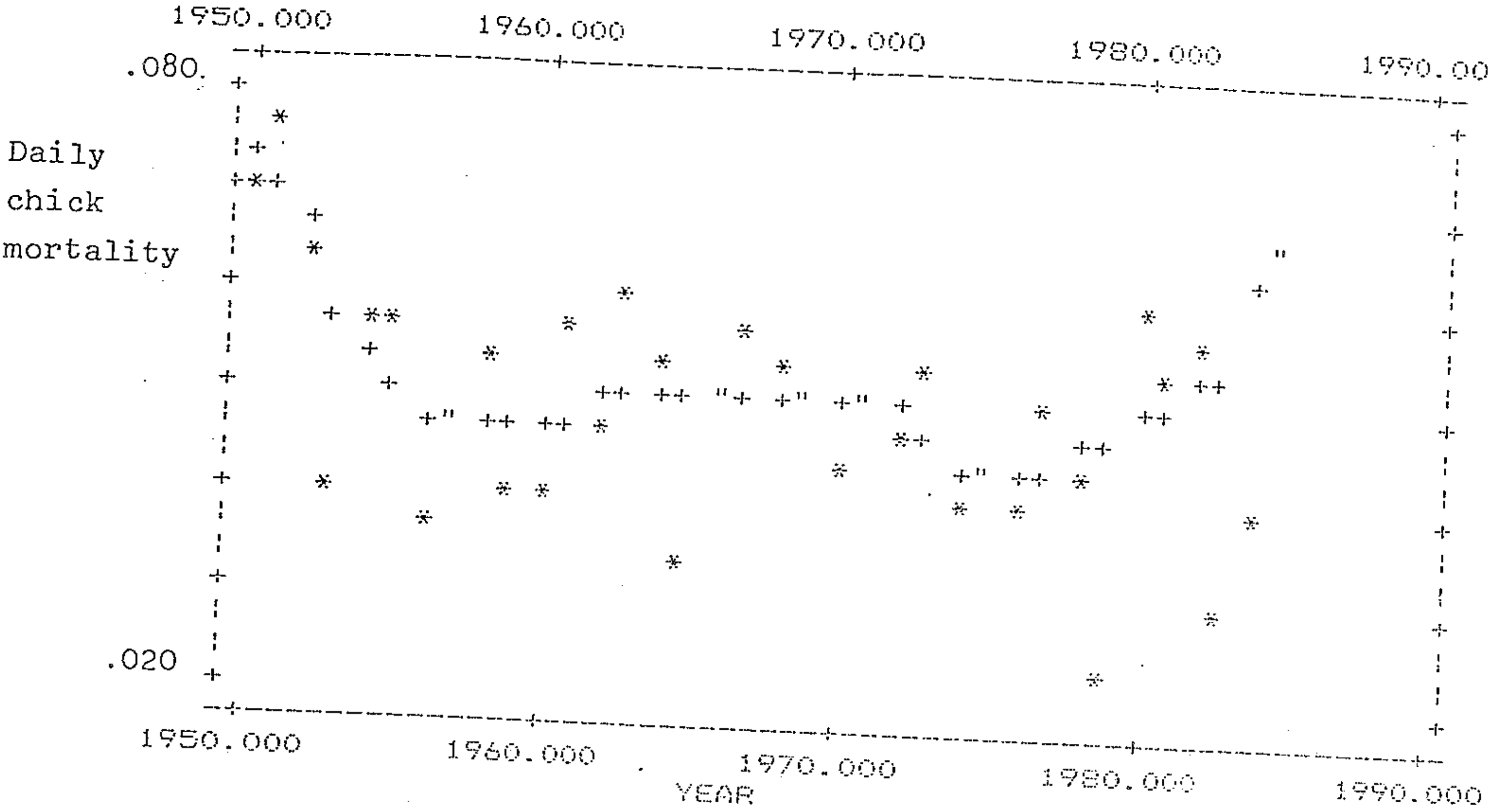

Figure 13.2 Temporal trends in chick mortality in the Greenfinch, 1950-85.

change in diversity over the period has been negative (r = -0.365, P<0.05). The annual figures for nest diversity and chick mortality are, however, poorly correlated statistically (r = -0.117, n.s.). The fact that clutch size also rose slightly in the late sixties and early seventies similarly suggests a link to habitat use, with declining populations concentrating into better habitats.

Glue (1982) documents an increasing tendency for Greenfinches to resort to artificial foods earlier each winter, a fact that O'Connor & Shrubb (1986a) relate to reduced seed supplies with the disappearance of autumn stubbles. Latterly, however, the advent of oilseed rape seems to be providing an alternative food supply, possibly sustaining a spread of the bird into a greater diversity of habitats of poorer quality (O'Connor & Shrubb 1986b).

14. Goldfinch

The Goldfinch is a species concentrating particularly on the seeds of weeds on waste ground rather than in agricultural crops and O'Connor & Shrubb (1986a) have attributed its relatively stable population levels to this independence of changes in agriculture. In this it differs substantially from its congeners on agricultural land. The data for egg mortality (Figure 14.1) and chick mortality (Figure 14.2) indicate a sharp increase in breeding sucess through the 1950s, since when egg mortality has been relatively stable. The net trend over the study period has been of improved success (r = 0.428, P<0.05). Chick mortality has increased noticeably since the mid-sixties with a steeper increase since the late 1970s. These changes must be viewed against significant changes in habitat use (Figure 14.3), with habitat diversity increasing sharply between 1950 and 1965, then falling slowly. Clutch size has tended to increase slightly through the late 1950s and to fall through the 1960s and early 1970s, rising again latterly, but this variation is only of the order of 10% or so. The general pattern for Goldfinches, therefore, has been one of improvement in the early part of the study period and stability in mid-period, with some suggestion of worsening success latterly. These changes are probably strongly habitat-linked.

15. Linnet

The Linnet is a species that depends heavily on the seeds of arable weeds and its numbers on arable land (but not elsewhere) have fallen sharply following the recent development of systemic herbicides targetted on these weed species (O'Connor and Shrubb 1986a). Given this dependence on weed seeds rather than on grain, egg success has been little affected by chemical use on farmland (Figure 15.1), though there is some suggestion of increased egg mortality in the 1980s. The species does feed its young on seeds from an early age (Newton 1972), however, which may account for a rise in chick mortality through the early 1950s (Figure 15.2); this fell away through the 1960s, however, and a subsequent increase in mortality was to a generally lower level than prevailed then. Its use of nesting habitats diversified between 1950 and 1970, fluctuating slightly since and is statistically significant over the period as a whole (Figure 15.3); (r = 0.700, P<0.01). It is possible that this diversification reflects changing land use even before the advent of systemic herbicides, for chick success was significantly correlated with habitat diversity across years (r = 0.346, P<0.05).

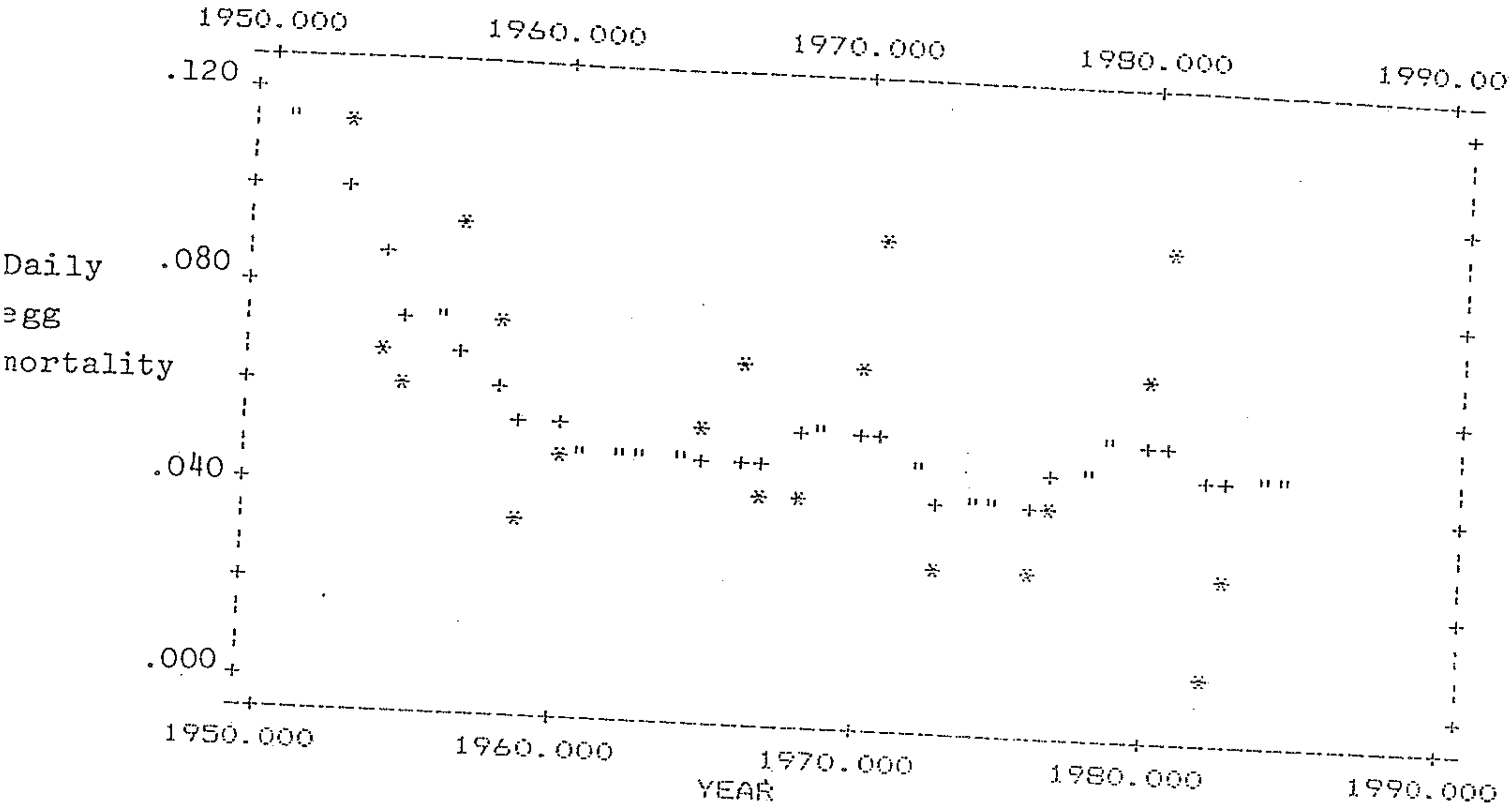

Figure 14.1 Temporal trends in egg mortality in the Goldfinch, 1950-85. Symbols as Figure 1.1

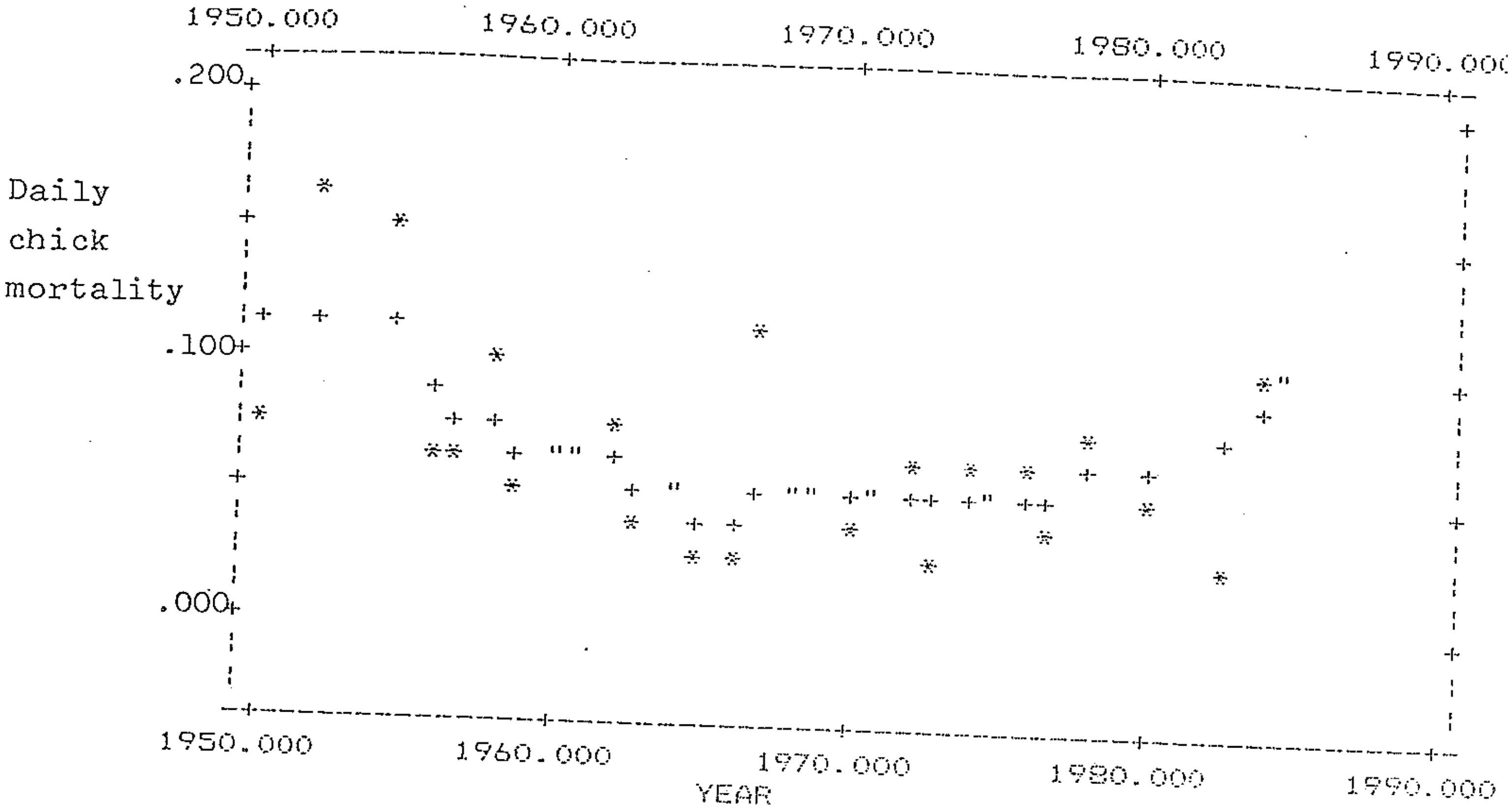

Figure 14.2 Temporal trends in chick mortality in the Goldfinch, 1950-85.

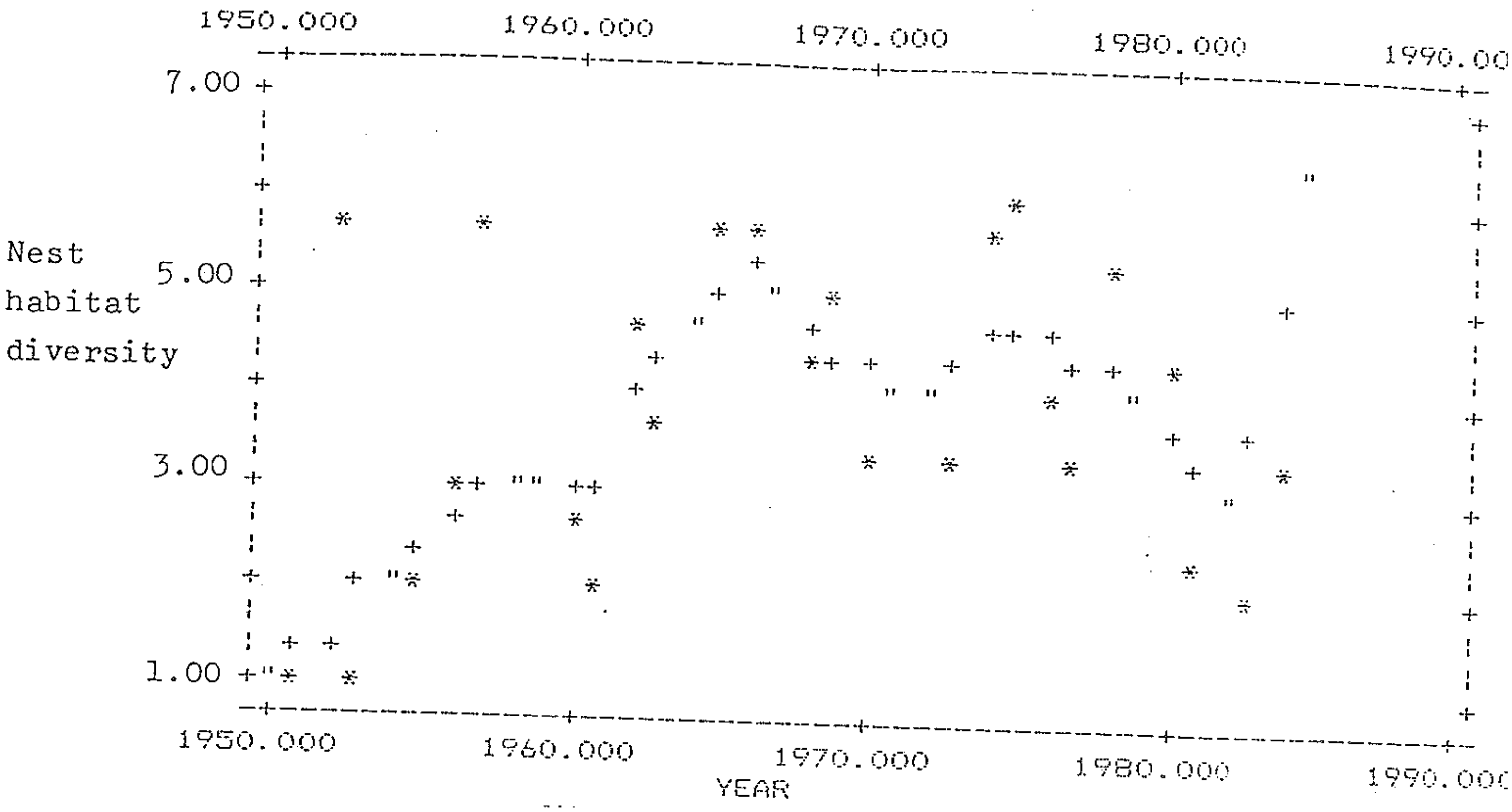

Figure 14.3 Trends in nest habitat diversity for Goldfinches, 1950-85.

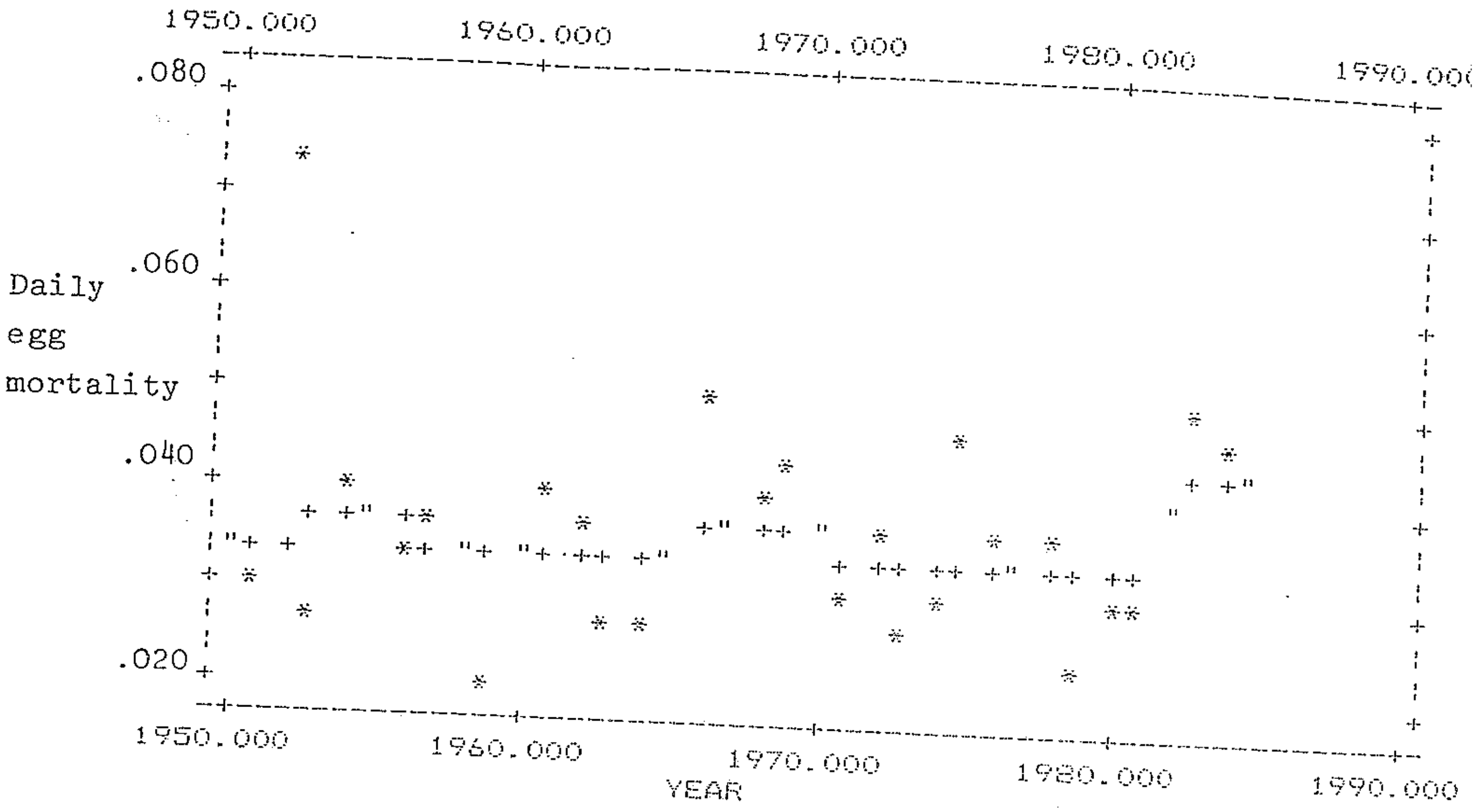

Figure 15.1 Temportal trends in egg mortality in the Linnet, 1950-85.

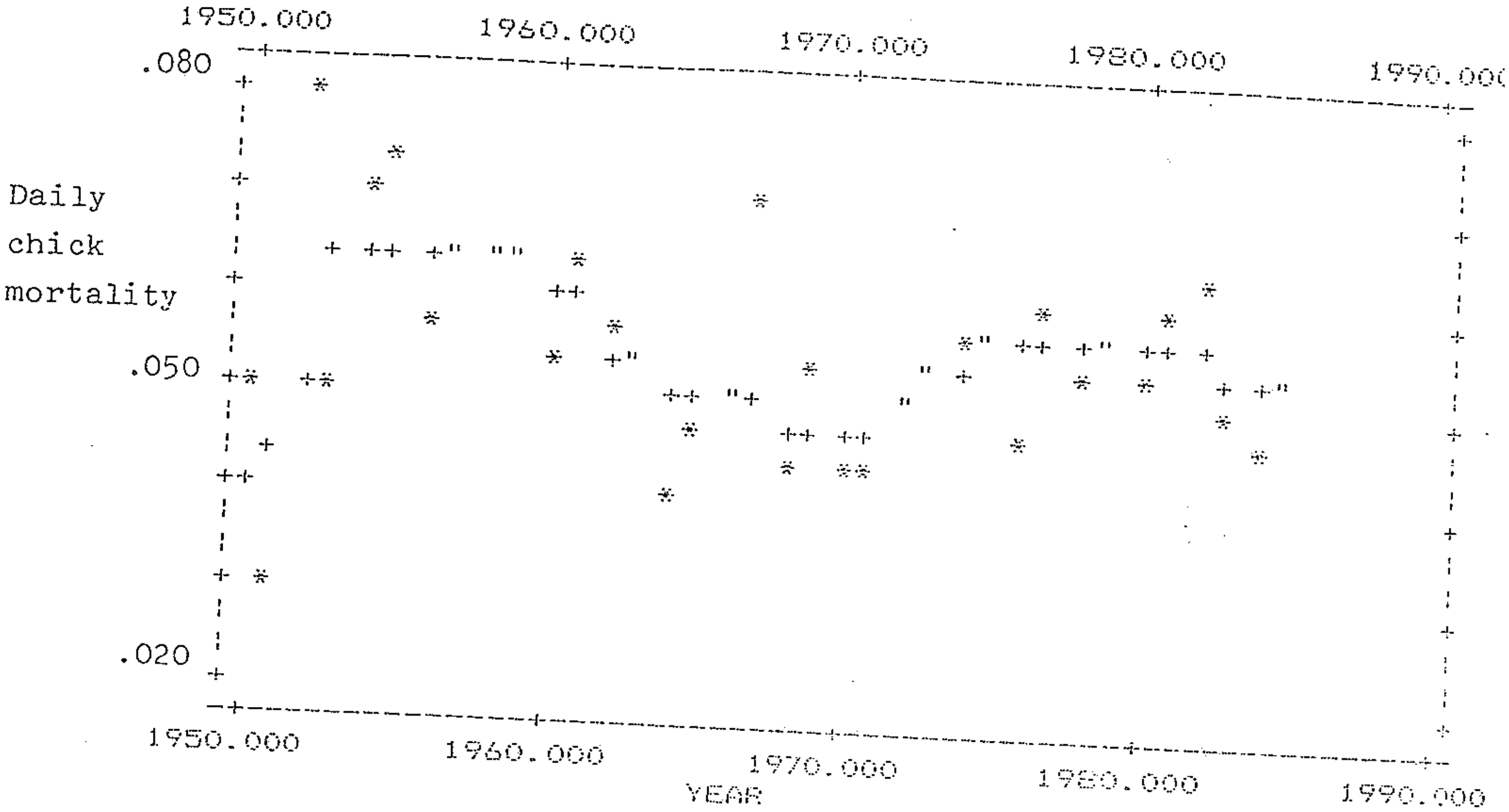

Figure 15.2 Temporal trends in chick mortality in the Linnet, 1950-85.

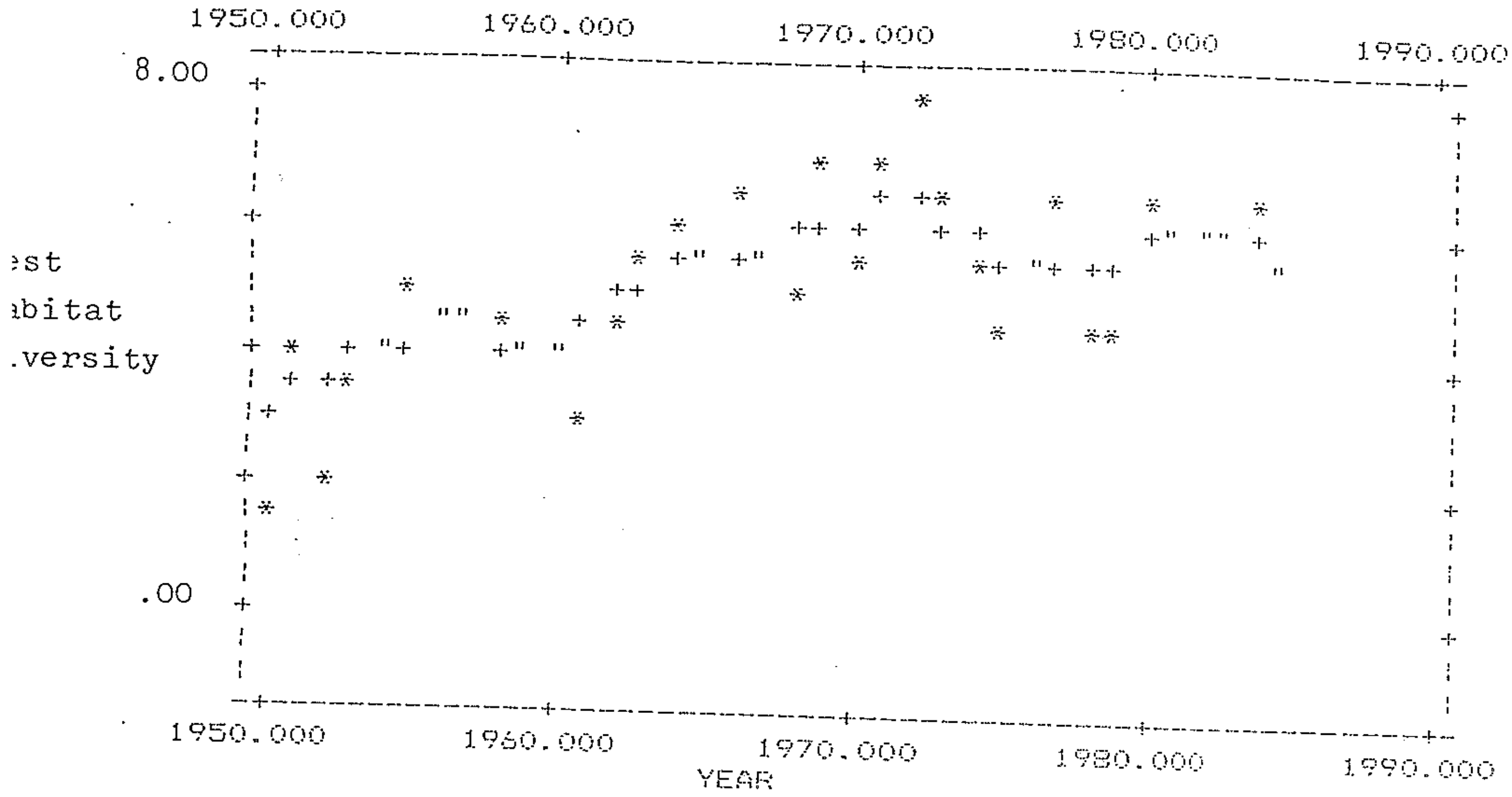

Figure 15.3 Temporal trends in nest habitat diversity for the Linner, 1950-85.

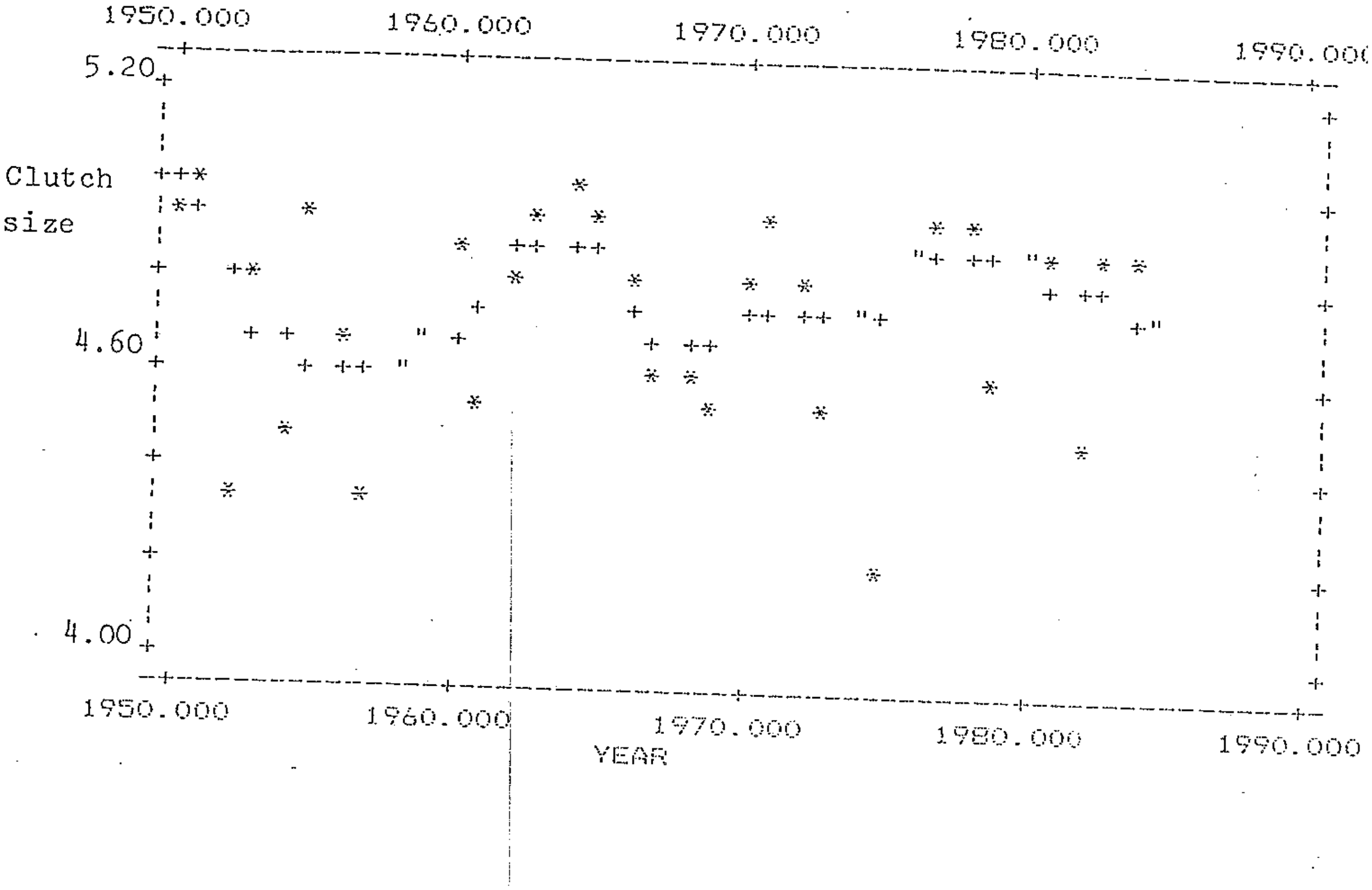

Figure 15.4 Temporal trends in clutch size in the Linnet, 1950-85.

That is, more chicks were reared in years (mostly recent) when a wider range of habitats were in use than when the population was more concentrated into a few agricultural habitats. Detailed examination shows that whilst typically 30-40 per cent of records were from grass fields in the 1950s, the proportion on arable rose sharply in the 1960s before decreasing gradually through the 1970s. This would be consistent with the conversion of pasture to arable, followed by the latter's deterioration as a breeding habitat as modern herbicides removed the bird's favoured weed species.

Figure 15.4 shows the pattern for clutch size, indicating a somewhat cyclic pattern of variation over time. Neither clutch size nor egg mortality are closely correlated with nest habitat diversity ($r = 0.174$ and 0.120 respectively) but chick mortality is weakly negatively correlated with species diversity ($r = -0.346$) and more strongly negatively correlated with clutch size ($r = -0.542$). Thus there is little evidence that egg mortality is affected by organochlorine use but chick losses were highest in large broods and when the population was breeding in the greatest range of habitats, relationships possibly driven by shifts in agricultural practice.

16. Bullfinch

Although this species is granivorous, much of its diet comes from woodland and trees and rather little from dressed grain (Newton 1967). Figure 16.1 shows that its egg mortality has consequently been little affected by events on farmland, with the smooth estimate of mortality fluctuating only gently, but possibly cyclically, over the study period. High mortality prevailed in 1959, 1969-70, 1977, and 1985, with lows about 1965, 1974, and 1980. However, there is considerably greater variance between estimates for individual years and little evidence of systematic trend.

In contrast, the data for chick mortality (Figure 16.2) suggest sharp improvement in conditions for young during the early 50s with a slow gradual continuation of this almost to date ($r = 0.525$, $P<0.01$) Examination of habitat diversity data (Figure 16.3) showed a steady increase in the variety of nesting habitats (on agricultural land) used by the Bullfinch over the period 1950 to about 1977, since when some reduction in diversity is apparent. The trend towards greater habitat diversity over the period as a whole is statistically significant ($r = 0.318$, $P<0.05$) and is somewhat correlated with an improvement in clutch success ($r = 0.303$, $P<0.10$). However, these changes in nest habitat diversity are poorly correlated with egg mortality ($r = -0.086$, n.s.).

Figure 16.4 shows that clutch size also fluctuated but in a manner out of phase with egg mortality, reaching lows about 1960 and again about 1975. These changes were uncorrelated with those in habitat ($r = -0.184$) and were also uncorrelated with egg mortality ($r = -0.046$) and with chick mortality ($r = -0.033$). Newton (1964) has shown that this species is particularly prone to fluctuation as a result of the natural cyclicity of seed production by masting tree species, a phenomenon which probably underlies the pattern seen here.

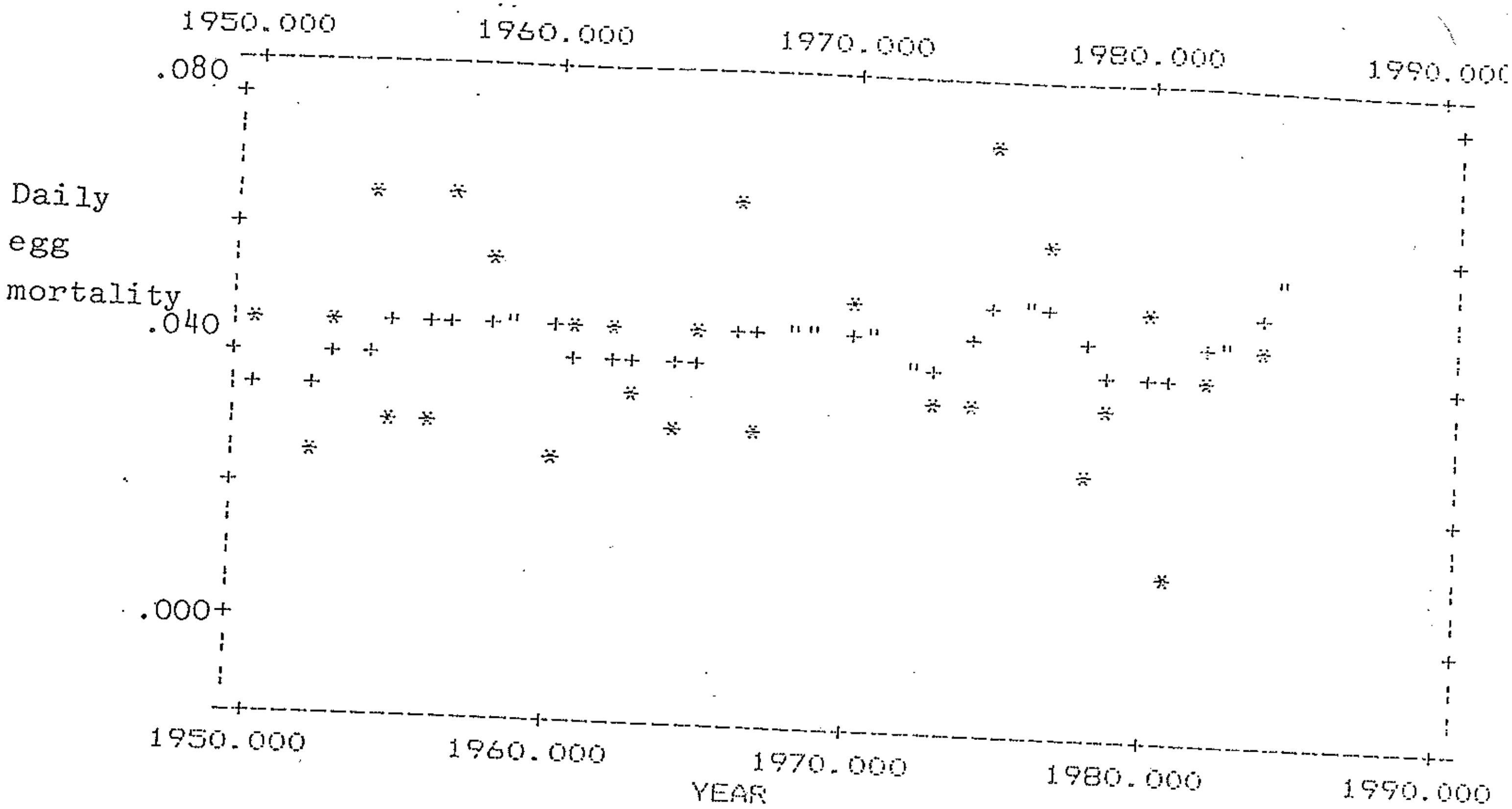

Figure 16.1 Temporal trends in egg mortality in the Bullfinch, 1950-85. Symbols as Figure 1.1

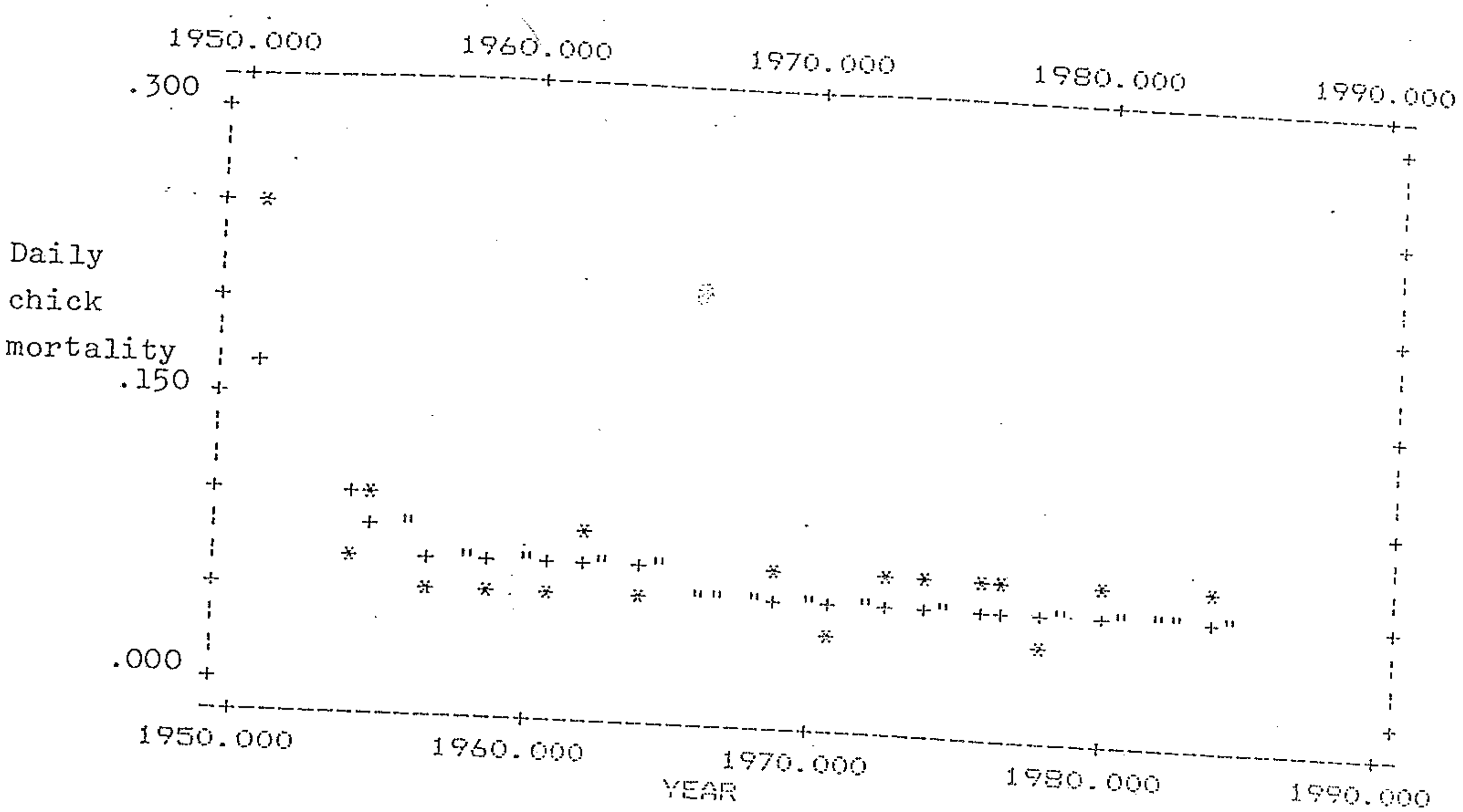

Figure 16.2 Temporal trends in chick mortality in the Bullfinch, 1950-85.

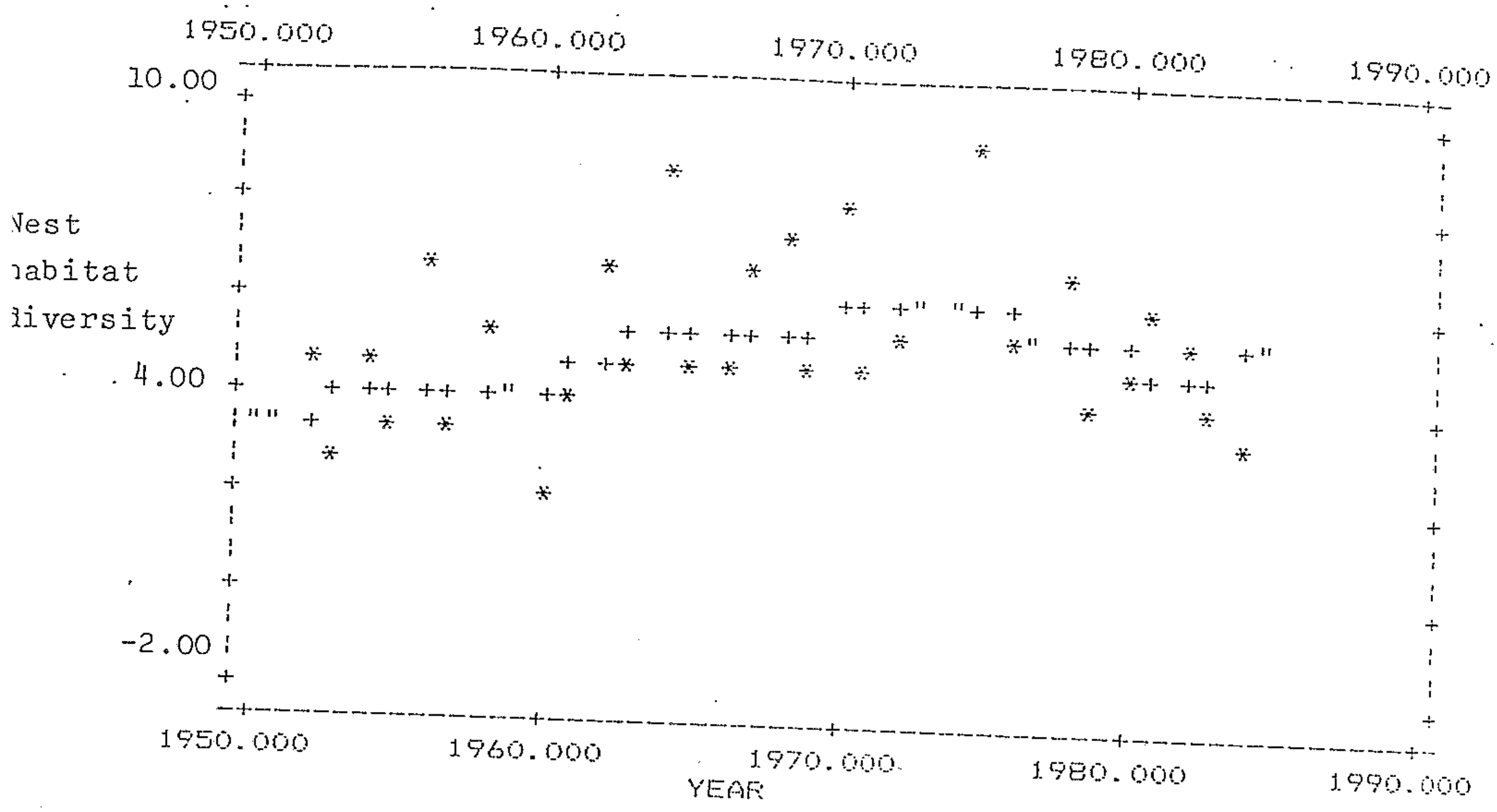

Figure 16.3 Temporal trends in nest habitat diversity for the Bullfinch, 1950-85.

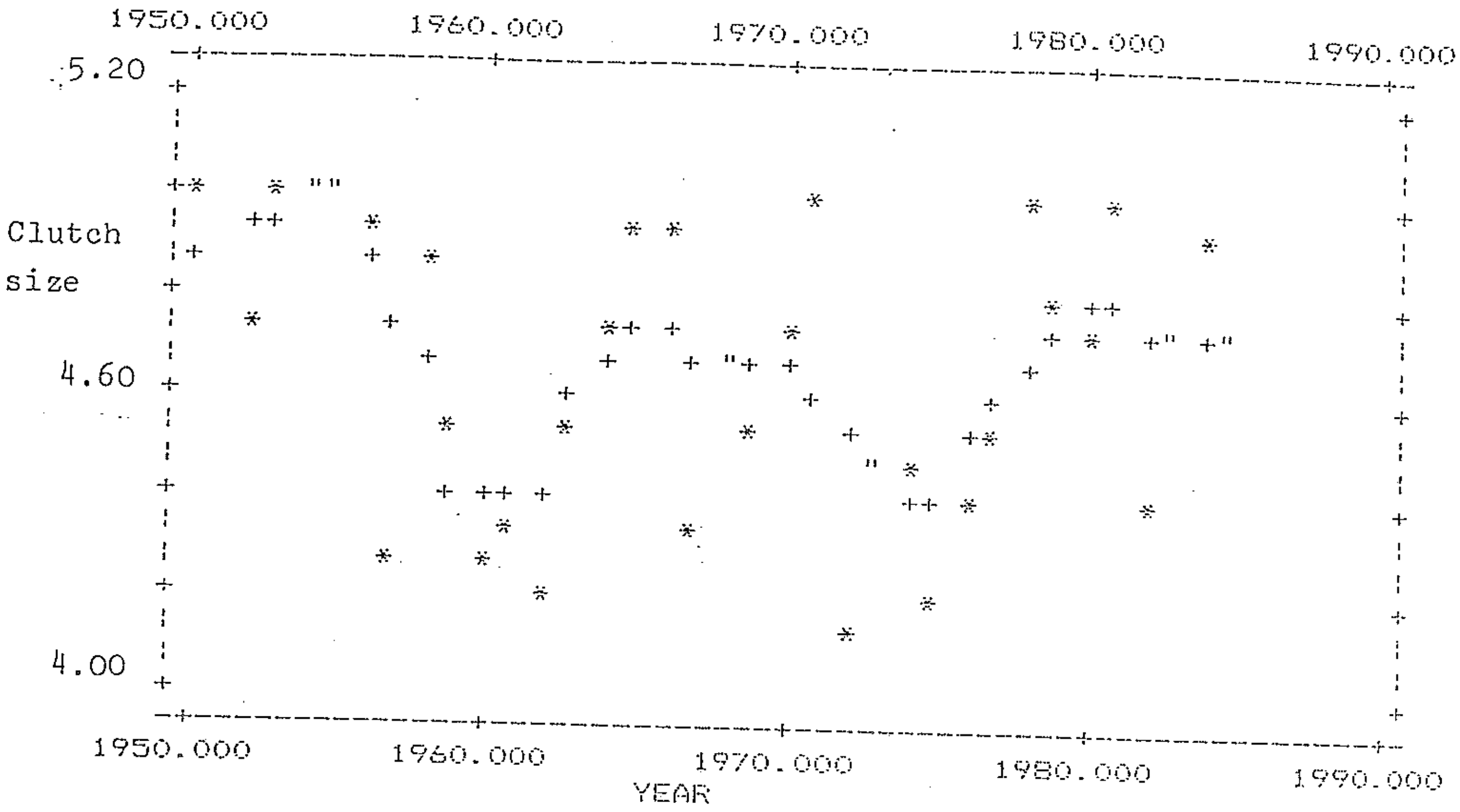

Figure 16.4 Temporal trends in clutch size in the Bullfinch, 1950-85.

17. Yellowhammer

The Yellowhammer is a prominent granivorous species on farmland, though it will resort to scrub and woodland edge for nesting, particularly in times of high population densities.

The data on egg mortality suggest that this species was badly affected by the use of organochlorines in the 1960s (Figure 17.1). Egg mortality rose steeply through the 1950s and was high in the early part of the 1960s, dropping more or less in step with the introduction of the 1966 restrictions. Egg success steadily improved through the 1970s but now appears to have levelled out at values comparable to those prevailing in the very early 1950s. Chick mortality, on the other hand, has tended to decrease steadily over the period, though there is some suggestion of a slight worsening in mortality during the early sixties (Figure 17.2), possibly due to losses of adults to poisoning, with consequent death of the nestlings through starvation. Chick success has thus experienced a net but small imporvement over the study period ($r = -0.307$, $P=0.06$). Clutch size data (Figure 17.3) have tended to oscillate slightly, with low values in the the late 1950s and again in the early 1970s. This may be associated with corresponding changes in habitat diversity (Figure 17.4) though the overall correlation with clutch size is negligible ($r = -0.050$). O'Connor (1980a) has previously shown that the diversification of habitat use by this species has been associated with population increase during a recovery from the 1962-63 severe winter, with birds using habitats that are individually poorer with respect to mean clutch size at times of high population density. Here we found that egg mortality was positively correlated with nest habitat diversity ($r = -0.423$, $P<0.01$), as would be expected if population overflow was into areas also low in egg success. Habitat use may therefore be the dominant influence on Yellowhammer success over the period as a whole, with a temporary effect of persistent organochlorines in the 1960s. Habitat use and clutch size may be more closely related. The systematic improvement in conditions for the rearing of young Yellowhammers is more difficult to account for.

18. Reed Bunting

The Reed Bunting is predominently an insectivorous species, taking only a small amount of grain during the winter. This is reflected in the data on egg success (Figure 18.1)which show a small increase (based on small samples) during the early 1950s, since when

its egg mortality has been extremely stable, at around 4% per day. Chick mortality has likewise been rather stable, though perhaps with a very slight increase in success over time (Figure 18.2). This last is largely due to a reduction in the loss rate of entire nests ($r = -0.629$, $P<0.01$) rather than to changes in chick starvation. Clutch size, on the other hand, has decreased slowly over time, with a recent recovery (Figure 18.3).

These changes have to be viewed against a background of changing habitat use by the species (Figure 18.4). The diversity of nesting habitat in use increased more or less steadily between 1950 and 1960, with a sharp decrease apparent in the 1960s; the increase resumed in the late sixties to a peak in the mid-seventies, since when habitat diversity has decreased once more. The early increase in habitat use by Reed Buntings has already been extensively discussed e.g. by Kent

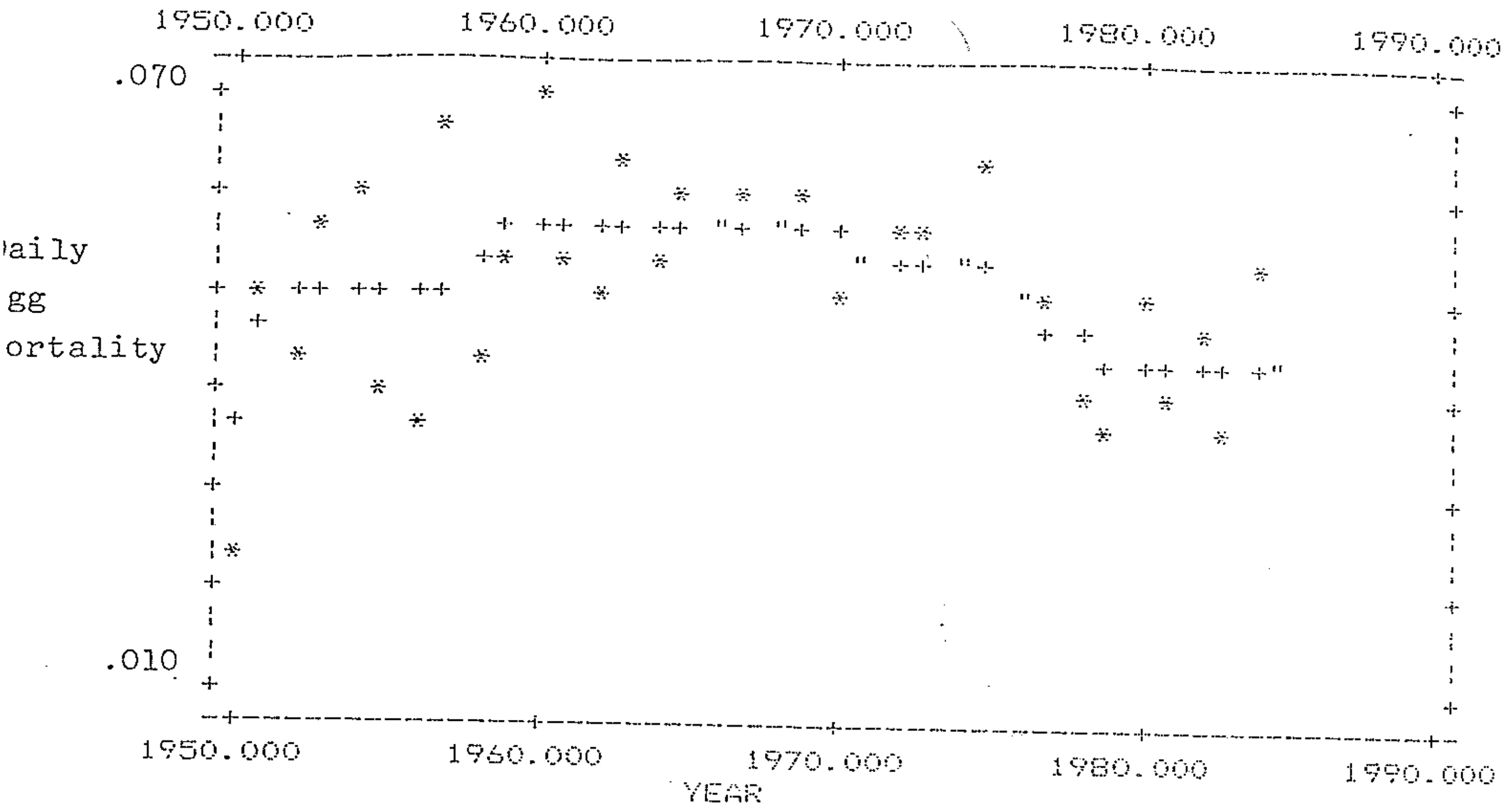

Figure 17.1 Temporal trends in egg mortality in the Yellowhammer, 1950-85. Symbols as Figure 1.1

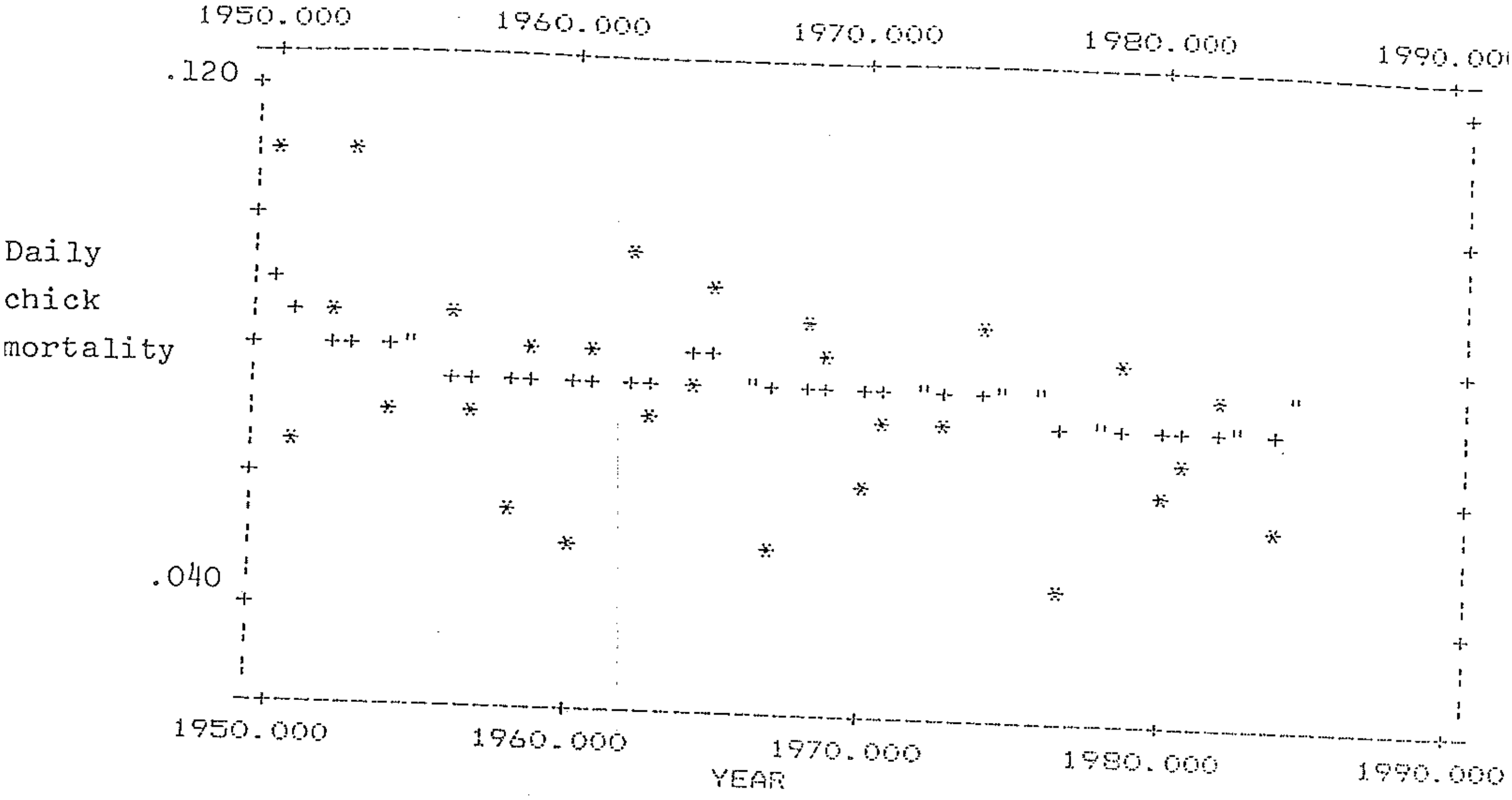

Figure 17.2 Temporal trends in chick mortality in the Yellowhammer, 1950-85.

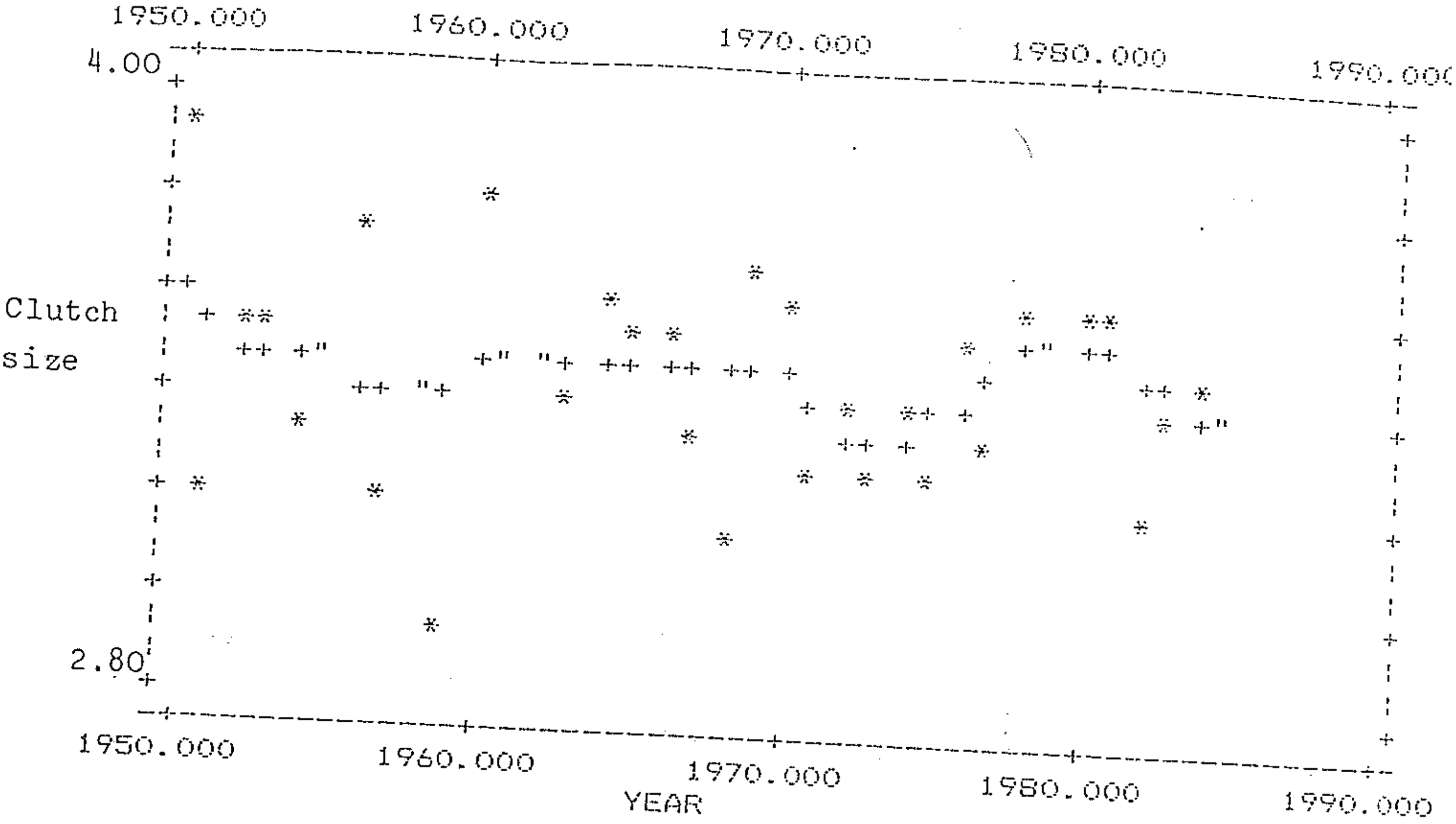

Figure 17.3 Temporal trends in clutch size in the Yellowhammer, 1950-85.

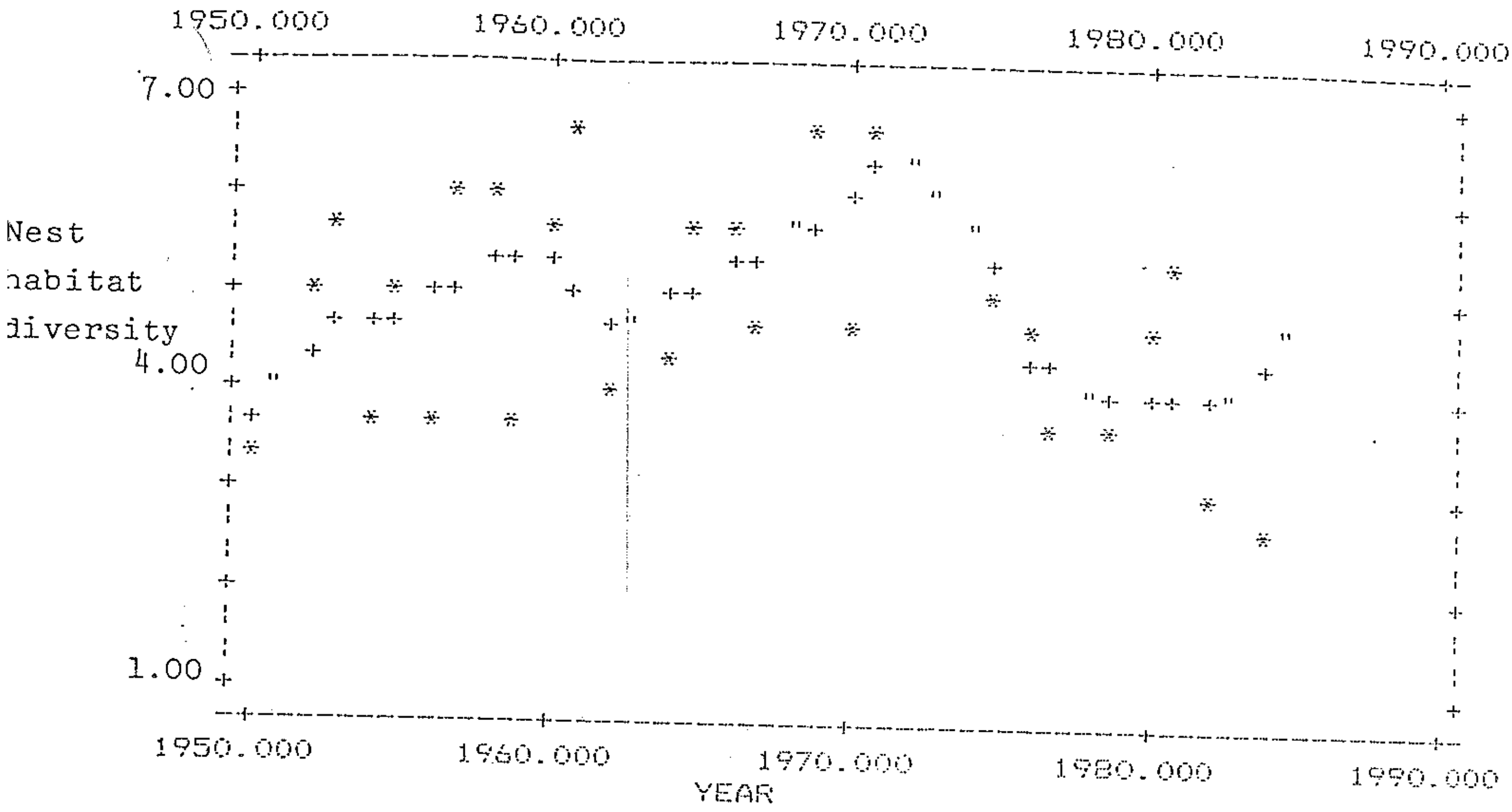

Figure 17.4 Temporal trends in nest habitat diversity for the Yellowhammer, 1950-85.

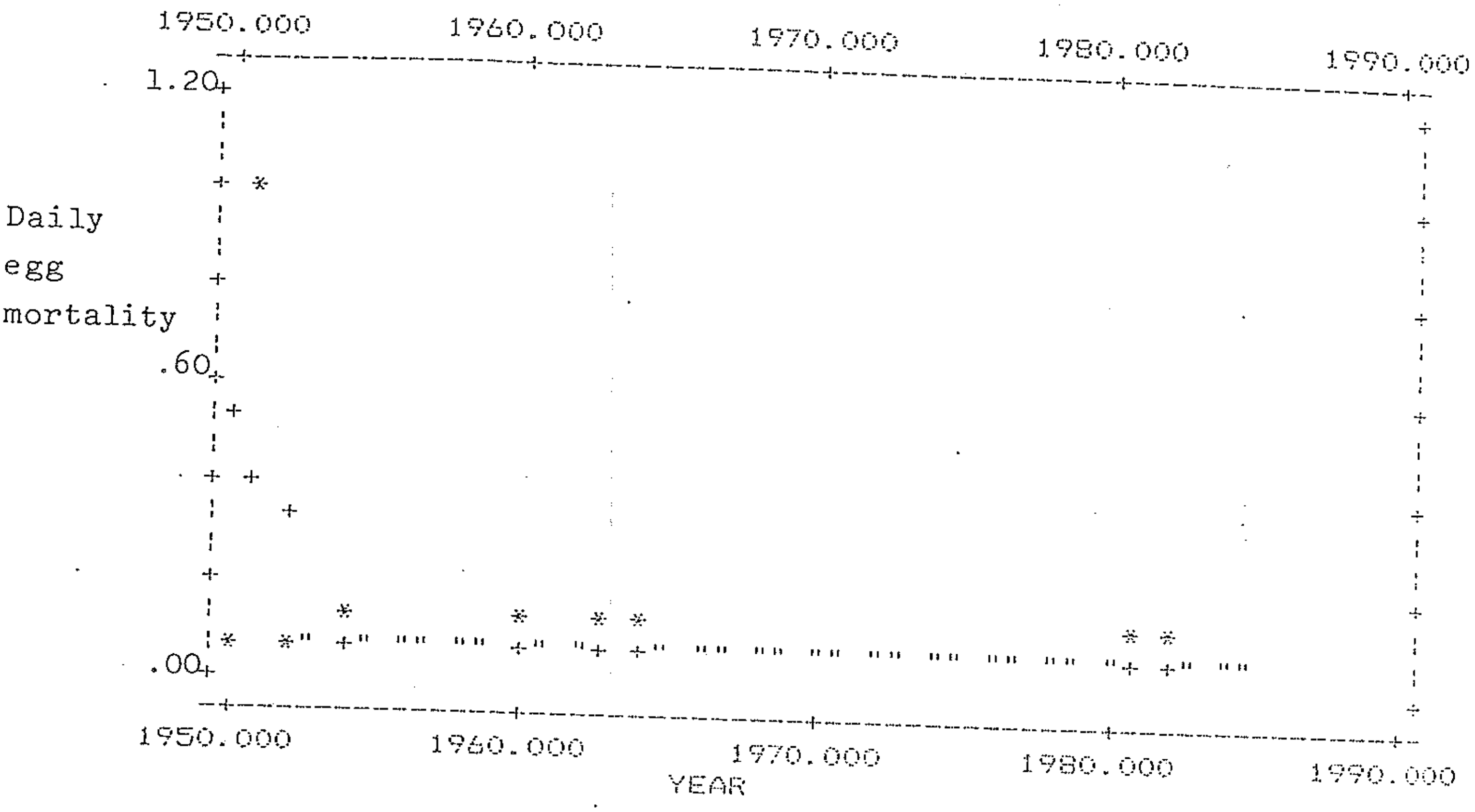

Figure 18.1 Temporal trends in egg mortality in the Reed Bunting, 1950-85. Symbols as Figure 1.1

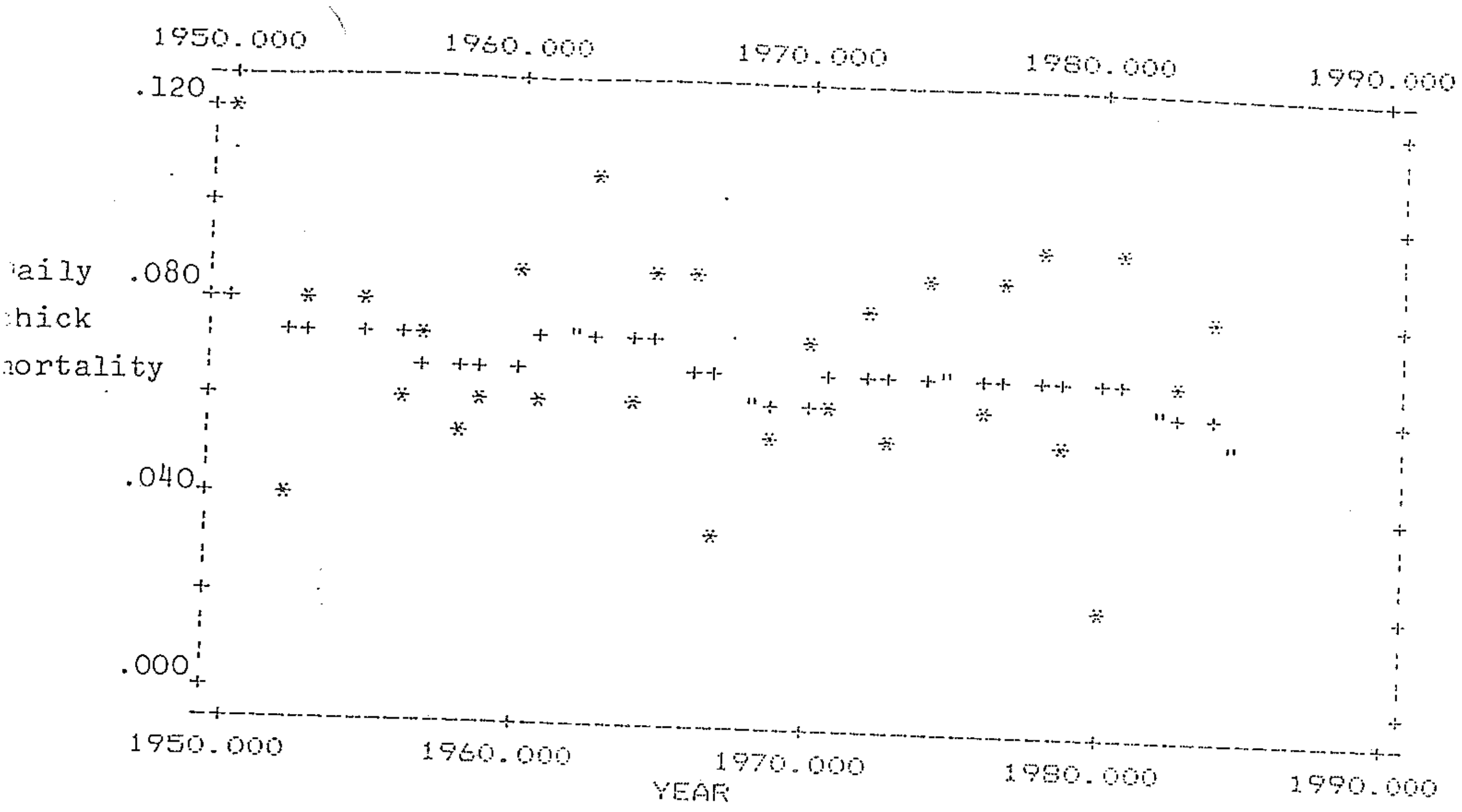

Figure 18.2 Temporal trends in chick mortality in the Reed Bunting, 1950-85.

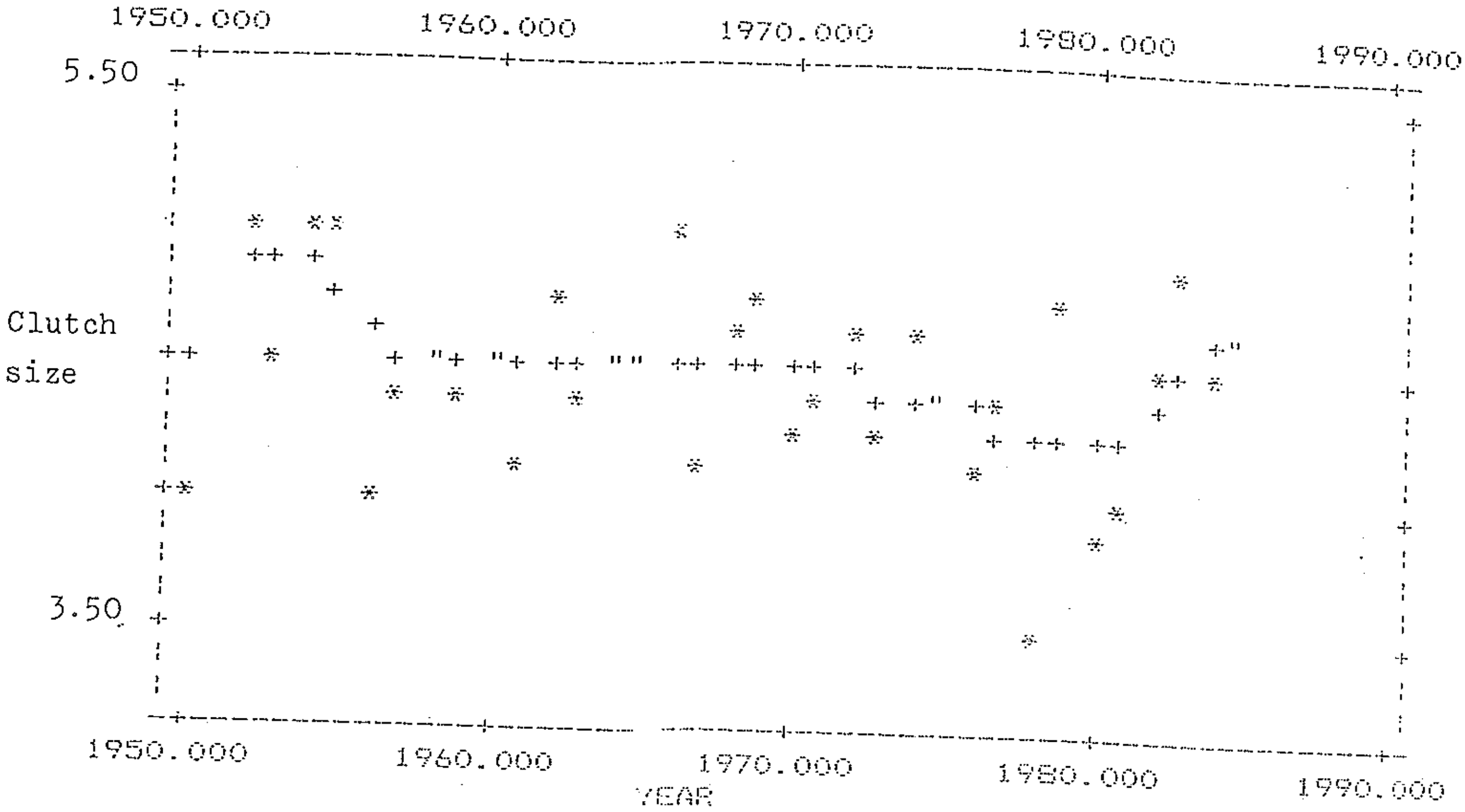

Figure 18.3 Temporal trends in clutch size in the Reed Bunting, 1950-85.

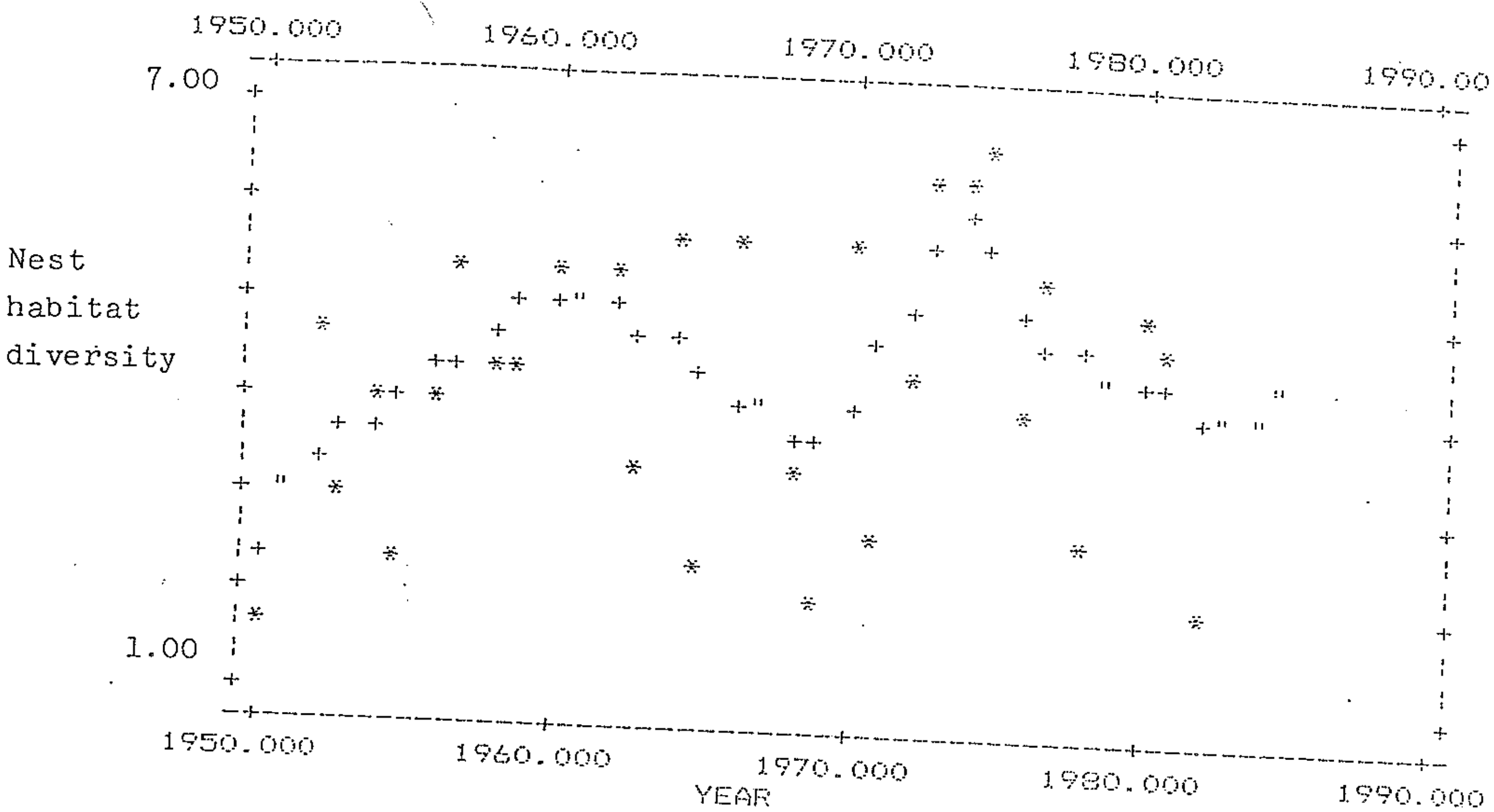

Figure 18.4 Trends in nest habitat diversity for Reed Bunting, 1950-85.

(1964) who suggested that the species was expanding into drier habitats formerly colonised by Yellowhammers. The severe winter of 1962-63 probably accounts for the reversal of this niche broadening. Reed Buntings are partial migrants, so that a proportion of the population will have escaped the severity of that winter in Britain, subsequently returning to reclaim their territories in their previously held habitats. As these adults subsequently die, they leave vacancies in less preferred habitats, reducing overall nest habitat diversity. First-time breeders, on the other hand, favour colonising the vacancies in preferred habitats. Bearing in mind that many preferred habitats, particularly wetland habitats, are not on agricultural land and so were excluded from the present sample, one can understand the decrease in net diversity through the 1960s, despite a net population growth which occurred at this time. As these wetland habitats saturated, however, further recruits were forced into farmland habitats, generating the continued increase in diversity. O'Connor & Shrubb (1986a) have suggested that conditions for Reed Buntings on farmland deteriorated significantly in the mid-seventies with the advent of new herbicides targetted on some of the weeds of arable crops previously providing nesting sites. This is perhaps reflected in the reduced diversity apparent from this time on in Figure 18.4, although it is not reflected in the national clutch size and breeding success figures.

Overview

The details of the various trends presented above are difficult to generalise and probably should be treated on a species by species basis. Treating the broader trends across the 35 year period examined, though, the data indicate a small overall improvement in breeding success by farmland birds. Egg mortality decreased significantly for four species, with less substantial evidence for as many again, and chick mortality decreased significantly for at least five species and probably did so in at least two others. Just over half of all species considered showed a net gain in either egg success or chick success and, more importantly, no species showed a net deterioration. Against this optimistic global view of trends, however, must be set the fairly high frequency of down-turn in fortune over the last ten years, presumably due to changes in the management of farm cropping. If these trends continue they will, for several species, wipe out the improvements brought about since the 1960s by modern pesticide screening procedures.

A second point of interest is how few species varied much in clutch size over time. Although the point requires more investigation, this result might indicate that clutch sizes, at least when measured nationally, are too robust to reflect environmental changes. This is a methodological issue, for a variety of previous studies have detected clutch size variations e.g. between habitats. In this respect a third point emerging from the present study - at least eight of the study species showing major changes in the pattern of their habitat use on farmland - may be relevant. The finding that niche diversification occurred in some species in response to intraspecific population pressure but in others, apparently in response to a reduction in the abundance of competing species is potentially of theoretical significance for models of habitat use by birds.

Table 1 Species and total numbers of farmland nest record cards analysed for the period 1950-85.

Species	Number of cards
Woodpigeon *Columbus palumba*	1351*
Skylark *Alauda arvensis*	1407
Dunnock *Prunella modularis*	1374
Song Thrush *Turdus philomelos*	3240
Mistle Thrush *T. viscivorus*	921
Whitethroat *Sylvia communis*	1282
Blackcap *S. atricapilla*	2300+
Great Tit *Parus major*	583
Magpie *Pica pica*	1513
Rook *Corvus frugilegus*	1711
Starling *Sturnus vulgaris*	2509
Chaffinch *Fringilla coelebs*	2400
Greenfinch *Carduelis chloris*	1076
Goldfinch *C. carduelis*	517
Linnet *C. cannabina*	1173
Bullfinch *Pyrrhula pyrrhula*	1021
Yellowhammer *Emberiza citrinella*	2485
Reed Bunting *E. schoeniclus*	669

* Of these, 782 were early season (January-June) nests

\+ All habitats (see text)

REFERENCES

Brown, J.L. (1969). The buffer effect and productivity in tit populations. *Am. Nat.* 103: 347-354.

Cramp, S & Conder, P.J. (1961). *The Deaths of Birds and Mammals connected with Toxic Chemicals*. Report No.1 of the BTO-RSPB Toxic Chemicals Committee.

Cramp, S., Conder, P.J. & Ash, J.S. (1962). *Deaths of Birds and Mammals from Toxic Chemicals*. Report No. 2 of the Joint Committee of the BTO and RSPB in collaboration with the Game Research Association.

Fretwell, S.D. & Lucas, H.L (1969). On territorial behaviour and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheoretica* 19: 16-36.

Glue, D.E. (Ed) (1970). *The Garden Bird Book*. London: Macmillan.

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

Karlsson, J. & Nilsson, S.G. (1977). The influence of nest-box area on clutch size in some hole-nesting passerines. *Ibis* 119: 207-211.

Kent, A.K. (1964). The breeding habitats of the Reed Bunting and Yellowhammer in Nottinghamshire. *Bird Study* 11: 123-7.

Lomas, P.D.R. (1968). The decline of the Rook population of Derbyshire. *Bird Study* 15: 198-205.

MacArthur, R.H. (1972). *Geographical Ecology*. New York: Harper & Row.

May, R.M. (1976). Patterns in multi-species communities. Pp. 142-162 *in* R.M. May (Ed), *Theoretical Ecology*, Philadelphia: W.B. Saunders.

Mayer-Gross, H. (1970). The Nest Record Scheme. *B.T.O. Guide*, 12: 1-36.

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

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

Murton, R.K., Isaacson, A.J. & Westwood, N.J. (1963). The food and growth of nestling wood-pigeons in relation to the breeding season. *Proc. Zool. Soc. Lond.* 141: 747-782.

Newton, I. (1964). Bud-eating by Bullfinches in relation to the natural food supply. *J. Appl. Ecol.* 1: 265-279.

Newton, I. (1967). The feeding ecology of the Bullfinch *Pyrrhula pyrrhula* L.) in southern England. *J. Anim. Ecol.* 36: 721-744.

Newton, I. (1972). Finches. London: Collins New Naturalist.

Newton, I. (1974). Changes attributed to pesticides in the nesting success of the sparrowhawk in Britain. J. Appl. Ecol. 11: 95-102.

Newton, I. (1979). Population Ecology of Raptors. Calton: Poyser

Newton, I. (1976). The Sparrowhawk. Calton: Poyser

O'Connor, R.J. (1980a). Population regulation in the Yellowhammer Emberiza citrinella. Pp. 190-200 in H. Oelke (Ed), Bird Census Work and Nature Conservation, Lengede: Dachverbandes Deutscher Avifaunisten.

O'Connor, R.J. (1980b). Pattern and process in Great Tit Parus major populations in Britain. Ardea 68: 165-183.

O'Connor, R.J. (1986). Dynamical aspects of avian habitat use. Pp. 235-240 in J. Verner, M.L. Morrison & C.J. Ralph, Modeling Habitat Reltionships in Terrestrial Vertebrates, Madison: University of Wisconsin Press.

O'Connor, R.J. (In press). Organisation of avian assemblages - the influence of intraspecific habitat dynamics. In J. Gee & P. Giller (Eds), Organisation of Communities - Past and Present. Oxford: Blackwell Scientific Publications.

O'Connor, R.J. & Fuller, R.J. (1985). Bird population responses to habitat. Pp. 197-271 in K. Taylor, R.J. Fuller & P.C.Lack (Eds), Bird Census and Atlas Studies, Tring: BTO.

O'Connor, R.J. & Mead, C.J. (1982). Population Level and Nesting Biology of the Stock Dove Columba oenas in Great Britain, 1930-1980. NCC CST Commission Research Report Series. Huntingdon: Nature Conservancy Council.

O'Connor, R.J. & Mead, C.J. (1984). The Stock Dove in Britain, 1930-80.. Brit. Birds 77: 181-201.

O'Connor, R.J. & Shrubb, M. (1986a). Farming and Birds. Cambridge: Cambridge Unversity Press.

O'Connor, R.J. & Shrubb, M. (1986b). Recent changes in bird populations in relation to farming practices in England and Wales. J. Roy. Agric. Soc. England 147: 132-141.

Perrins, C.M. (1979). British Tits. London: Collins New Naturalist.

Ratcliffe, D. (1970). Changes attributable to pesticides in egg breakage frequency and eggshell thickness in some British Birds. J. Appl. Ecol. 7: 67-115.

Ratcliffe, D.A. (1980). The Peregrine Falcon. Calton: Poyser.

Ricklefs, R.E. (1969). An analysis of nesting mortality in birds. Smithsonian Contrib. Zool. 9: 1-48.

Stanley, P.I. & Bunyan, P.J. (1979). Hazards to wintering geese and other wildlife from the use of dieldrin, chlorfenvinphos and carbophenothion as wheat seed treatments. Proc. Roy.Soc. Lond 205B: 31-45.

Tukey, J.W. (1977). Exploratory Data Analysis. Reading, MA: Addison-Wesley.

Velleman, P.F. & Hoaglin, D.C. (1981). Applications, Basics, and Computing of Exploratory Data Analysis. Belmont, C.A: Duxbury Press.

Winstanley, D., Spencer, R. & Williamson, K. (1974). Where have all the Whitethroats gone? Bird Study 21: 1-14.