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Population Level and Nesting Biology of the Stock Dove *Columba oenas* in Great Britain, 1930-1980

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ABSTRACT

(1) An assessment of historical population trends and current status of the Stock Dove *Columba oenas* has been made on the basis of data held by the British Trust for Ornithology.

(2) In Britain the Stock Dove is primarily a bird of rural lowland areas, breeding on agricultural land, in broad-leaved woodland, in areas of open vegetation, in coastal habitats and, to some extent, in suburban and urban areas (parks,gardens,etc). Breeding densities decrease exponentially with altitude, with 96 per cent of the recorded nests located below 300m.

(3) Stock Dove populations in Britain are concentrated in the South and East of England. During the 1950s the species contracted southwards and coastally but has since largely but not entirely re-colonized the areas then depleted.

(4) Population levels dropped substantially between 1950 and 1960, particularly on arable and intensively managed agricultural land, but persisted or even increased in woodland (except coniferous woods), in coastal areas, and in suburbia.

(5) Trends in nest habitat diversity show that Stock Doves have not yet fully recovered their pre-crash habitat distribution. Elm trees were extensively used for nesting during the immediate post-crash years when nesting success in elms was significantly higher than in other nest-sites, but this pattern has reversed as elm use decreased during the 1970s.

(6) The breeding season is prolonged, with eggs laid as early as late February and young in the nest in November on occasion. Three peaks of laying occur in rural areas but only the first two are present in suburban and urban nests. The most successful months are March and July but this is subject to latitude effects. The start of breeding was delayed during the population depression of the 1950s.

(7) Much intraspecific parasitism occurs but clutches of two eggs are both the most frequent and the most successful. Egg losses are commoner in rural areas than in suburbia and nests on agricultural land are more successful than those in woodland or coastal sites. Breeding success was poor during the 1950s population low.

(8) First year survival is about 40 per cent and adult survival is about 53-57 per cent but was lower during the late 1950s and early 1960s. Young birds from early broods seem to fare better in autumn than do those from late broods.

(9) Stock Doves in Britain are largely sedentary, with little interchange with Europe. Young birds disperse rather more than do adults.

INTRODUCTION

This report presents an assessment of the current status of the Stock Dove *Columba oenas* in Britain, with special emphasis on its population dynamics and breeding biology. The report has been prepared at the request of Dr.L.Batten (NCC Belgrave Square), to provide background information for an assessment of the desirability or otherwise of classifying the species as a quarry species within Britain in respect of the EEC Directive on Bird Conservation. The report primarily addresses only the relevant aspects of the bird's biology - its distribution and population level, breeding biology, movements and survival - and does not treat the more purely scientific aspects of the information available.

MATERIALS AND METHODS

Data analysed were obtained from the files of the British Trust for Ornithology. The principal sources were three major monitoring schemes conducted by the Trust under contract with the NCC: (1) the Common Bird Census which has monitored Stock Dove (and other species) populations in woodland in Britain since 1964 (2) the Nest Record Scheme run by the Trust since 1939 and (3) the National Ringing Scheme which first started in 1909. Each scheme collects data from an extensive network of volunteer field workers throughout Britain (and Ireland). The Common Bird Census (CBC) provides information on population trends and on bird density based on annual censussing of some 300 or so (all habitats) plots spread throughout Britain, though with a bias towards more intensive coverage of the Midlands and the South-East. The Nest Record Scheme collects cards recording habitat and nest content data for an annual intake of ca.25,000 nests inspected by BTO observers on one or more visits. These records provide estimates of date of laying, clutch size and breeding success for each nest, the precision of each estimate varying with the timing and frequency of the inspections made to each individual nest. The National Ringing Scheme provides for the collation and interpretation of reports of ringed birds recovered in the British Isles following ringing in Britain or abroad. Most reports provide a precise place and date for the recovery which information, in conjunction with the files of ringing date and place data held by the BTO, provide estimates of movement and survival of the birds concerned.

Data from all three sources are subject to a number of biasses but with appropriate analysis can yield information comparable to that obtained from studies conducted on an intensive basis by professional ecologists (see O'Connor (1980) for a validation study). For studies such as the present one of Stock Dove, for which such intensive studies have not been conducted (though see Murton 1966a) these data sources are the only ones available and cannot be directly validated, but all

known biasses were routinely considered in the course of the analysis conducted here.

Census Data

The Common Bird Census data are collected by observers visiting a census plot of defined boundaries and plotting onto large-scale maps the position of all registrations of (here) Stock Doves, including those pertaining to territorial interactions, to nestling feeding, and to family parties after fledging. With 8-12 visits to the plot enough registrations accumulate to allow identification of clusters of sightings (or hearings) corresponding to the number of breeding territories. Fieldwork is largely confined to May through early July. Not all territories are identified by this method but validation studies have shown generally high correlations between the clusters determined by CBC methods and those obtained in intensive calibration work based on colour-ringing, nest-finding, and playback experiments (review in O'Connor and Marchant 1981). Observers are required to hold their census effort constant (in respect of number of visits to the plot, timing of visits, hours in field, etc) since this allows removal of between observer differences in census ability by pairing plot (observer) data across years to obtain an umbiassed estimate of the proportional change in the population. These changes are then used to calculate a CBC index whose value in 1966 was set arbitrarily to a value of 100. For analysis of regional population trends the process is repeated using only data from that region.

Whilst the pairing of plots across years removes from the CBC index any observer bias due to census skill or effort it also removes the information on absolute Stock Dove densities. Density estimates vary with observer ability but may not be excessively biassed: in the only experimental study on this point inexperienced census workers were only 20-25 per cent below more experienced census workers in their estimates of breeding pairs present on the census plot (O'Connor and Marchant 1981).

Nest Record Data

Nest Record cards vary considerably in the quality of information they carry. A single visit provides information on habitat and nest site requirements but contributes little to the assessment of laying dates, clutch size and breeding success. But a sequence of suitably spaced visits allows all these data be determined precisely whilst a less well spaced sequence contributes with less precision. The rationale of the analysis conducted is that observations from each successive visit impose constraints on the possible dates of first egg date, etc, given initial estimates of laying interval, incubation period, nestling period, etc. By setting minimum and maximum limits to these latter variables successive approximation procedures eventually yield the narrowest possible limits to egg date, (clutch size, etc) consistent with the observations. These values were tabulated for each nest and analysed in respect of variables of interest (annual variation, seasonal and habitat differences, etc.).

Certain nest records proved to contain mutually inconsistent observations when analysed as above. In a small proportion of cases the cause of the inconsistency could not be attributed to any biological factor and must represent observation error (mis-counting of eggs or young, etc). But for Stock Doves the majority of records containing inconsistencies contained evidence of intraspecific nest parasitism - two or more females laying into the same nest. Although such dump nesting may be a regular feature of Stock Dove breeding the records concerned do not contribute information on clutch size or laying dates. Accordingly, all nests containing mutually inconsistent observations were discarded from the analysis.

For the present study, date of first egg was established wherever possible and used if the estimates of the earliest possible and latest possible laying date were no more than five days apart. Analysis was based on the earlier of the two limiting dates. For a substantial number of records the pattern of observations was such that egg dates could not be assessed but date of hatching could. First egg dates were estimated for these records by subtracting a mean incubation period of 17 days from hatching date, where this estimate of incubation period was obtained from those cards providing both egg and hatching dates. Checks showed that incubation periods calculated in this way were independent of laying date.

Estimates of breeding success were obtained in two ways. First, the maximum number of young recorded in a nest was used to provide minimum estimates of hatching success. These estimates are crude because our computer programs do not yet include routines to discount entries of zero young for nests to which no visits were paid during the nestling period. Second, and more reliably, the observers inspecting possibly successful nests after the expected fledging date are asked to record any evidence available as to success and observers inspecting failed nests are asked to record evidence as to stage (egg or nestling) and cause of failure. The relative frequency of these various success codes provided information on seasonal, habitat or other variations in breeding success.

RESULTS

DISTRIBUTION

Figure 1 is reproduced from Sharrock (1976) and shows the distribution of Stock Doves in the British Isles during the 1968-72 fieldwork for the BTO's Atlas of Breeding Birds in Britain and Ireland. The species were widespread in the south and east of Britain and scarce or absent in the west and north. Sharrock (1976) suggests this distribution was similar to the recent historical distribution of the bird prior to an organochlorine pesticide induced collapse of the population in the late 1950s. This is supported to some extent by

Figure 2 in which are plotted by 1x2 degree latitude-longitude blocks the ringing co-ordinates and recovery co-ordinates of Stock Doves ringed and subsequently recovered. These maps represent only an approximate plotting of distribution for the species since they are based on the co-ordinates only of those birds recovered subsequently and not of a random sample of the Stock Dove population as a whole. Nevertheless, the general lack of movement by this species (see below) makes it unlikely that the overall pattern of major concentration to the south and east of Britain is a mis-representation of the true position.

The three maps indicate that a significant shift in distribution did indeed take place between 1951 and 1967, the centre of gravity of the population moving southwards. In the east-west direction the distribution became more coastal, with proportionately fewer birds in the Midlands. Since 1968 the birds have redistributed themselves back towards their pre-1951 pattern, as suggested by Sharrock. The three distributions are statistically heterogenous both in respect of latitudinal pattern (X =33.2, d.f.=10, P<0.001) and in respect of longitudinal trend (X =53.1, d.f.=6, P<0.001). Despite the redistribution, however, latterly the birds are still not as widespread as previously, for comparison of the pre-1951 pattern with the 1967-80 one shows the population has not yet re-colonized the northern end of its early range to the same degree as before (X =11.4, d.f.=5, P<0.05) and that it is still over-represented(relative to the pre-1951 level) in the east and west coastal squares (X =11.7, d.f.=3, P<0.01). The possibility of concentrations of ringing effort in particular areas must be borne in mind as a caveat in making these interpretations,however.

Figure 3 provides a third source of information as to recent distribution of Stock Doves in Britain. Here the breeding densities on CBC plots are used to map population density and confirm the other evidence for the birds being most numerous in the south and east and scarce or absent to the north and west.

Table 1 provides further evidence for changes in the distribution of Stock Doves in Britain between 1942 and 1980 in so far as distribution is reflected in the totals of nest record cards from different regions. The relative distribution of cards between regions is a biassed indicator of distribution because observers are not spread evenly over Britain as a whole but temporal changes in the relative proportion of cards from any particular region are indicative of changes in the relative density of Stock Doves in the region. Table 1 confirms that Southern England and Eastern England were the main strongholds of the species in the 1940s. Birds from Western England and Wales decreased relative to other areas during the 1950s but have since recovered. Northern England has also become more important since 1960 and Scottish populations also seem to have grown steadily.

POPULATION TRENDS

CBC index

Figure 4 shows how the Stock Dove population in Britain has varied since 1964. The trend shown by the CBC index is one of more or less steady increase, with average densities increasing eight-fold between 1964 and 1980. (The CBC method measures population changes more precisely than it does absolute densities, so all densities are routinely expressed in the index relative to an arbitrarily set value of 100 for 1966. The figure plots this index on a logarithmic scale to equalize the emphasis on equal relative changes at different points on the scale e.g. to weight equally a change from 50 to 60 and from 200 to 240). A priori, this increase is likely to be primarily a recovery from unusually low population levels. First, many other species suffered severe mortality during the cold winter of 1962-63 and took several years to recover to their probable 1961 levels (references and discussion of cold winter effects on British birds in Cawthorne and Marchant 1980). Secondly, much anecdotal evidence indicates that Stock Dove populations were badly depressed (and even locally extinct) between 1957 and 1960, perhaps later (Sharrock 1976).

Figure 5 analyses the CBC data on a regional basis, using the standard groupings of counties described by Batten and Marchant (1976). Stock Doves were too infrequent on census plots outside two regions - Southern England (comprising Cornwall, Devon, Somerset, Dorset, Wiltshire, Berkshire Hampshire, Surrey, Sussex and Kent) and Eastern England (comprising Norfolk, Suffolk, Essex, Cambridgeshire, Bedfordshire, Oxfordshire, Huntingdonshire, Buckinghamshire, Hertfordshire, Middlesex, Northamptonshire, Leicestershire, Nottinghamshire, Lincolnshire and Rutland (or their modern equivalents)) - to permit construction of a continuously running CBC index. The figure shows that populations both in the Southern England and in the Eastern England region have increased roughly in parallel with the national population index of Figure 4. There is nevertheless some slight suggestion that the population increase in the south may be levelling off relative to the east. One might expect a core region to saturate before a less preferred region (cf. Williamson 1969) were the population nationally recovering from the type of population collapse suggested by Sharrock(1976).

Evidence from ringing data

Since the CBC scheme commenced for woodland only in 1964 census data with which to document such a collapse are not available. However, Ginn(1969) provides a method of using ringing totals and nest record totals to describe population trends. His techniques are not as precise as that of the CBC scheme but are valuable for a retrospective assessment of major population shifts. His rationale is to seek species pair comparisons in which one species is that of immediate interest (here Stock Dove) and the other is an a priori indicator of relevant ringing effort (e.g. of effort concentrated on species breeding in nest-boxes, of effort concentrated on nestling ringing, etc.). For Stock Doves, the relatively constant clutch size and breeding season (see below) allow use of standardized nestling ringing totals as a population index. To standardize the Stock Dove totals each of the following was used:

a) Annual total of nestlings of all species ringed. These totals alter with ringer effort but with a large number of species involved are otherwise likely to average out species-specific fluctuations. The remaining bias is the risk that many common species might simultaneously increase or decrease with a major environmental change (a particularly fine or bad summer; use of pesticides; etc.).

b) Tawny Owl Strix aluco. A species which may use nest-boxes (as Stock Dove may) but which , again like Stock Dove, probably has a majority of the chicks ringed every year located in natural sites. Its disadvantage is that a number of intensive ringing studies of the species have resulted in increased ringing effort (e.g. Southern 1970). Tawny Owls are also subject to very violent country-wide fluctuations in breeding output.

c) Wood Pigeon Columba palumbus. This is the species most closely related to Stock Dove and has a similarly extended breeding season. It was also the subject of a specialist study (which included Stock Dove) in the period between the late 1950s and the mid-1960s (Murton 1966a).

d) Dunnock Prunella modularis. This is a typical small bird species with an open nest. It is a resident species not subject to violent fluctuations and is a fairly good indicator of general nest-finding and nestling ringing effort by the majority of ringers.

e) Mistle Thrush Turdus viscivorus. A rather more charismatic open-nesting species unlikely to be ignored even by blase ringers. It therefore controls for any saturation effect which might occur with the common Dunnock (whereby ringers level off in effort as the bird becomes more common).

These five sets of ringing totals thus provide a selection of comparisons for the Stock Dove totals capable of controlling for several sources of bias.

Figure 6 shows the relative number of pullus Stock Doves ringed annually since 1931 (when the practice of reporting separate annual totals for pulli began). Prior to the war years nestling Stock Dove accounted for between 0.1 and 0.2 per cent of all nestlings ringed. The year 1951 was unusually productive of Stock Dove young but was immediately follwed by a steep and systematic decline through 1960. Since the other species were also affected adversely by organochlorine use in these years the relative decline of Stock Dove nestlings reared is underestimated by the ratio used as y-axis here. Between 1960 and

1966, the population of Stock Doves (and/or their breeding success) has recovered, though perhaps less steadily so over the last 12 years. Comparison of the relative totals for 1971-80 and for 1931-40 shows that Stock Doves might be 30-40 per cent more numerous (or successful) now than 40 years ago.

Figure 7 presents the trend in Stock Dove to Tawny Owl pullus totals ratio from 1931 through 1980. These values fluctuate greatly, probably because of the factors already noted as likely to affect the owl totals, and are clearly too variable to document even the order of magnitude decline in Stock Dove totals suggested by Figure 6. Even so, Figure 7 does suggest a decline in Stock Dove nestlings relative to Tawny Owls between 1950 and 1960.

Figure 8 compares Stock Dove totals for pulli to those of Wood Pigeon. Both species were the subject of intensive study by Murton (1966a,b) and his colleagues. The data shown a three-fold variation in the ratio of the two species' nestlings between 1931 and 1950, with a decline in relative abundance from the early 1950s through 1961. Stock Doves have subsequently increased relative to Wood Pigeons and their ratio is currently at its highest ever.

Figure 9 compares Stock Dove pullus totals with those of Dunnocks since 1931 and again shows features noted in earlier plots - a relative high at the end of the 1940s, a decline through the 1950s and a subsequent recovery and increase through 1980. In many ways the Dunnock is a better comparison than the all pulli totals used in Figure 6, for the former reflects ringing effort for natural, terrestrial nests alone whilst the latter includes birds nesting in nestboxes and seabirds nestings ringed in large numbers on islands. Relatively small increases in the number of extensive nest-box schemes and in seabird ringing expeditions can therefore alter the grand total of all pulli for a year and could account for this point of difference between Figure 6 and Figure 9.

Figure 10 for Stock Dove to Mistle Thrush pulli ratio is rather similar to the Dunnock pattern and controls in large measure for any risk that Dunnock totals might have fallen with decline in ringer interest in such a common sedentary species.

Evidence from nest records

An alternative source of data on historical population trends is the totals of nest record cards submitted for Stock Doves over the years. Figure 11 presents these in relation the corresponding annual grand total (all species) of cards submitted to the BTO, thus standardizing observer effort at nest finding. However, the relative totals for 1942 and 1943 may be artificially high because of the war-time Wood Pigeon Enquiry in those years. The Wood Pigeon totals have been excluded from the grand totals for the two years but it seems likely that the concentration of effort onto Wood Pigeons will have boosted the totals of Stock Dove cards from similar habitat. For 1942, for example, the 51 Stock Dove cards exceed even the total of Blackbird

(44 cards) and Song Thrush (41 cards), though these are two very common birds whose nests are found easily. Subject to these reservations Figure 11 suggests that Stock Dove numbers were relatively high at the end of the 1940s but then decreased precipitously until about 1961, since when their relative abundance has recovered more slowly. Extrapolation of this trend suggests the species will not fully recover its early abundance until about 1990 or slightly later if the 1942-43 data are in fact unbiassed. The current relative abundance is about half that of 1950 and one-third that of the 1942-43 index.

The data presented in Figures 6-11 thus vary substantially in their assessment of the current (1981) position of Stock Dove populations in Britain. All measures indicate that the population was relatively high about 1949-50 and fell sharply through the next decade, with a steady recovery since. It seems likely, though, that the nest records totals used in Figure 11 over-estimate the early population. Ringing totals are harder to assess for this sort of bias in view of the distortions brought about by the war but their general implication is that Stock Doves are now about 1.5 - 3.0 times are frequently ringed as they were before the war. An important point common to all the data is that the present population trend shows little evidence of levelling off. Hence (1) the species is now expanding into a previously unavailable or recently expanded niche or (2) the early population data greatly <u>under</u>estimate the true population in the 1930-40 period or (3) the population at that time was already decreasing from some earlier population high.

BREEDING HABITAT

Altitude

Stock Doves are primarily lowland birds but without a sharp cut-off as to altitude. The frequency of nest records decreased exponentially with altitude according to the equation

$$N = 1099\exp(-0.012)$$

between 50m and 300m ($r = -0.998$, d.f.=3, $P<0.001$). Some 96 per cent of all nests were located below 300m. This includes a proportion of underground nests built in war-time bunkers and other subterranean locales.

Habitat use

The vast majority (88 per cent) of the Stock Dove nests analysed were from rural areas. Table 2 shows the breakdown of the nests analysed according to their classification to rural, suburban or urban status. A small percentage of the nests found were in suburban areas but extremely few were found in areas classified by the observer as predominantly urban. The residual ''other'' catergory covers nests for which the observer provided no gross habitat classification.

Table 3 provides a more detailed breakdown of the major habitats used for nesting by Stock Doves in Britain. Agricultural habitats accounted for the majority of nests found (41 per cent). Woodland habitats of various sorts were much less frequent (15 per cent) and were followed in turn by open vegetation (9.7 per cent), coastal habitats (6.2 per cent), and parks and gardens (4 per cent). The remaining nests (22 per cent) were in a variety of miscellaneous habitats.

For about half the nests found on agricultural land no further details of land use were provided. Amongst those for which agricultural practice was specified pasture, arable, and mixed farmland were more or less equally common. Use of agricultural buildings and of orchards was only one-third to one-half as frequent as use of these three habitats. Rough grazing was rather infrequently recorded.

About half the woodland nests recorded were described as being in broad-leaved woods, with mixed woodland in second place. Coniferous woods were relatively infrequently used.

The open vegetation nests were primarily in unspecified field vegetation, in many cases probably more properly coded to an agricultural habitat of some sort. Moorland and breckland nests were, however, notably frequent.

Amongst the nests in coastal habitats the most frequent coding was '64' (exposed rock, sand, shingle), probably better regarded as 'unspecified coastal'. After this group nests on stacks or islands were commonest, as might be expected. The low frequency of cliffs and of coastal buildings suggest that the birds were not particularly given to use of the rocky habitats more characteristic of Rock Doves.

More than half the nests recorded from park and garden habitats came from private gardens, probably reflecting a bias towards the recording of such nests.

Temporal changes in habitat distribution

Although the vast majority of nests were found in rural sites the proportion of nests in suburban and urban sites has varied over the years (Figure 12). Prior to 1950 few years saw more than about 2 per cent of the nests reported from urban and surburban sites but between 1950 and 1965 this proportion seems to have risen. Since then there has been a more or less steady decrease in the relative incidence of urban nesting (Figure 12). Such a pattern could arise either through an absolute increase in the numbers of birds nesting in suburban areas or because of a decrease in the absolute numbers of birds nesting in rural sites. If birds in rural areas survived less well or bred less successfully than those nesting in suburban and urban areas the percentage of nests recorded from surburbia would increase. For Stock Doves the increase in Figure 12 coincides with the appearance of organochlorines on agricultural land, suggesting that the latter effect - a decrease in the size of the rural population of Stock Doves - was responsible.

Figure 13 presents data on the corresponding trends within individual habitats. Fewer than ten nests were available between 1944 and 1948 but samples of 51 nests for 1942 and of 90 nests for 1943 provide reasonable indications of habitat use prior to 1950. Figure 13 shows that in areas described as arable few Stock Dove nests were recorded from 1949 onwards until the late 1960s, when numbers there rose, even though 10-15 per cent of the 1942-43 nests had been from this habitat. A much larger sample of nests from areas described by the observer as agricultural (BTO code 70) - and one which undoubtedly contains many nests from arable areas - reveals a sharp drop in nesting there from 1949 to 1960, with a slow recovery thereafter. In areas classified as pasture (BTO code 72) the proportion of nests found has, if anything increased between 1949 and the late 1960s, decreasing sharply thereafter as the proportion of nests in arable and other habitats recovered. This is consistent with the lighter use of organochlorines on pasture than on arable land.

A similar increase holds for the proportion of nests found in woodland (pure conifer woods excluded), again reflecting the absence of pesticide use there (Figure 13). The same effect is probably also behind the high incidence of coastal nesting by Stock Doves between 1953 and 1962. Records of Stock Doves from stacks and islands also increased, though doing so slightly later than the rise in mainland coastal habitats. One might well expect some delay on offshore islands if differential dispersal is involved. It is also worth noting that the increased use of coastal habitats is an increase in absolute rate of use and not the result of a constant number of nests forming a larger proportion of the whole as use of agricultural habitats declined.

This evidence as to changing relative use of habitats has relevance to the continuation of the recent increase in Stock Dove population levels noted above (Figure 4). Expanding populations frequently colonize secondary or tertiary habitats of relatively poor breeding success (Fretwell and Lucas 1969) and relatively few young may be reared in these habitats to join future breeding populations. The number of different habitats noted in the nest record samples for each year was strongly correlated with the number of nest record cards in the sample, according to the equation

$$\ln H = 0.121 - 0.625 \ln N \qquad r = 0.945,\ P<0.001$$

where H and N are numbers of habitats and of cards respectively, and ln denotes the natural logarithm. If N is correlated with population level this relationship might imply that more habitats are used for nesting as the population increased. But a common statistical artefact is present in these data, in that a population permanently (i.e. independent of population pressure) distributed amongst the available habitats would also yield a greater count of habitat types under more intense sampling. To control for this possibility the annual nest record samples N and their habitat counts H were adjusted to 100 cards per year by pro-rating N to 100 with a 0.625 exponent. i.e.

$$S = (n/100)$$

where S is the standard (sampling effort independent) habitat count. This standard count - effectively of diversity of nesting habitat - is plotted for 1942-198 in Figure 14. This diversity was initially low but rose sharply between 1950 and 1960 (implying proportionately more of the birds then nested in formerly less favoured habitats - cf. the reduced proportion of the population on arable land at that time (Figure 13)) and then decreased again as agricultural habitats re-filled with birds. Inspection of the Figure shows that habitat diversity has not yet fallen to the lowest levels prevailing in the 1940s, thus indicating the population has yet some distance to go before it has recovered to reach the levels of habitat saturation (possibly incomplete) then prevailing. As these data are derived only from nest record cards for the Stock Dove alone these trends are less likely to be biassed by such events as the Wood Pigeon Enquiry. They thus suggest a population recovery from a 1950s depression rather than any expansion into a previously increased niche.

Summarizing these results, it is clear that the Stock Dove population nesting in agricultural habitats fell sharply during the pesticides era of the 1950s, with the decrease more marked in arable areas than in pastures. During this period proportionately more of the Stock Doves breeding in Britain used suburban and urban habitats and habitats such as woodland and coastal sites outside the immediate influence of agricultural practice. In some cases the numbers (and not just proportions) of Stock Doves recorded from these habitats increased. The subsequent recovery is not yet complete in respect of the bird's distribution amongst the available habitats.

BREEDING BIOLOGY

Breeding season

A total of 796 nest record cards permitted the calculation of laying date for the first egg of the clutch to at least five days precision. The earliest first egg date recorded was day 52 (21 February) whilst the latest was day 286 (13 October). Figure 15 shows the distributions of these laying dates within individual decades from 1942 through 1980. Within each distribution there is a suggestion of three peaks of egg laying each year, at around day 110 (20 April), day 170 (19 June) and day 220 (8 July). These dates are very approximate given the 20 day intervals of Figure 15, but would correspond to a nest cycle of about 60 days. This is consistent with the species' incubation period of 16-18 days and nestling period of about 25-28 days. Inspection of the five distributions further suggests that the nest cycles may have been more distinct in earlier years than they are now but this could as easily reflect changing observer standards (e.g. less intensive nest recording over the whole of the nest season) as reflect a real biological phenomenon.

Figure 15 shows that about 83 per cent of all nests for which the first egg date of the clutch could be established started laying between mid-April and the end of August. However, a small proportion of nests began laying in late September or even in October in some years and these nests are likely to contain young up to six weeks later i.e. until early November. Ringing recoveries also provide information on the length of the nestling period, in the form of date of ringing of pulli later recovered. The sample is biassed since the probability of a nestling being recovered varies with its egg date (Murton 1966a) but is adequate for the present purpose. Table 4 summarizes the ringing data for the 207 nestlings recovered from known ringing dates (two other nestlings with inadequate data were omitted from the analysis) and confirms the extended breeding season. Young of ringable age (about 10 days old) were in the nest from late March to mid-October. With a 17 day incubation period the earliest eggs must have been laid about 1 March and the last young fledged in the second half of October, a nesting span of more than seven and a half months.

Laying dates varied between habitats, with suburban and urban habitats having a shorter breeding season than in rural areas (Figure 16). The difference was largely due to the absence of late nests in suburban and urban areas (X =18.0, d.f.=4, P<0.01). The possibility of under-recording of nests from built-up areas should be borne in mind as a possible bias here, though the main drop in the Stock Dove records (Figure 16) occurred after day 180 (29 June), a very early date for such a marked cessation of nest recording in these areas. One might expect Stock Doves in rural areas to continue breeding later in the year as the autumn cereal crops come available as a food source.

Figure 15 showed some variation as to the start of the breeding season between decades but the variation was not meaningful with the scale of plotting used in the diagram. Figure 17 shows how the date of first egg has varied between 20-day periods each year. Interpretation is made difficult by low sample sizes before 1949 and again between 1958 and 1963 but the five-year moving averages suggest that the start of laying may have been delayed (relative to other years) between 1955 and 1965. Much the same pattern is further apparent in Figure 18 for date of ringing of nestlings. These data are not completely independent of the nest record data used for Figure 17 because some ringers complete nest record cards for nests at which they ring. In addition the probability of a Stock Dove nestling surviving varies seasonally (Murton 1966a) so the recoveries provide a biassed assessment of the timing of the breeding season. Nevertheless, the appearance in both data sets of the same delay in the breeding seasons during the late 1950's strengthens the evidence provided by each. Figure 17 suggests that breeding seasons have now returned to their normal timing.

The breeding season of Stock Doves varied with latitude, according to analysis based on ringing recoveries (Table 5). Northern latitude recoveries contained the largest proportion of early brood recoveries and the smallest proportion of late brood recoveries, with southern latitude nests showing the opposite pattern. The latitudinal trend is most pronounced in respect of September-October broods. This is the reverse of what might be expected with northern areas warming later in spring and having later grain harvests. Again, though, the risk of bias through differential recovery rates at different times of year must be borne in mind. Reference to Figure 2 shows that the distribution of recoveries moved southwards during 1951-67 and thus, on the basis of Table 5, would induce a delay in breeding season such as recorded (Figure 17).

Clutch size

Table 6 summarizes the distribution of clutch sizes determined from the Stock Dove nest record cards and additionally analyses them by rural and suburban-urban habitat categories. As already noted, evidence for dump nesting was obtained in a number of records consequently omitted from analysis. Dump laying is indicated if two or more eggs are laid in a nest on the same day or (less conclusively) if additional eggs appear in a nest some days after a normal laying sequence has been recorded (or inferred). It remains possible, however, for dumping to take place and not be detected in the checks for these indicators. For example, three eggs appearing at daily intervals could be a genuine clutch of three but could alternatively be due to two females laying into the one nest. As the vast majority of Stock Doves lay only two eggs (Table 6) records of clutches of three and of four eggs give cause for caution. Table 6 suggests that proportionately more one-egg clutches were detected for suburban and urban nests and that rural clutches were slightly larger, but neither trend is statistically significant (rural nests versus all others X =0.38,n.s.; suburban-urban nests versus all others X =1.94,n.s.).

Table 7 sets out equivalent data in respect of the maximum number of young recorded in individual nests. The column for zero young includes cases where no visits were made during the nestling stage and is therefore not an indicator of nest failure. The distribution of brood counts across all three habitats is rather similar (X =3.72, d.f.=4,n.s.). About 40 per cent of all nests counted two young and 8-9 per cent recorded only one young (but may have had unhatched eggs on the last visit paid to the nest by the observer). The various biasses introduced into this table by incomplete recording make the analysis rather unsatisfactory as evidence of breeding success; a better analysis is presented below (Table 9).

Table 8 summarises the relationships between the number of young produced and the clutch size recorded for the nest concerned. Clutches of two eggs had the highest success, with only 34 per cent failing to yield records of young. Of the clutches recorded as of one egg some 69 per cent subsequently failed to yield records of a nestling. However, some of these clutches were probably of ''dumped'' eggs, rather than a full breeding attempt. A proportion may have been of incomplete clutches where laying was unduly prolonged. Among clutches of three eggs some 52 per cent subsequently failed to yield records of young and among clutches of four some 86 per cent of the nests so failed. These findings would be consistent with a degree of dump nesting. In this analysis, nests into which eggs were laid after a delay greater than that appropriate for laying by a single female were rejected before analysis commenced. Nevertheless, it was possible for some dump nests to be included where the additional eggs appeared on dates consistent with laying by a single female. (As clutches of four eggs were more likely to be the result of two females laying than were clutches of three the greater failure rate in the nests with the larger clutch is to be expected).

Table 9 examines the success of clutches of different size on the basis of their final recorded outcome. (Observers recorded the nest as successful, failed at egg stage, failed at nestling stage or failed to unknown cause according to evidence available on the first visit after eggs or young disappeared e.g. predated egg shells, fledglings seen nearby, etc). The conclusions are similar to those drawn from Table 8. Clutches of two were most successful (17 per cent successfully fledging young, 8 per cent of clutches of three eggs fledging young). Except in clutches of two, failure at the egg stage was commonest, as expected on the basis of discussion above. Failure at the nestling stage was similar in clutches of two and in clutches of three.

Table 10 examines the relative success of nests in different habitats, according to the eventual assessment of success or failure made by the observer for individual nests. Nests in suburban-urban environments were slightly more likely to be recorded as successful than were nests in rural areas ($X = 4.93$, d.f.$=1$, $P<0.05$). The difference was mainly due to failure at the egg stage, with rural nests being nearly twice as likely to lose their eggs than was the case in suburban nests. Rural nests were also slightly more likely to lose their young than were the nests in suburbia but the difference was relatively smaller than at the egg stage.

Clutch size in different habitats

Table 11 summarises the distribution of clutch sizes in habitats of different types. The vast majority of all nests contained two eggs, and at least 85 per cent of the nests found in any habitat held a clutch of this size. It seems likely that clutches larger than this were the result of more than one female laying into the same nest. Clutches of one were generally rare, in most agricultural habitats accounting for less than 5 per cent of the total clutches examined, and this was true also of nests in coastal habitats. In woodland of all types, however, clutches of one were relatively more frequent, suggesting that these habitats might be less satisfactory as breeding habitat. However, the possibility of bias, in the form of incomplete clutches being recorded differentially between the habitats, cannot be completely ruled out here.

Table 12 summarises the distribution of brood size by different habitats, for those nests in which young were recorded at some stage during the sequence of observer visits. No major differences between the habitat categories as to the incidence of broods of one, two or three young are apparent. However, this analysis is not by itself conclusive since nests from which no young were recorded at all are excluded from this analysis. Table 13 examines the distribution of the final success codes recorded by the observers for nests in these habitats. Nests on arable land were the most successful, with 16 per cent of the nests being recorded as successful. Mixed farmland was the poorest in respect of breeding success of the various types of habitats examined but this may have been an artefact of observer activity, for the rate of egg failure and the rate of nestling failure on mixed farmland were similar to those recorded for the other habitats. Woodland and coastal habitats were generally rather less successful for Stock Dove nests than were the agricultural habitats, with egg failure and nestling stage failure rates both running to higher values than was the case in the main agricultural habitats.

Seasonal variations in breeding success

Table 14 summarises the seasonal distribution of clutch sizes over all habitats combined. In all months clutches of two eggs were commonest but the frequency of clutches of three eggs was highest and the frequency of one egg lowest in July. These large clutches were also relatively frequent in the adjacent months of June and August. These months are therefore the months of maximum egg production but it is not possible to distinguish from these data whether individual Stock Doves laid more eggs per clutch in July or whether the frequency of egg dumping rose in that month.

Table 15 presents similar information in respect of the brood sizes recorded in different months (for nests for which young were recorded at some stage). Broods of two were always commonest but the proportion of single young records increased from March through May, decreased in June and rose again through August. The only cases with three young in a single nest were recorded in June.

Supplementary data on thare point is provided by Table 16 which presents a seasonal breakdown of the brood sizes recorded for 161 of the 207 nestlings and subsequently recovered. Distributions computed from such ringing recoveries can be highly biassed if survival has seasonal or clutch size dependencies, so caution is needed in their interpretation. Nevertheless, it is noteworthy that four of the five recoveries from broods of three were from June nests, in line with Table 10. Recoveries from broods of one young were few and their relative frequency within the time periods shown do not differ significantly from the corresponding nest record card data of Table 10 (March-May X =1.60; June-July X =0.21; August-October X =2.30; all n.s.). The ringing data are thus consistent with the nest record data despite the possible biasses of the former.

Breeding success

Such data might be taken to suggest that March and June-July were the most successful periods for producing young and this is confirmed by the data on individual nest success (Table 17). Nearly one nest in three in March was recorded as successful in producing young but this proportion had fallen substantially in May (15 per cent) before rising again to peak once more in July (22 per cent): August nests were relatively unsuccessful (12 per cent). Egg stage failures were therefore low at the two extremes of the breeding season and were high in April and May and again in July, probably the periods of maximum egg predation activity. Inspection of the rate of failure at the nestling stage shows a sharp increase in failure rates between March and April (but note the small sample size for March) and a seasonal decline thereafter until August when the rate increases sharply once more. As cereal crops ripen through the summer one might expect to find the birds increasingly well able to forage whilst attending nestlings.

Temporal variation in breeding success

Figure 19 documents the pattern of breeding success and failure over the period 1942-1980. Prior to 1950 samples were rather small and only a few, rather variable, years are recorded. Between 1950 and 1960 nest success was rather low, generally in the region of 4-7 per cent but since about 1962 the proportion of successful nests seems to have risen steadily. Regressing the untransformed percentage success on date gives a regression

$$S = 0.355Y - 13.268 \quad r=0.595,\ n=18,\ P<0.05$$

where S is the percentage of nests found to be successful and Y is the date (62 for 1962, 63 for 1963, etc.). Figure 19 thus suggests that nest success was rather low during the period 1950-1961 with a steady recovery thereafter.

Table 18 summarises breeding success and failure (due to various causes) by decade and confirms this pattern: between 1950 and 1959 nest success averaged only 7.5 per cent, less than half that of the period 1942-49 when organochlorine pesticides were not in use. The decadal figures show the subsequent increase in nest success. Related data from the ringing recoveries, in the form of decadal brood size distributions for nestlings recovered later (Table 19) do not show this trend. The table suggests brood sizes may be slightly more variable in the last two decades than earlier, which might be expected if rather more birds breed now than earlier and if dump laying is now rather more frequent. As noted earlier (Figure 15), there is some evidence that laying has become more irregular latterly. Again, though, the possible sources of bias in the use of recoveries here are numerous.

Table 18 shows that the sharp drop in nest success around 1950 was associated with a quadrupling of egg failures at this time (from 3.7 to 17.1 per cent). Failure rates for the egg stage decreased around 1960 but are still (in 1980) substantially above 1942-1949 figure (Table 18). Nest failures whilst young were in the nest and failures for unknown reasons also increased sharply between 1950-1959 and fell back subsequently. Figure 19 presents the percentage of egg failures and of nestling failures on an annual basis and shows the increase in egg failure rate during the early 1950s. Changes in nestling failure rates are less marked but still apparent in this figure. Although, as noted above, nest success increased significantly over the period 1962-1980 there was no systematic trend in average rate of nest failure over this period, the percentage if anything rising ($r = 0.315$, n.s.). However, this conceals certain trends, for during the period 1960-1980 both the failure rates shown in Figure 19 increased significantly: for egg failure rates the analogous regression equation to that above was

$$E = 0.104Y + 4.731 \qquad r=0.477,\ n=18,\ \text{n.s.}$$

where E is the percentage of nests recorded as failing at egg stage. For failures at nestling stage the equation obtained was

$$N = 0.308Y - 15.222 \qquad r=0.565,\ n=18,\ P<0.05$$

where N is the percentage of nests recorded as failing at the nestling stage. However, these detailed trends were offset by a decrease in the percentage of nests failing with the stage of failure unknown ($r = -0.138$, n.s.). The possibility of a recording bias due to the observers becoming more competent in their recording, so that proportions in more of the nests failing are recorded as such should be borne in mind in interpreting these results.

Nest success and elm use

An alternative explanation of the recent trends just noted might be a relationship between breeding success and the use of elm trees for breeding. Elms were used for 292 (10.0 per cent) of the 2916 Stock Dove nests analysed here. As this is a relatively high proportion of all nest sites any differential in nest success between elm and other nest sites would create a trend in average nest success as elm use decreased with the spread of Dutch elm disease. Figure 20 shows the annual proportion of nests in elm trees between 1942 and 1980. The 1942-43 data suggests a 15-20 per cent incidence of elm nests at that time but the proportion was low by 1950 and then increased steeply through the early 1950s. By 1964 the proportion of all nests in elms had reached 24 per cent but it has since decreased to only 10 per cent in 1980. Thus, the use of elms has varied substantially over the period reviewed but shows the expected decline over the last decade.

Table 20 examines breeding success in relation to elm and other sites. Overall, there is no relationship between elm use and nest success or failure ($X = 0.46$, n.s.) but there has been significant temporal variation in the relationships involved. Until about 1959 success and failure were independent of nest-site but during the 1960s elms were significantly more likely to be successful than were nests in other sites ($X = 4.24$, d.f.=1, $P<0.05$). In the 1970s and through 1980 this pattern reversed. Examination of the lower part of Table 20 shows no evidence of changes in the differential success of egg and young between nest sites over the period considered.

Summarizing these results on breeding biology, Stock Doves have an extended breeding season in Britain, particularly in rural areas. Nests in suburban and urban areas are more likely to produce young than are rural nests and nests on arable land are more successful on average than nests in woodland or in coastal sites. Breeding success varies seasonally, in part dependent on latitude. During the 1950s a notable decrease in breeding success took place, particularly in arable and more intensively farmed habitats, and the breeding season shortened. During the subsequent recovery elms were heavily used for nesting and were relatively more successful as nest-sites than were other nest locations.

MORTALITY

Causes of death

The reported causes of death are tabulated in Table 21. The most common cause (which is more likely, though not significantly so, to happen to young birds) is shooting. Overall 71 per cent of deaths were attributed to this cause. This is probably an under-estimate since some of the 23 per cent 'found dead' category are likely to have died from shooting and without the cause being ascertained when found. Accidents and predation together account for only 6 per cent of all recoveries.

Timing of mortality

Figure 21 shows the monthly totals of young and of old Stock Doves recovered. The 'young birds' category includes all nestlings up to the start of their second August; the 'old birds' catergory contains all birds definitely older than this. A few individuals are omitted from the histogram as being of uncertain age. During the first five months of the breeding season shooting pressure is not as high as at other times of the year (44 out of 71 adults: 62 per cent) but is high for the last part of the breeding season (July, August and September 27 out of 33 adults: 82 per cent). Of the total of 95 adult Stock Doves reported shot 72 (76 per cent) had been killed at sometime during the extended breeding season. Such shooting creates a risk of eggs and young of these birds being left to perish in the nest. Figure 22 shows the cumulative frequency diagram for mortality to young Stock Doves up to the start of their second August of life. Allowance has been made here for those recoveries which can be expected to be reported later for birds ringed in recent years (Haldane 1955). Early season, mid-season and late breeding season nestlings are plotted separately. Rather heavy initial mortality experienced by the early brood youngsters during the late spring and early summer is followed by a [illegible] of good survival until mid-winter. This period sees the overall mortality/survival from all three parts of the breeding season running at much the same level. It is possible that later, in their second summer of life, early - fledged youngsters fare better than those reared in the middle or later part of the breeding season. First year survival rates (up to 1st August of the second year of life) are about 40 per cent.

Survival rate

Table 22 shows the mortality lattice for older birds and yielded survival estimates of 57.7 per cent on complete data and 52.7 per cent on incomplete data (See Haldane (1955) for details of 'complete' and 'incomplete' analyses). The latter estimate is sensitive to the possibility of one or two old birds from the period being recovered later. The two figures are not significantly different from the estimate of 53 per cent made by Murton (1966b) for the period up to 1964 (using both complete and incomplete data). Interestingly , the additional two old (9 and 13 years respectively) birds in the complete data used for the calculations here would completely account for the 4.7 per cent discrepancy between Murton's estimate and the 57.7 per cent quoted above. Investigations of annual variations in survival of Stock Doves are impossible since the data are too sparse. Even combining results by half-decade, which show some considerable differences (61 per cent in the best half-decade, 44 per cent in the worst), sample sizes are too small to show any significant differences. The data are given in Table 23 for the period 1950 - 1970. The survival figures were highest in the first and last periods. The first period included a time of high population level and the start of the decline in numbers, the last period was when recovery was well under way. Annual or half-decade figures were not produced for the 1970s as the allowance needed for birds already ringed but not yet recovered make the figures even more speculative.

DISPERSAL

Distant movements (more than 120 kilometres) are unusual amongst Stock Doves with only three birds ringed in Great Britain moving this far (one within Britain and one each to south-west France and north-east Spain). These are plotted in Figure 23 along with the only two Stock Doves ringed abroad and recovered in Britain (one from Finland and one from the Netherlands). All five birds had been ringed as nestlings. The seven movements of Stock Doves ringed as full grown birds and recovered more than 25 kilometres away within Britain are plotted in Figure 24. Two were of experimentally transported birds returning to (or towards) the point of capture. Of the other five records three show southern winter movements and two northern ones.

There are rather more nestling movements of similar distance. Winter recoveries are plotted in Figure 25 and summer ones in Figure 26. No evidence of oriented southward movement during the winter is apparent. Instead, the pattern seems to indicate relatively short distance dispersal by these birds. Young Stock Doves thus constitute the more mobile fraction of the population. However, this dispersal is rather limited: only 27 of 205 nestlings ringed and recovered were subsequently found more than 25 kilometres from their birthplace.

DISCUSSION

The analyses presented here indicate that the Stock Dove population in Britain has passed through three phases: (1) a period of apparently relative stability between 1930 and 1950 but for which we have rather poor information (2) a period of severe population depression and reduced breeding success in the 1950s, and (3) a period of recovery from this depression, with the recovery apparently still (to some extent) in progress.

The evidence for the 1950s population crash is quite substantial. All ringing indices examined (Figures 6-10) and the nest record totals (Figure 11) indicate a population reduction at that time and the data on distribution (Figures 1-3, Table 1) also point to a contraction of range during this period. Our evidence indicates that nest success was badly reduced at this time, particularly because of increased egg failure but including some reduction in nestling success as well (Figure 19, Table 18). Nevertheless, it is also worth noting the lower survival rates for adults in the late 1950s and early 1960s (Table 23). Such trends can obviously be attributed to the impact of organochlorine residues on this seed-eating bird. This explanation is also in accord with the differential reduction in nest totals recorded from agricultural (especially arable) habitats and increased representation of coastal and woodland habitats (Figure 13) and of suburban and urban habitats (Figure 12). Apart from their direct effects on reproduction and survival, organochlorine chemicals are likely to interfere with egg production most severely at the start of the breeding season, when conditions may still be marginal for breeding. Such an effect is consistent with the delay in the breeding season suggested by Figures 17 and 18.

Several indicators (Tables 6-9) point to the standard clutch size of two eggs as being the most successful. This is typical of doves but results in the number of breeding attempts per season becoming the determinant of annual productivity, particularly when, as here, egg losses are the major channel of failure (Table 9). The Stock Dove correspondingly has a very extended breeding season, with eggs or young in the nest from perhaps late February through October (Figure 15, Table 4). These are, however, seasonal variations in breeding success: March and June-July appear to be the most successful months for breeding (Tables 15-17) but the causes of nest failures vary seasonally also, egg loss being higher in April and May and in July than at other times and nestling losses being lowest between May and July (Table 17). [illegible] also [illegible] with latitude (Table 5).

Stock Doves are predominantly lowland birds of agricultural and other park-like habitats (Tables 2,3), through a significant proportion of nest record cards for the species come from woodland (but not coniferous woods). In keeping with this, breeding success on arable land and in other agricultural habitat is generally higher than in woodland and coastal habitats (Tables 11-13). Despite this, the incidence of egg losses is greater in rural areas than in suburban and urban areas. It is possible that re-nesting is easier in rural areas than in built-up areas because of the greater availibility of seeds through the year, so that birds can repeatedly nest until successful (cf.Foster 1974). It is not clear, though, whether the breeding season in rural areas is prolonged relative to urban areas (Figure 16) of necessity, to ensure the birds produce enough young to replace themselves each year, or opportunistically, to exploit autumn cereal crops available in rural but not in urban areas.

Stock Doves in Britain are clearly rather sedentary, though with young birds moving more than adults (Figures 24-26); there is little interchange with birds from Continental Europe (Figure 23). In such conditions the size of the population is determined largely by the balance of birth and death process. First year survival averages about 40 per cent, adult survival about 53-57 per cent (Table 22), requiring about three fledglings per pair for population stability. The major source of adult mortality is due to birds being shot, with a large proportion of the deaths taking place during the extended breeding season (Table 21, Figure 21). A proportion of these deaths must result in eggs or young dying in a deserted nest.

How much margin for population increase do these figures leave Stock Doves? Ignoring nests whose outcome was unknown, some 337 nests were noted as successful and 883 as having failed, an average of 38.2 per cent successful over the period 1942-1980. For three breeding attempts each year this would yield an average of 2.3 young annually, rather below the 3 young suggested above for population balance. But the 38 per cent success ratio is undoubtedly an under-estimate of the true situation since a) failed nests are more likely to be recorded than successful ones b) this figure includes the reduced success of the 1950s and c) birds losing eggs or small young probably undertake a replacement nest attempt. It thus seems likely that Stock Doves can continue to increase in population size on the basis of current birth-death balances, though the margin is unlikely to be great. On this basis the reduction in adult survival during the late 1950s and early 1960s would have contributed significantly to the population collapse of that time.

The CBC index for Stock Doves (Figure 4) shows that the species has increased since 1964 in the country as a whole, with only the slightest suggestion of any slowing down of increase in Southern England (Table 5). The various data presented in Figures 6-11 vary in their assessment of the present population levels vis-a-vis those prevailing before 1950, but make it unlikely that current densities in the main part of the birds range are much below their 1940s level. However, the analysis of the pre-1951 and the post-1967 distributions (Figure 2) indicate that distribution in recent years is still significantly different from that before the crash. Similarly, the analysis of within-habitat distributions (Figure 14) indicates the recovery is still (though only slightly so) incomplete. It is not clear to what extent this latter is due to changes in the availability of elms as nest-sites following the spread of Dutch elm disease. Elms were clearly extensively used in the late 1960s when breeding success there was temporarily elevated above that prevailing in other sites (Figure 20, Table 20) but both their use and their relative advantage for breeding seem to have declined in recent years. Whether this will restrict the further recovery of the population in any way remains to be seen.

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Table 1. Regional origin of nest record cards received in different decades.[1]

Region	1942-1949	1950-1959	1960-1969	1970-1979	1980
Southern England	59 (31.4)	177 (30.8)	101 (19.7)	258 (19.4)	28 (16.8)
Western England	25 (13.3)	26 (4.5)	122 (23.8)	278 (19.8)	25 (15.0)
Eastern England	76 (40.4)	277 (48.2)	158 (30.8)	477 (34.0)	60 (35.9)
Northern England	19 (10.1)	63 (11.0)	103 (20.1)	280 (20.0)	34 (20.4)
Scotland	1 (0.5)	16 (2.8)	14 (2.7)	48 (3.4)	6 (3.6)
Wales	8 (4.2)	15 (2.6)	15 (2.9)	61 (4.4)	14 (8.4)
Totals	188	574	513	1402	167

[1] This analysis is based on all Stock Dove cards with nest-site data, irrespectiv of the consistency of the visit data. The totals here thus do not tally with those analysed elsewhere in the report.

Table 2. Distribution of Stock Dove nests amongst rural, suburban and urban sites.

Sites	Number	(per cent)
Rural	2562	(87.9)
Suburban	98	(3.4)
Urban	14	(0.5)
Other[a]	242	(8.2)

[a] Not categorised to rural/suburban/urban class by the observer

Table 3 Month of ringing of Stock Dove nestlings subsequently recovered.

	March	April	May	June	July	August	September	Oct.
Total	1	17	27	41	43	44	29	5
Percentage	0.5	8.2	13.0	19.8	20.8	21.3	14.0	2.4

Total number recovered 207

Table 4. Latitudinal variation in seasonal distribution of ringing date for birds ringed as nestlings and subsequently recovered.

Latitude °N	March-April N	March-April %	May-June N	May-June %	July-August N	July-August %	September-October N	September-October %	Total
55.0+	5	23.8	11	52.4	5	23.8	1	4.8	21
54.0-54.9	1	4.2	9	37.5	12	50.0	2	8.3	24
53.0-53.9	6	11.1	17	31.5	24	44.4	7	13.0	54
52.0-52.9	0	0.0	10	28.6	16	45.7	9	25.7	35
51.0-51.9	2	4.9	7	17.1	20	48.8	12	29.3	41
50.0-50.9	4	12.5	14	43.8	11	34.4	3	9.4	32
Totals	18	8.7	68	32.8	87	42.0	34	16.6	207

Table 5. Clutch size distribution in Stock Dove nests in various habitat categories.

Habitat	1		2		3		4		Total
	N	%	N	%	N	%	N	%	
Rural	37	4.8	700	90.4	23	3.0	14	1.8	774
Suburban/urban	4	11.4	30	85.7	1	2.8	0	0.0	35
Other	1	2.9	32	94.1	1	2.9	0	0.0	34
Total	42		762		25		14		843

Table 6. Maximum numbers of young recorded in Stock Dove nests in various habitats.

Habitat	0 N	0 %	1 N	1 %	2 N	2 %	3 N	3 %
Rural	1304	(50.9)	223	(8.7)	1032	(40.3)	3	(0.1)
Suburban-urban	63	(48.5)	7	(5.4)	58	(44.6)	2	(1.5)
Other	117	(54.2)	18	(8.3)	80	(37.0)	1	(0.5)
Total	1184	(51.2)	248	(8.5)	1170	(40.1)	6	(0.2)

Table 7. Stock Dove nesting-success in rural and in suburban-urban environments[a] during the 1950's and at other times.

		1950-1959		All other years	
		N	(%)	N	(%)
Nests successful	Rural	39	(6.83)	257	(12.91)
	Suburban-urban	6	(28.57)	14	(15.38)
Nest failure	Rural	232	(40.63)	592	(29.73)
	Suburban-urban	3	(14.28)	19	(20.88)
Egg stage failure	Rural	96	(16.81)	245	(12.31)
	Suburban-urban	1	(4.76)	6	(6.59)
Nestling stage failure	Rural	57	(9.98)	149	(7.48)
	Suburban-urban	0	(0.00)	6	(6.59)
Unknown outcome	Rural	300	(52.54)	1142	(57.36)
	Suburban-urban	12	(57.14)	62	(68.13)

Notes

[a] Nests from areas unclassified or classified as rural-suburban are omitted from this table.

[b] As percentage of all rural (or suburban-urban) nests for the period.

Table 8. Number of young produced from different clutch siz

Number of young	Clutch size 1 N	%	Clutch size 2 N	%	Clutch size 3 N	%	Clutch size 4 N	%
0	29	(69.0)	262	(34.4)	13	(52.0)	12	(8
1	13	(31.0)	63	(8.3)	2	(8.0)	0	(0.
2	0	(0.0)	437	(57.3)	8	(32.0)	1	(7
3	0	(0.0)	0	(0.0)	2	(8.0)	1	(
Total	42		762		25		14	

Table 9. Incidence of success and failure in relation to clutch size in Stock Dove. Percentages are given in brackets.

Outcome	Clutch size 1	2	3	4
Failure - unknown stage	4 (9.52)	65 (8.5)	1 (4.0)	3 (21.4)
young stage	2 (4.76)	107 (14.0)	3 (12.0)	0 (0.0)
egg stage	12 (28.57)	99 (13.0)	8 (32.0)	5 (35.7)
Successful	0 (0.0)	129 (16.9)	2 (8.0)	0 (0.0)
Outcome unknown	24 (57.14)	362 (47.5)	11 (44.0)	6 (42.8)
Total	42	762	25	14

Table 10. Nest success and failure in rural and suburban-urban environments.

	Rural		Suburban-urban		(	
	N	%	N	%	N	
Success	296	11.6	20	14.5	21	
Failure	824	32.3	29	21.0	30	[illegible]
Egg stage	341	13.3	11	8.0	8	3.
Nestling stage	206	8.0	7	5.1	10	4.
All stages	824	32.2	29	21.0	30	13.
Unknown outcome	1442	56.3	89	64.5	165	76.

χ^2 for success versus failure = 9.75, d.f. = 2, $P < 0.01$

Table 11. Variation in clutch size in Stock Dove nests in various habitats

	1		2		3	
	N	%	N	%	N	%
Agricultural						
Arable	1	3.0	32	97.0	0	
Pasture	1	2.2	40	87.0	4	
Mixed	1	2.7	35	94.6	1	2.7
Other	12	4.8	219	87.6		4.8
Woodland						
Broadleaved	7	10.6	58	87.9	0	0.0
Coniferous/ mixed	4	7.7	46	88.5	2	3.8
Unspecified	2	6.4	28	90.3	0	0.0
Coastal	2	2.7	71	94.7	0	0.0
Other	12	4.7	233	92.1	7	2.8

Table 12. Variation in brood size (maximum c[illegible]oung) in S[illegible]

Doves in relation to nesting habitat.

	Number of young recorded					
	1		2		3	
Habitat	N	%	N		N	
Agricultural						
Arable	8	11.3	63	88.2	0	0.
Pasture	17	19.5	69	79.3	1	1.2
Mixed	12	16.0	63	84.0	0	0.0
Other	60	15.4	328	84.3	1	0.2
Woodland						
Broad-leaved9	19	18.6	83	81.4	0	0.0
Coniferous/mixed	11	16.9	53	81.5	1	1.6
Unspecified	8	17.0	38	80.9	1	2.1
Coastal	20	22.5	69	77.5	0	0.
Other	93	18.6	40.4	81.0	2	0.4

Table 13. Incidence of nestling success and failure in various habitats.

Habitat	Nest failure at Egg stage N	%	Nestling stage N	%	All stages N	%	Nest success N	%	Unknown outcome N	%	Total
Agricultural											
Arable	14	10.7	6	4.6	35	26.7	21	16.0	75	57.2	131
Pasture	27	15.5	10	5.7	59	33.9	22	12.6	93	71.0	174
Mixed	18	11.6	9	5.8	45	29.0	16	10.3	94	60.6	155
Other	100	27.0	69	9.3	251	33.8	101	13.6	391	52.6	743
Woodland											
Broad leaved	34	14.0	17	7.0	72	29.6	17	7.0	154	63.4	243
Coniferous/mixed	21	14.5	14	9.6	54	37.2	15	10.3	76	52.4	145
Unspecified	13	11.3	3	2.6	28	24.3	11	9.5	76	66.1	115
Coastal											
Mainland	20	15.5	10	7.8	50	38.8	10	7.8	69	53.5	129
Stacks/islands	8	12.3	2	3.1	14	21.5	2	3.1	49	75.4	65
Other											
Miscellaneous	105	10.3	83	8.2	275	27.1	122	12.0	6.9	60.9	1016

Table 14. Seasonal variation in clutch size in Stock Doves

Clutch size	Mar.		Apr.		May		Jun.		Jul.		Aug.	
	N	%	N	%	N	%	N	%	N	%	N	%
1	2	5.1	5	3.5	7	6.2	7	6.3	1	1.1	3	3.6
2	37	94.9	133	94.3	103	91.1	101	90.2	79	87.8	74	89.1
3	0	0.0	2	1.4	1	0.9	4	3.6	9	10.0	4	4.8
4	0	0.0	1	0.7	2	1.8	0	0.0	1	1.1	2	2.4
	39		141		113		112		90		83	

Table 15. Seasonal distribution of maximum contents of young per nest in Stock Doves.

	Number of young						
	1		2		3		
Month	N	%	N	%	N	%	Total
March	4	10.5	34	89.5	0	0.0	38
April	15	13.8	94	86.2	0	0.0	10[illegible]
May	19	20.0	76	80.0	0	0.0	[illegible]
June	10	10.4	84	87.5	2	2.1	9[illegible]
July	10	12.2	72	87.8	0	0.0	[illegible]
August	14	16.3	72	83.7	0	0.0	[illegible]

Table 16. Seasonal distribution of brood-size for Stock D...

subsequently recovered.

Period	Brood size 1		2		3		Tc
	N	%	N	%	N	%	
March-May	2	(5.9)	32	(94.1)	0	(0.0)	3
June-July	5	(7.6)	57	(86.4)	4	(6.1)	6
August-October	4	(6.6)	56	(91.8)	1	(1.6)	6
Total	11	(6.8)	145	(90.1)	5	(3.1)	161

Table 17. Seasonal variation in nest success in Stock Doves

	March		April		May		June		July	
	N	%	N	%	N	%	N	%	N	%
Successful	18	(31.0)	35	(19.7)	24	(15.2)	29	(19.9)	28	(21
Failed										
Egg stage	3	(5.2)	31	(17.4)	26	(16.4)	16	(11.0)	9	(
Nestling stage	4	(6.9)	31	(17.4)	18	(11.4)	13	(8.9)	9	(
All stages	10	(3.9)	76	(29.8)	54	(21.2)	41	(16.1)	37	(14
Outcome unknown	30	(51.7)	67	(37.6)	80	(50.6)	76	(52.0)	63	(49

Table 18. Nest success of Stock Dove in different decades

Decade	Failed[a]						Successful	
	At egg stage		At nestling stage		All failures			
	N	%	N	%	N	%	N	%
1942-49	7	3.7	12	6.3	28	14.7	28	14.
1950-59	103	17.1	57	9.5	242	40.2	45	[illegible]
1960-69	58	10.5	32	5.8	147	26.5	50	[illegible]
1970-79	174	12.3	109	7.7	415	29.4	190	13
1980	23	13.8	13	7.8	56	33.6	24	[illegible]
Overall	360	12.3	223	7.6	883	30.3	337	[illegible]

a According to observer's final assessment of the success of the nes

For a further total of 1696 nests (58.2 per cent) no assessment wa [illegible] sil

Table 19. Brood size distribution by decade derived from ringing of nestling Stock Doves subsequently recovered.

Period	Brood size 1		Brood size 2		Brood size 3		Total	Size not recorded
	N	%	N	%	N	%		
1909-1939	0	(0.0)	15	(100.0)	0	(0.0)	15	5
1940-1949	0	(0.0)	15	(93.8)	1	(6.2)	16	6
1950-1959	2	(5.1)	37	(94.9)	0	(0.0)	39	26
1960-1969	5	(14.7)	26	(76.5)	3	(8.8)	34	6
1970-1980	4	(7.0)	52	(91.2)	1	(1.8)	57	3
Total	11	(6.8)	145	(90.1)	5	(3.1)	161	46

Table 20. Temporal changes in relative breeding success of Stock Doves nesting in elm trees and in other sites. * $P < 0.05$.

Nest success	Nest site	1942-49	1950-59	1960-69	1970-79	1980	Totals
Successful	Elms	3	2	14	15	0	34
	All other sites	25	43	36	175	24	303
Failure	Elms	2	14	22	35	5	78
	All other sites	26	223	125	380	51	805
	χ^2	0.22	0.15	4.24*	0.05	2.29	0.46
Egg stage failure	Elms	1	5	7	13	1	27
	All other sites	6	93	51	161	22	333
Nestling stage failure	Elms	0	2	7	9	2	20
	All other sites	12	55	25	100	11	203
	χ^2	0.75 (1942-59 combined)		1.51	.06	1.32	0.40

Table 21. Reported recovery methods for ringed Stock Doves.

Age at recovery	Up to 1 August of second year		Older		Unknown		Total	
	N	%	N	%	N	%	N	%
Shot[a]	90	72.5	95	69.8	12	70.6	197	71
Found dead[b]	28	22.6	30	22.0	5	29.4	63	2
Accidents:								
Road traffic	1	0.8	3	2.2			4	
Railway	2	1.6					2	
Wires			2	1.5			2	
In buildings[c]	2	1.6	2	1.5			4	1
Predation:								
Cat			2	1.5			2	7
Dog			1	0.7			1	[illegible]
Sparrowhawk	1	0.8					1	[illegible]
Tawny Owl			1	0.7			1	0.4
Totals	124		136		17		277	

Recoveries for which the circumstances are wholly unknown have been omitted.

a Two birds reported as 'hunted' and a single from a cage trap are included

b One young bird reported as 'starved' and leg and ring only reported of one older bird.

c The two older birds were found in chimneys - potential breeding sites.

Table 22. Mortality lattice for Stock Doves using August 1st as starting date of mortality year.

Year ringed *	Total	Age at death											
		1	2	3	4	5	6	7	8	9	10	11	
1913-66 (Complete data)	88	37	26	10	6	4	1	.	1	2	.	.	
1967	4	1	3	.	.	.	.	.	.	.	.	.	.
1968	5	.	4	.	1	.	.	.	.	.	.	.	.
1969	4	2	1	.	1	.	.	.	.	.	.	.	
1970	3	1	1	1	.	.	.	.	.	.	.		
1971	7	6	1	.	.	.	.	.	.	.			
1972	1	.	.	.	.	1	.	.	.				
1973	2	1	1	.	.	.	.	.					
1974	3	1	.	.	1	.	1						
1975	4	2	1	.	1	.							
1976	6	4	1	.	1								
1977	1	1	.	.									
1978	2	.	2										
1979	4	4											
Totals for 1967-79	46	23	15	1	5	1	1	.	.	.	.	.	.

This lattice includes all birds ringed as full-grown, out of the nest, which have survived through one August 1st subsequent to being ringed. It also includes nestlings and juveniles which have survived past the August 1st of their second calendar year of life: for such birds the actual ringing year will be on earlier than that shown in the initial column (1). For full-grown birds the actual year of ringing runs from, for example 1.8.70 to 31.7.71 for a bird entered as 1971.

Survival estimates are as follows:

Complete data	57.7%	s.e. 3.4%
Incomplete data	52.7%	s.e. 6.0%

Table 23. Adult survival by half-decade between 1950-1970.

	Total years survived	Total birds dying	Annual survi- %
1950-1954	31	20	61
1955-1959	22	21	51
1960-1964	14	18	44
1965-1969	22	15	59
Pooled	89	74	55

Figure 1

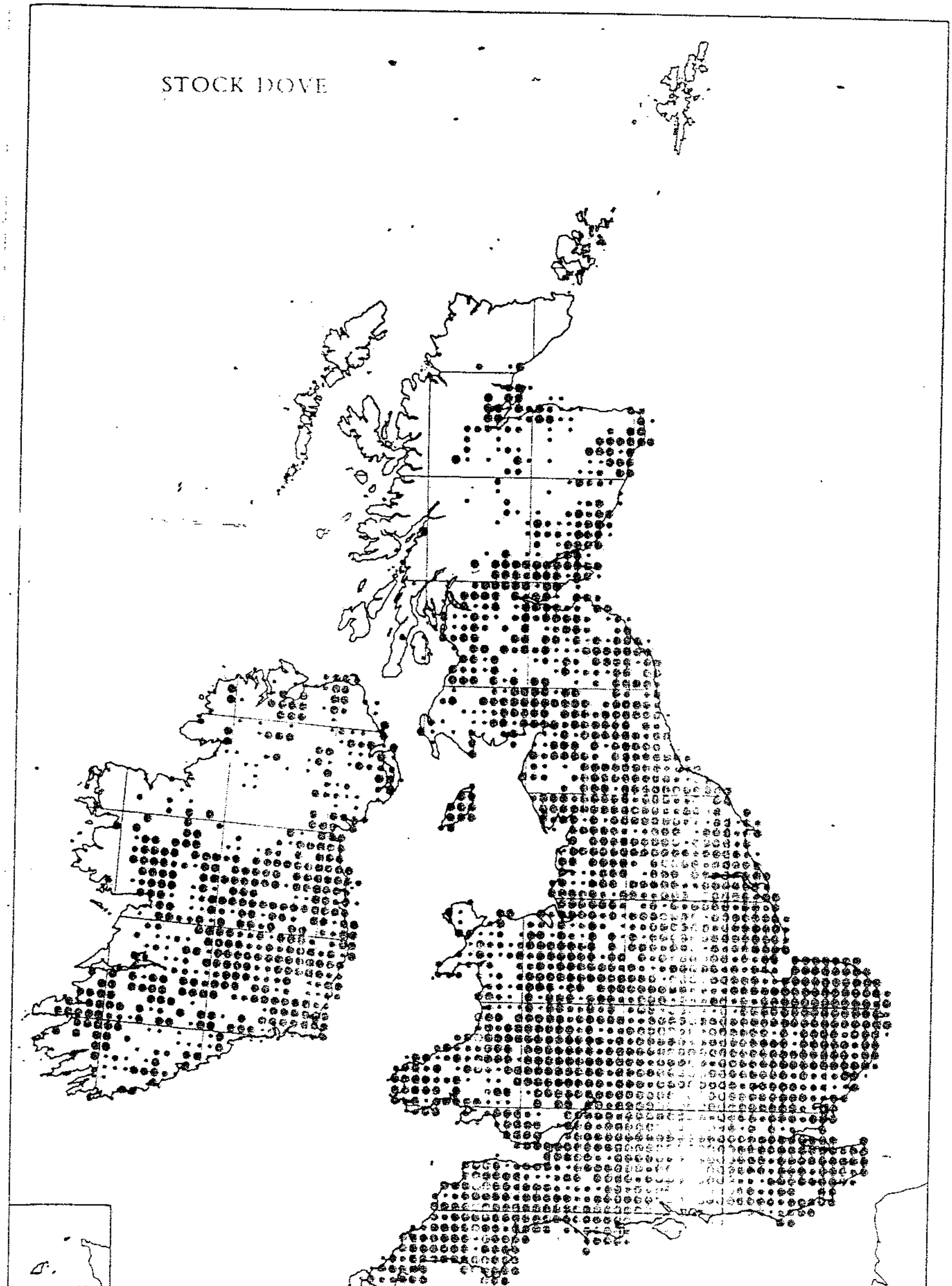


Figure 2a. Areas of ringing of Stock Doves (all ages) marked up to and including 1950.

Star marks centre of gravity of ringing sites (in degrees). Each area, bounded by individual degree lines of lattitude and by even numbered lines of longitude, covers an area of about 15,000 km^2.

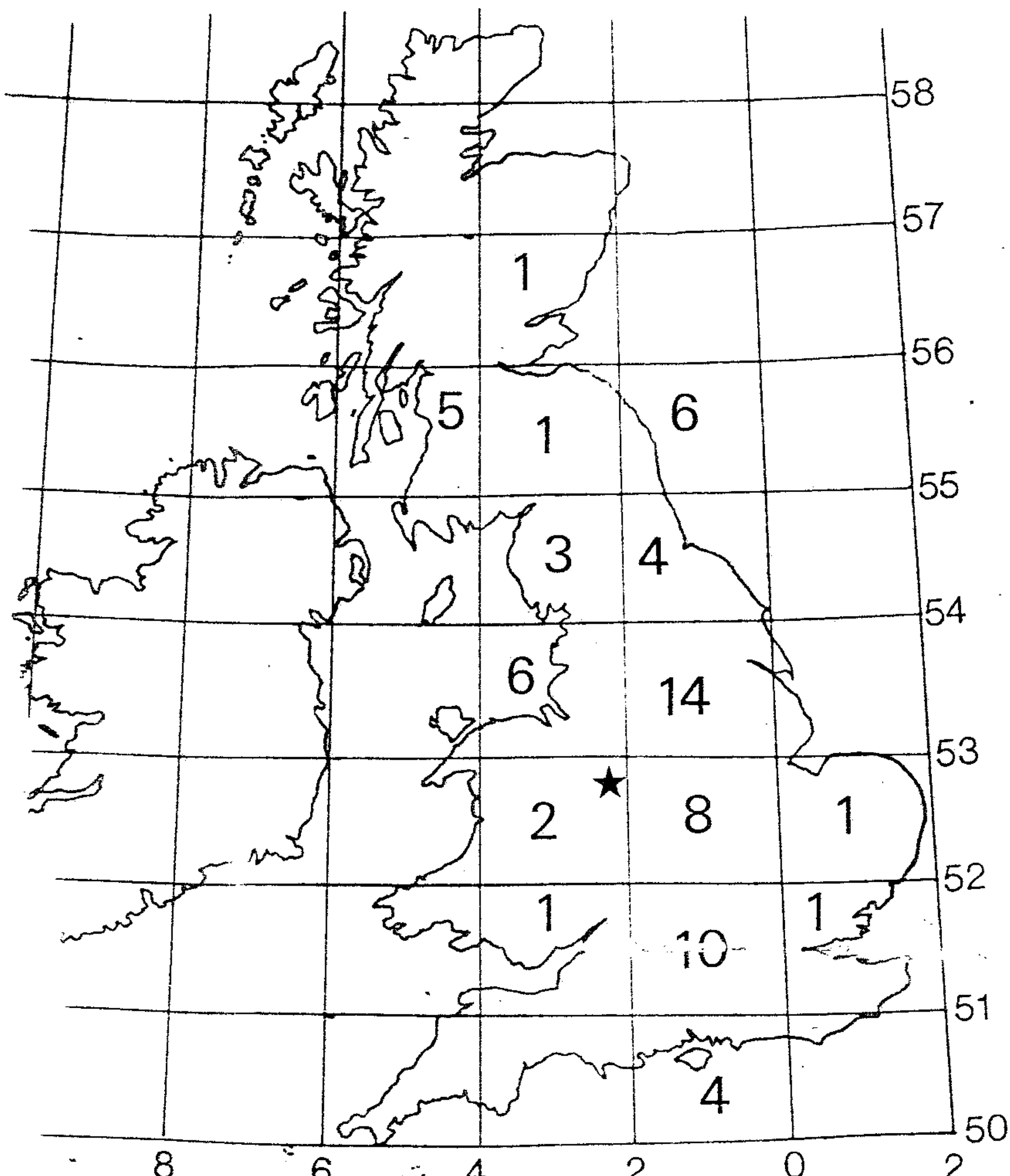


Figure 2b. Areas of ringing of Stock Doves (all ages) from 1951 to 1967 inclusive.

The star marks the centre of gravity of ringing sites (in degrees). Each area is bounded by individual lines of lattitude and by the even numbered lines of longitude, each covers about 15,000 km^2.

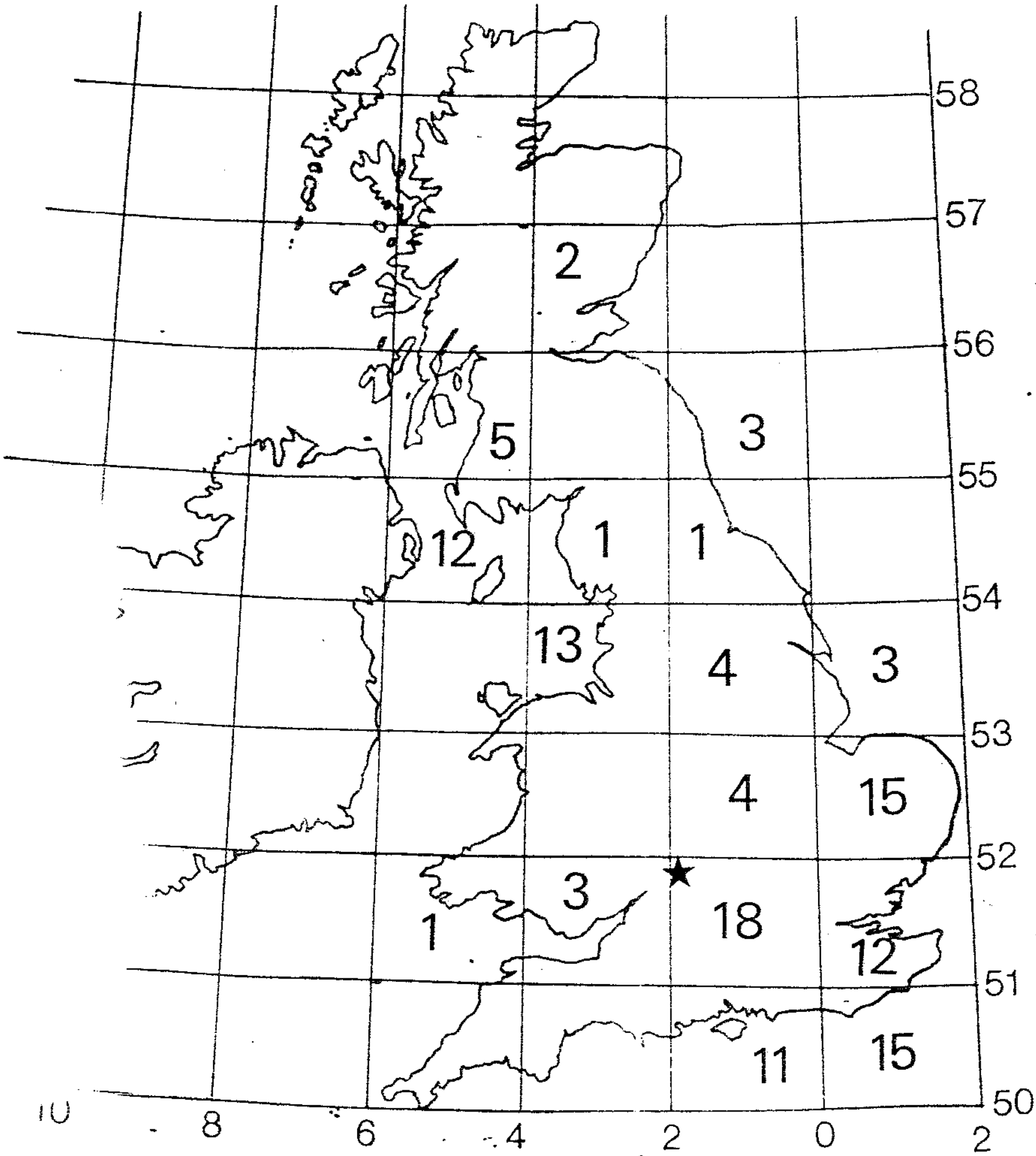
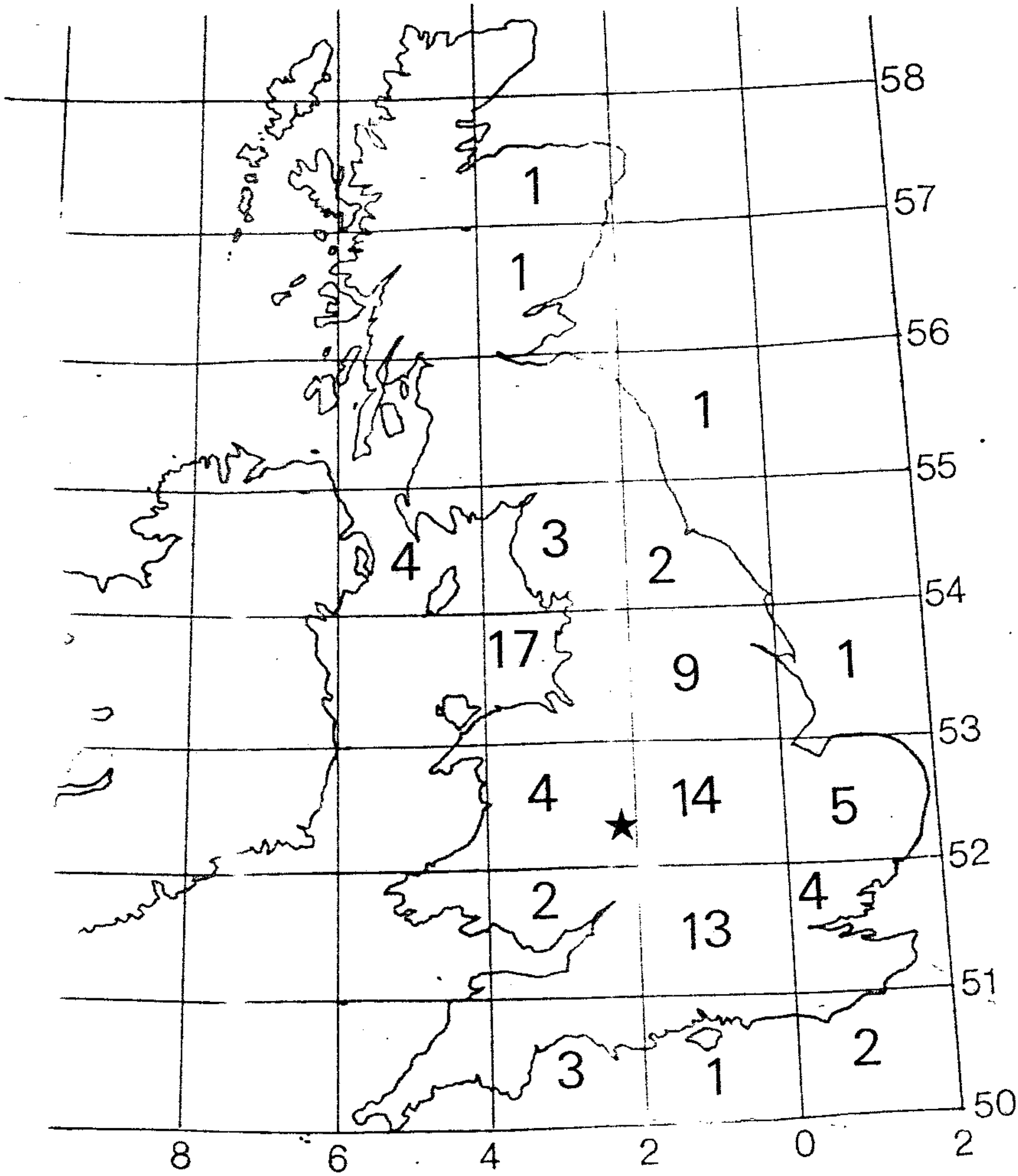


Figure 2c. Areas of ringing of Stock Doves (all ages) from 1968 and later years.

The star marks the centre of gravity of ringing sites (in degrees). Each rectangle is bounded by individual degree lines of lattitude and by even numbered lines of longitude, each covers about 15,000 km^2.



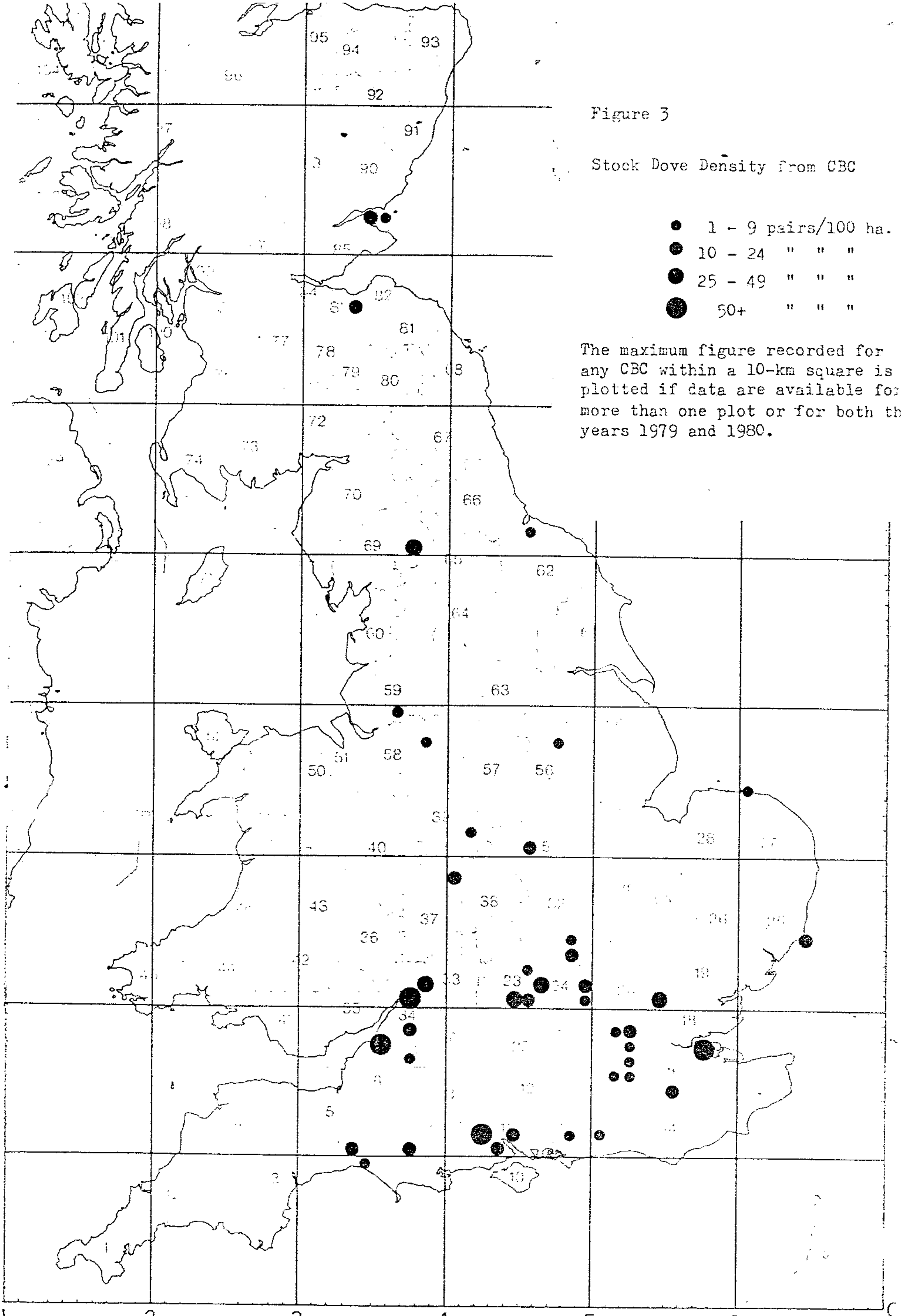


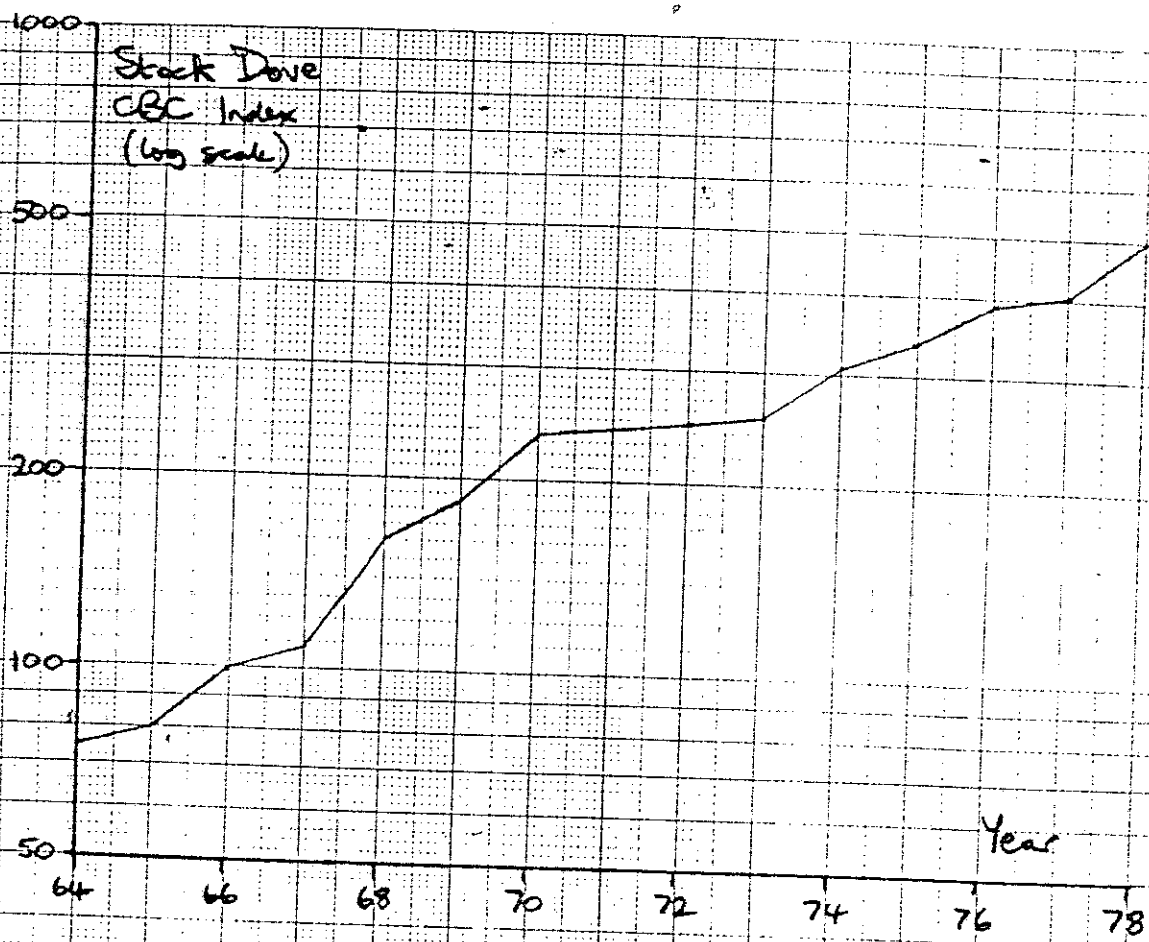
Figure 3

Stock Dove Density from CBC

- 1 - 9 pairs/100 ha.
- 10 - 24 " " "
- 25 - 49 " " "
- 50+ " " "

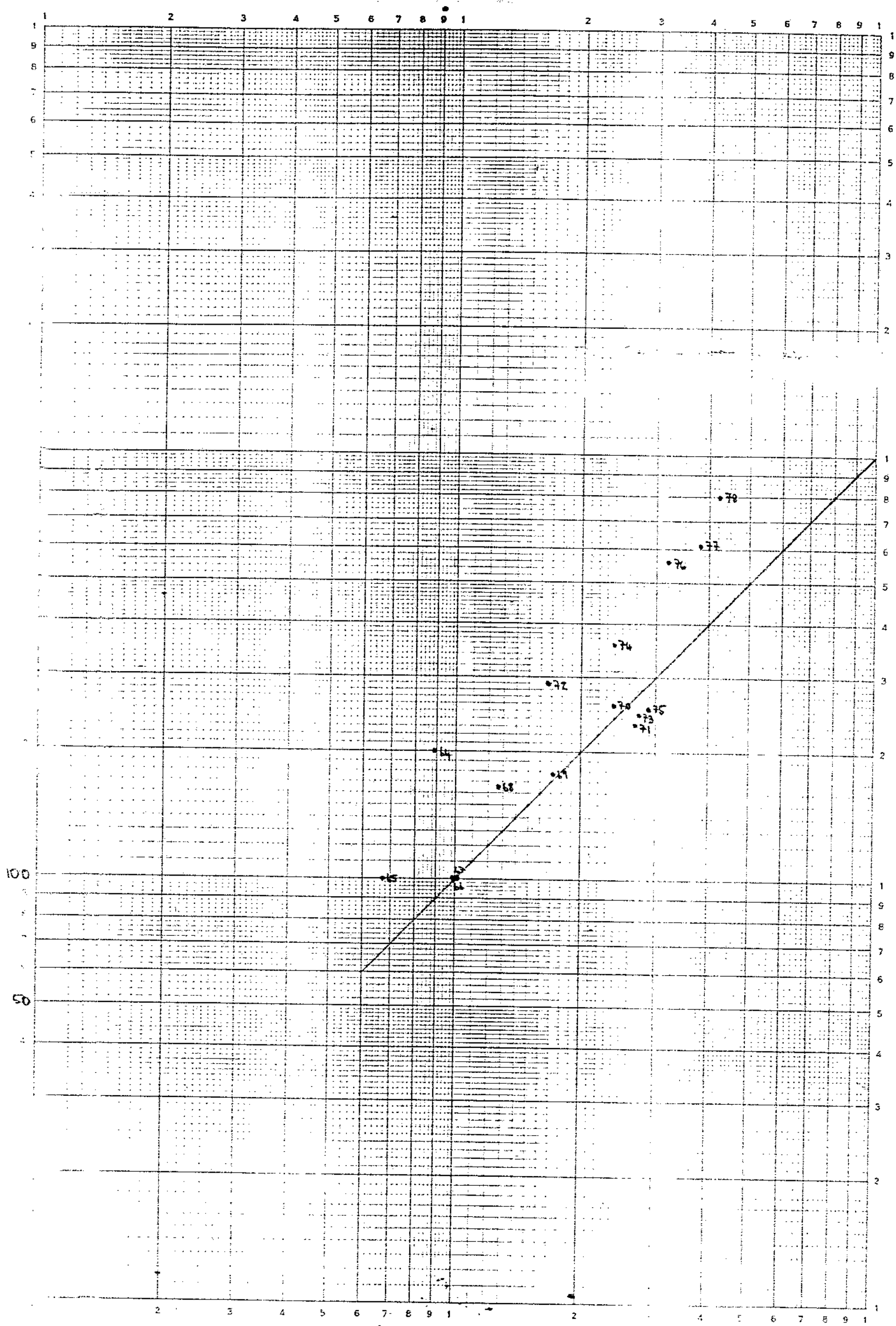
The maximum figure recorded for any CBC within a 10-km square is plotted if data are available for more than one plot or for both the years 1979 and 1980.

Figure 4



Stock Dove
CBC Index
(log scale)
1000
500
200
100
50
64
66
68
70
72
74
76
78
Year

Figure 9.



CBC Index Southern England

Figure 6. Number of pulli Stock Doves ringed annually 1000 pulli ringed nationally 1931 to 1980

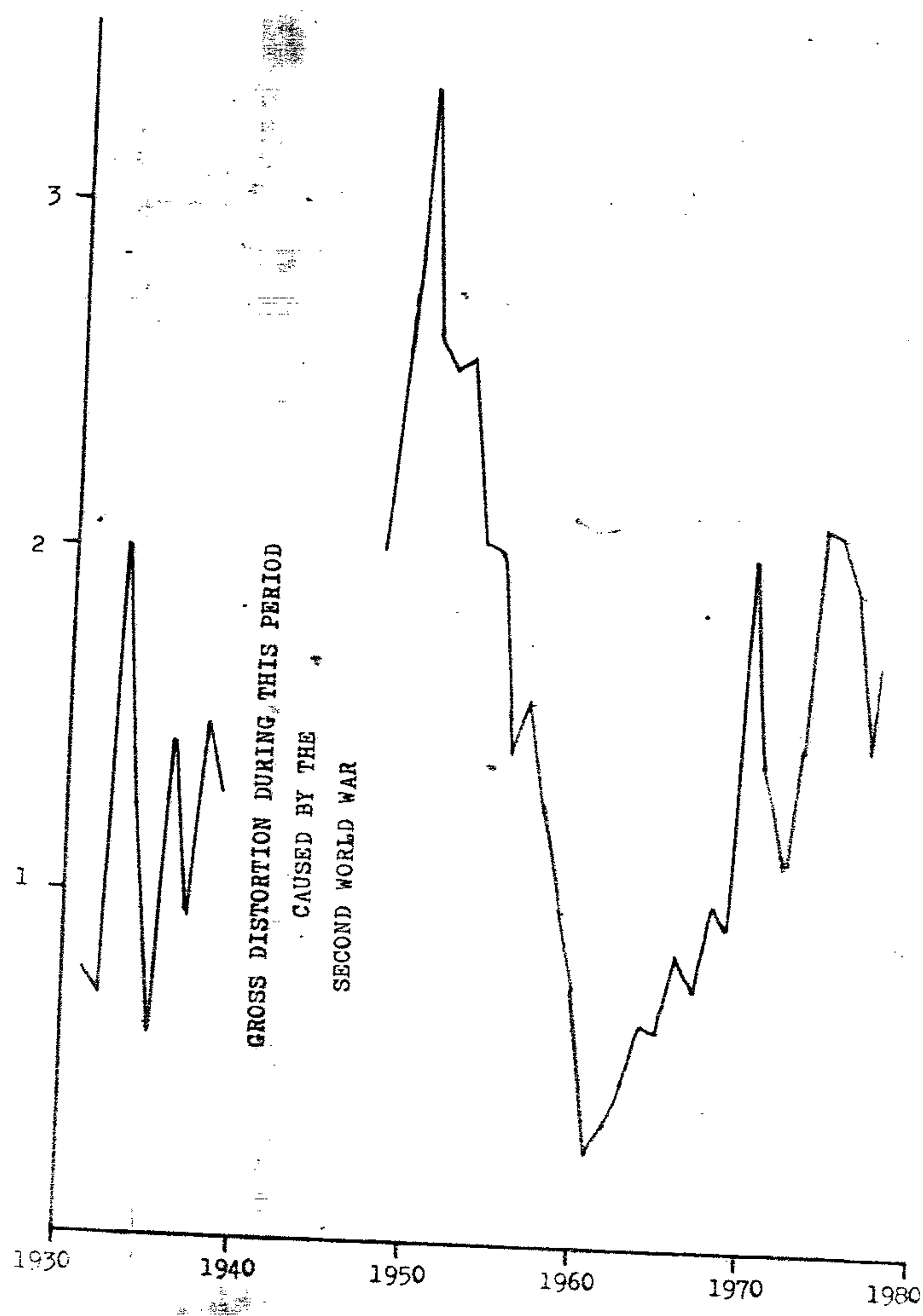


Figure 7. Annual ratio Stock Dove to Tawny Owl pulli ringed 1931 to 1980

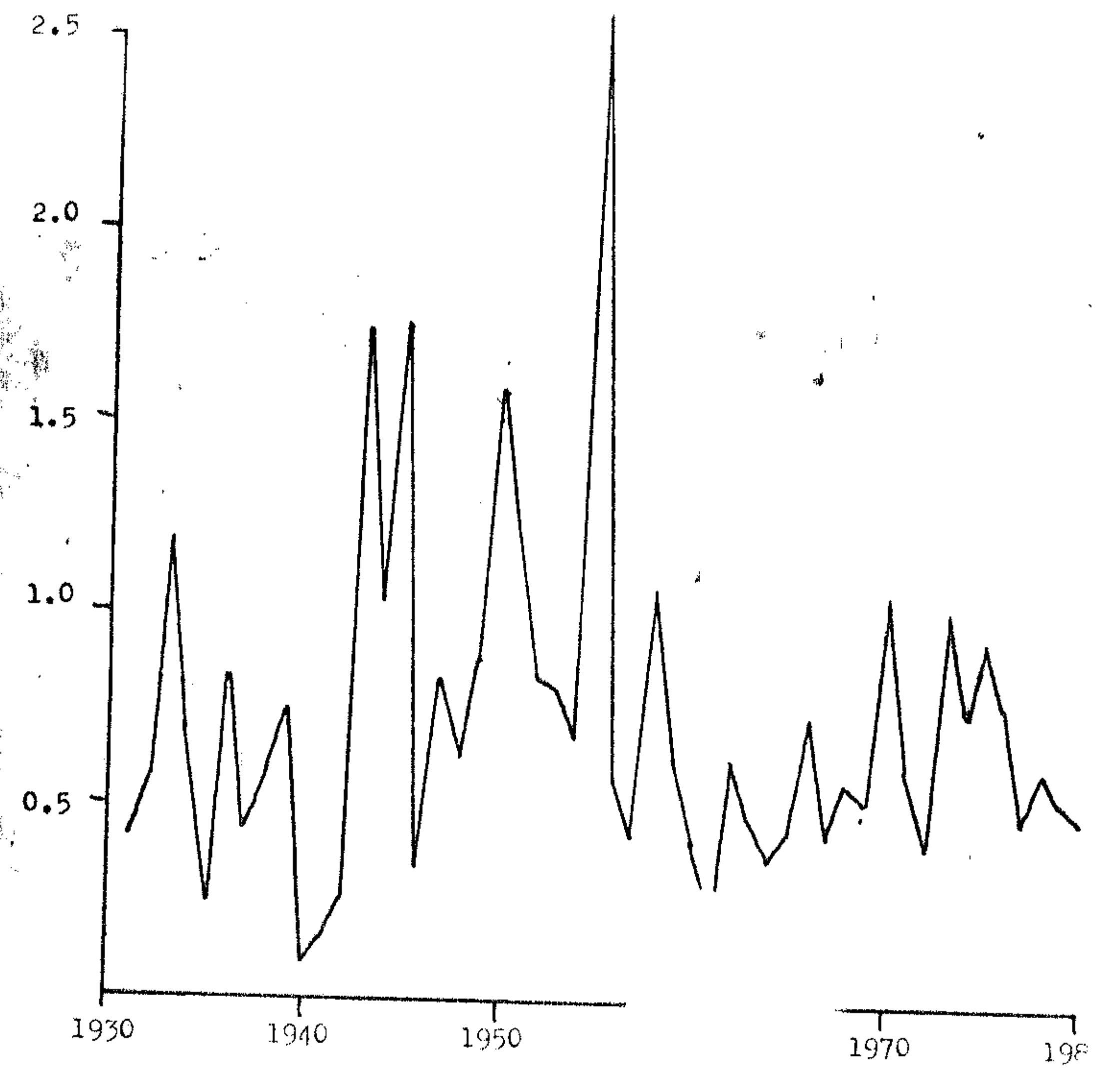


Figure 8. Annual ratio Stock Dove to Woodpigeon pulli ringed 1931 to 1980

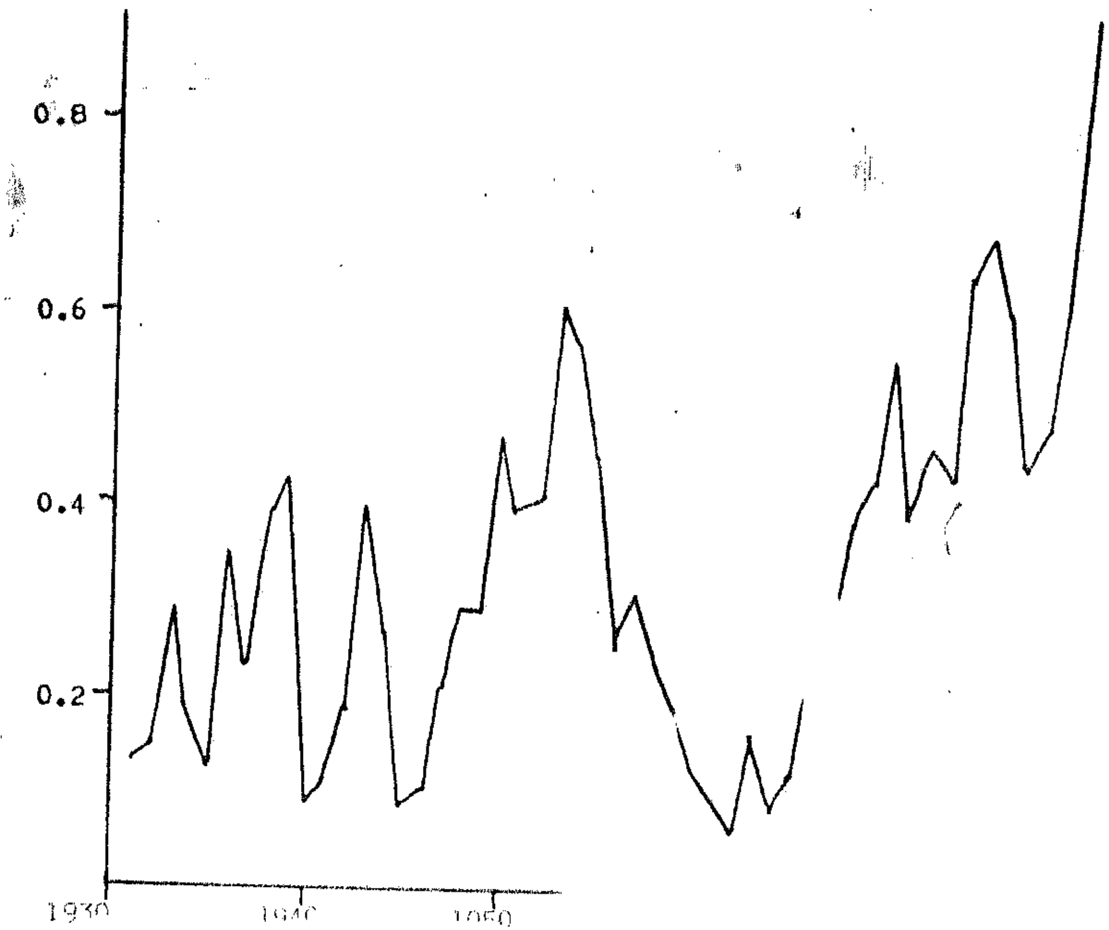


Figure 9. Annual ratio Stock Dove to Dunnock pulli ringed 1931 to 1980

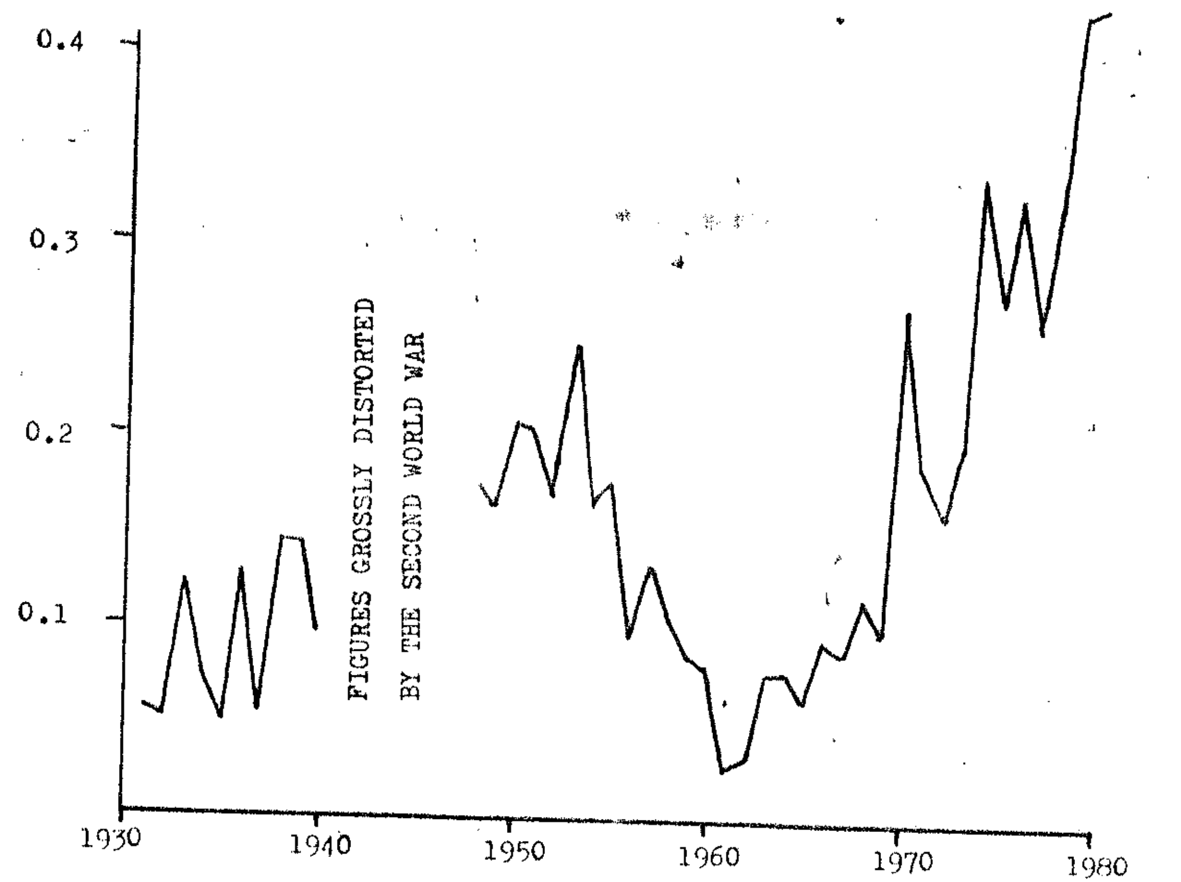


Figure 10. Annual ratio Stock Dove to Mistle Thrush pulli ringed 1931 to 1980

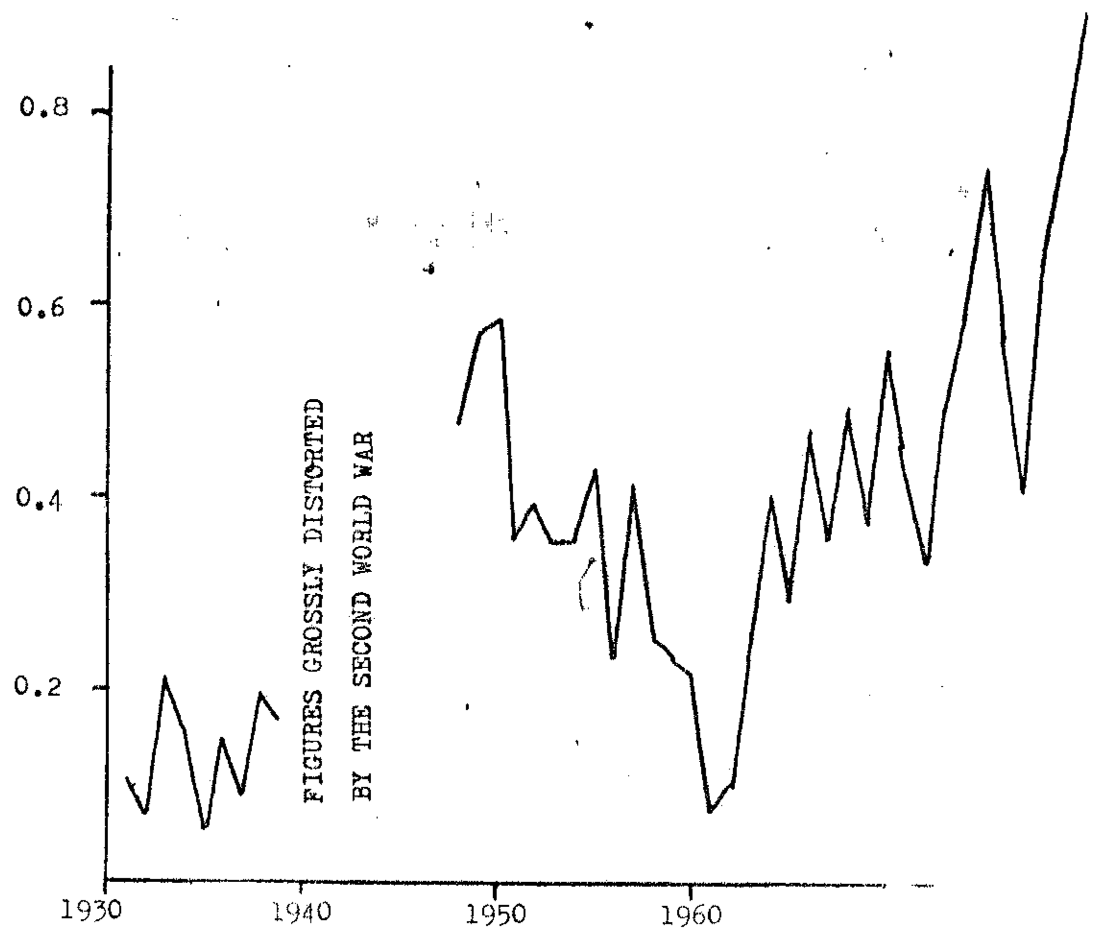
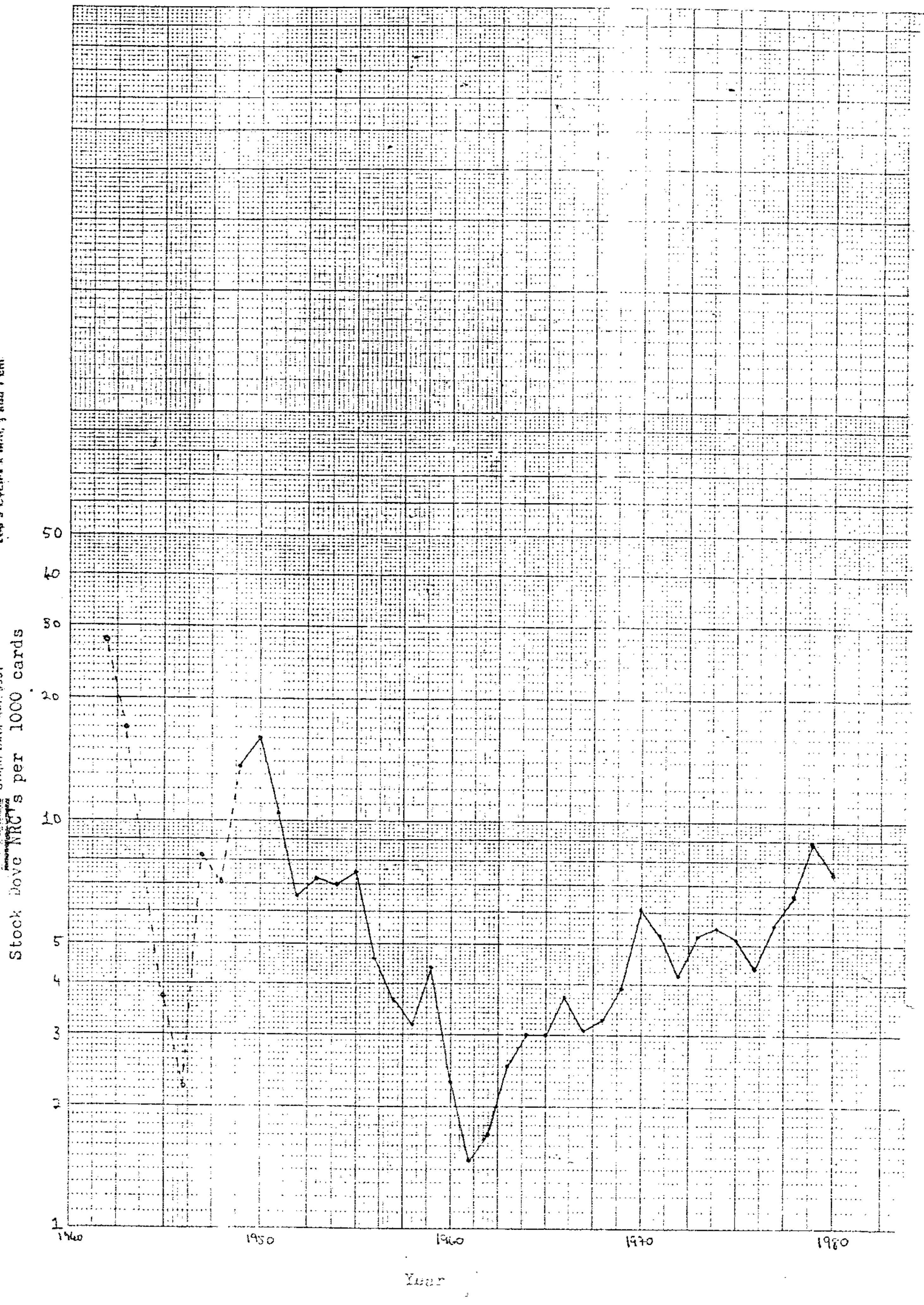


Figure 11


Stock Dove NRC's per 1000 cards
50
40
30
20
10
5
4
3
2
1
1940
1950
1960
1970
1980
Year

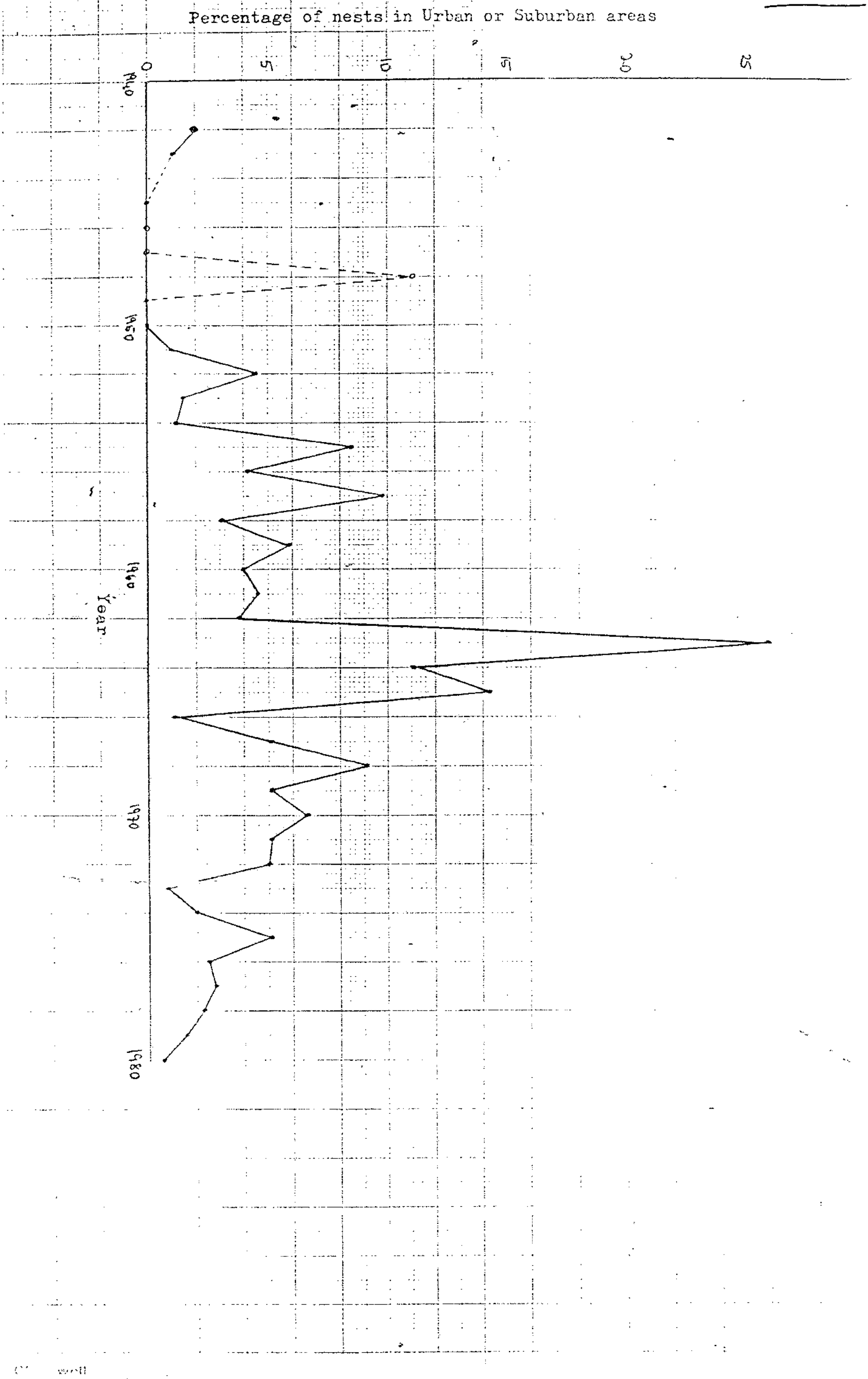
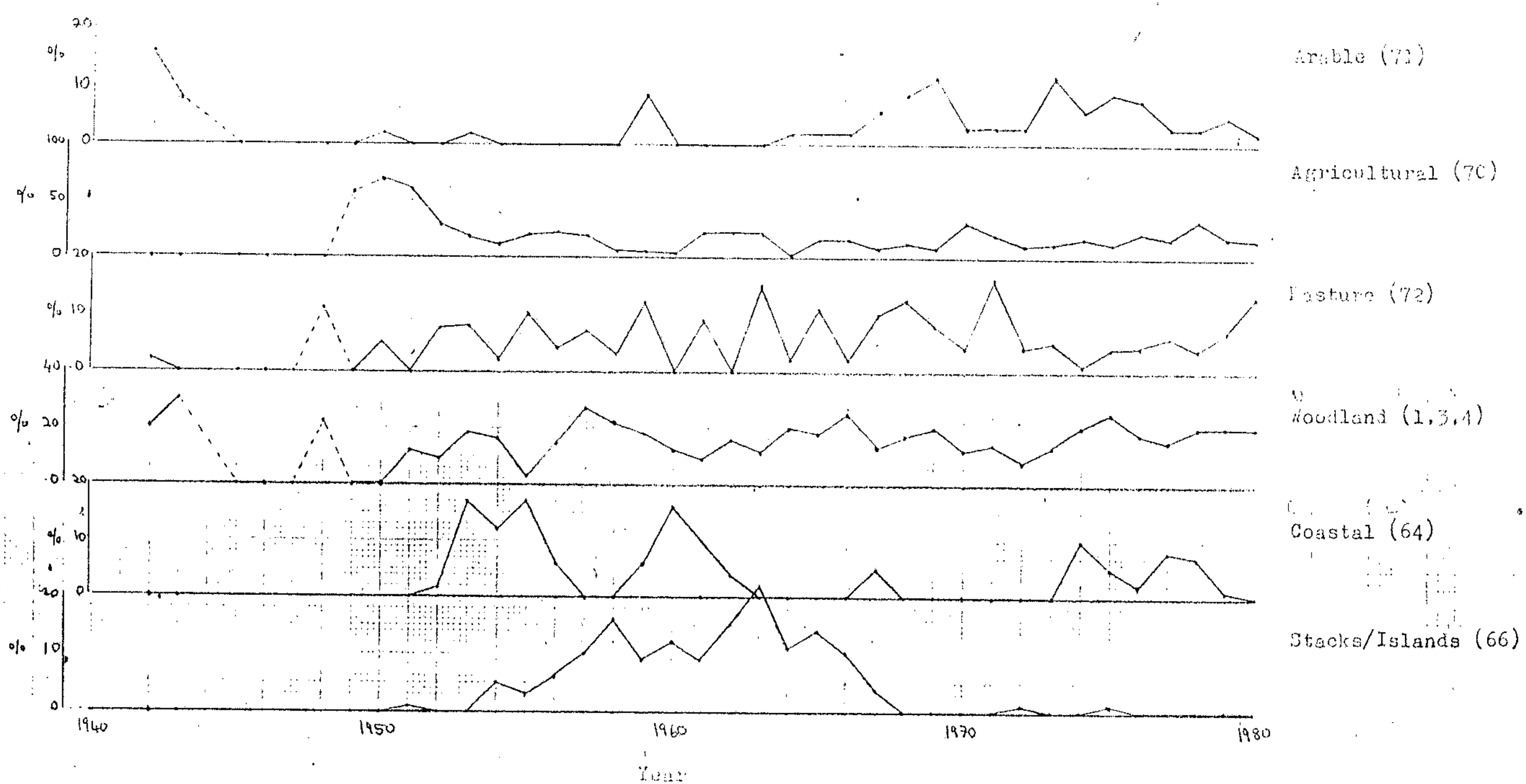
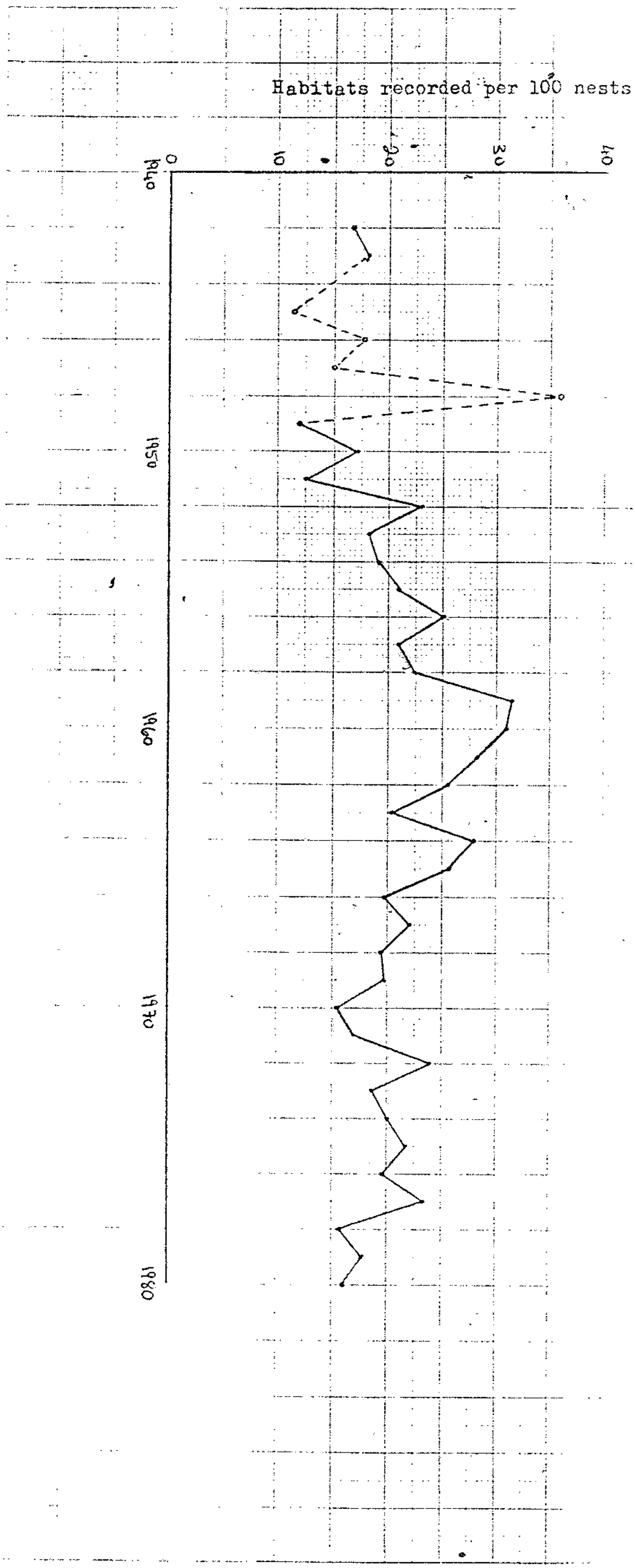

Percentage of nests in Urban or Suburban areas
0
5
10
15
20
25
Year
1940
1950
1960
1970
1980

Fig. 13



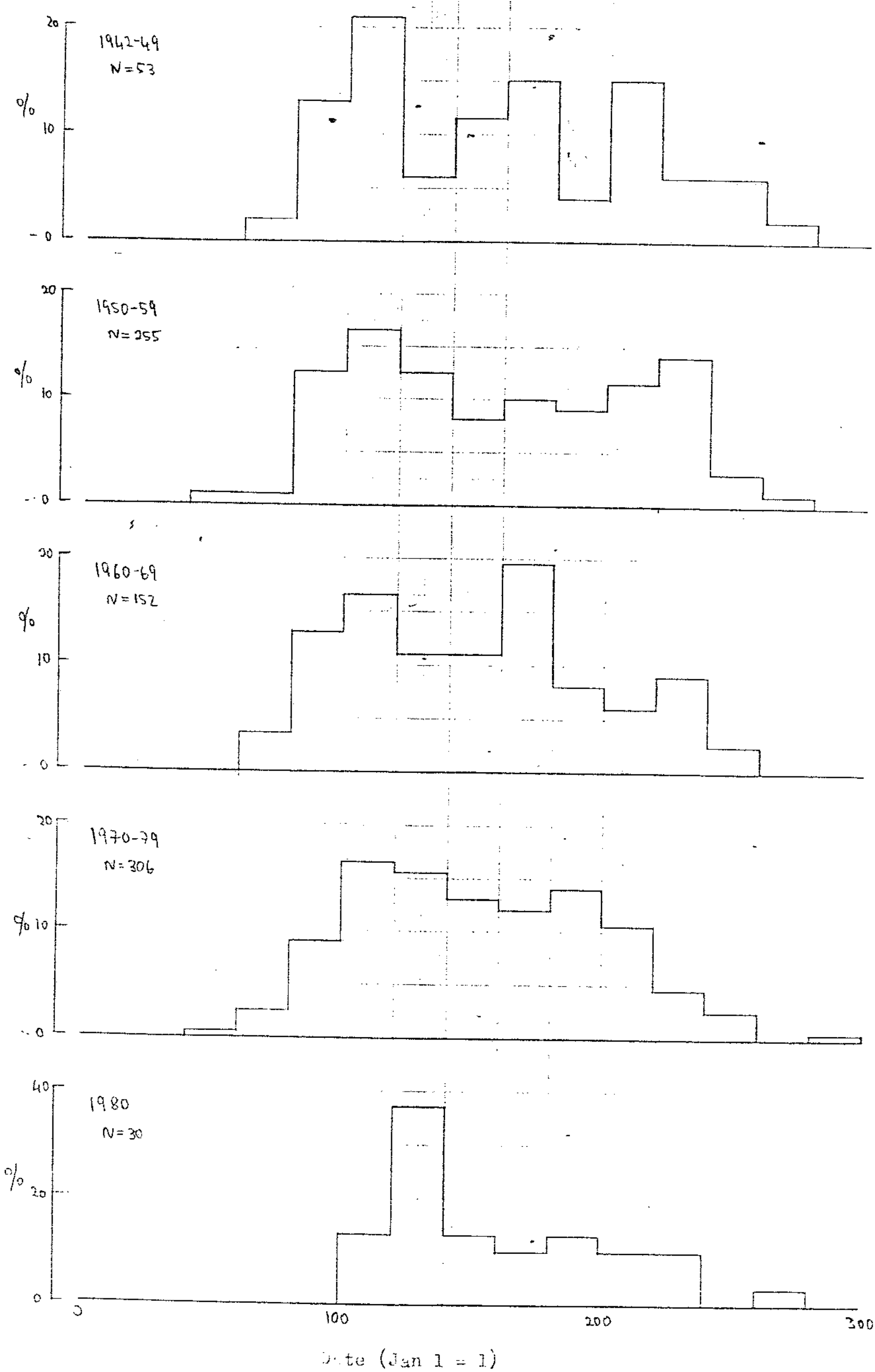
Arable (71)
Agricultural (70)
Pasture (72)
Woodland (1,3,4)
Coastal (64)
Stacks/Islands (66)
%
1940
1950
1960
1970
1980
Year

Fig. 14



Habitats recorded per 100 nests
0
10
20
30
40
1940
1950
1960
1970
1980

Figure 15



1942-49
N=53
1950-59
N=255
1960-69
N=152
1970-79
N=306
1980
N=30
%
0
10
20
40
100
200
300
Date (Jan 1 = 1)

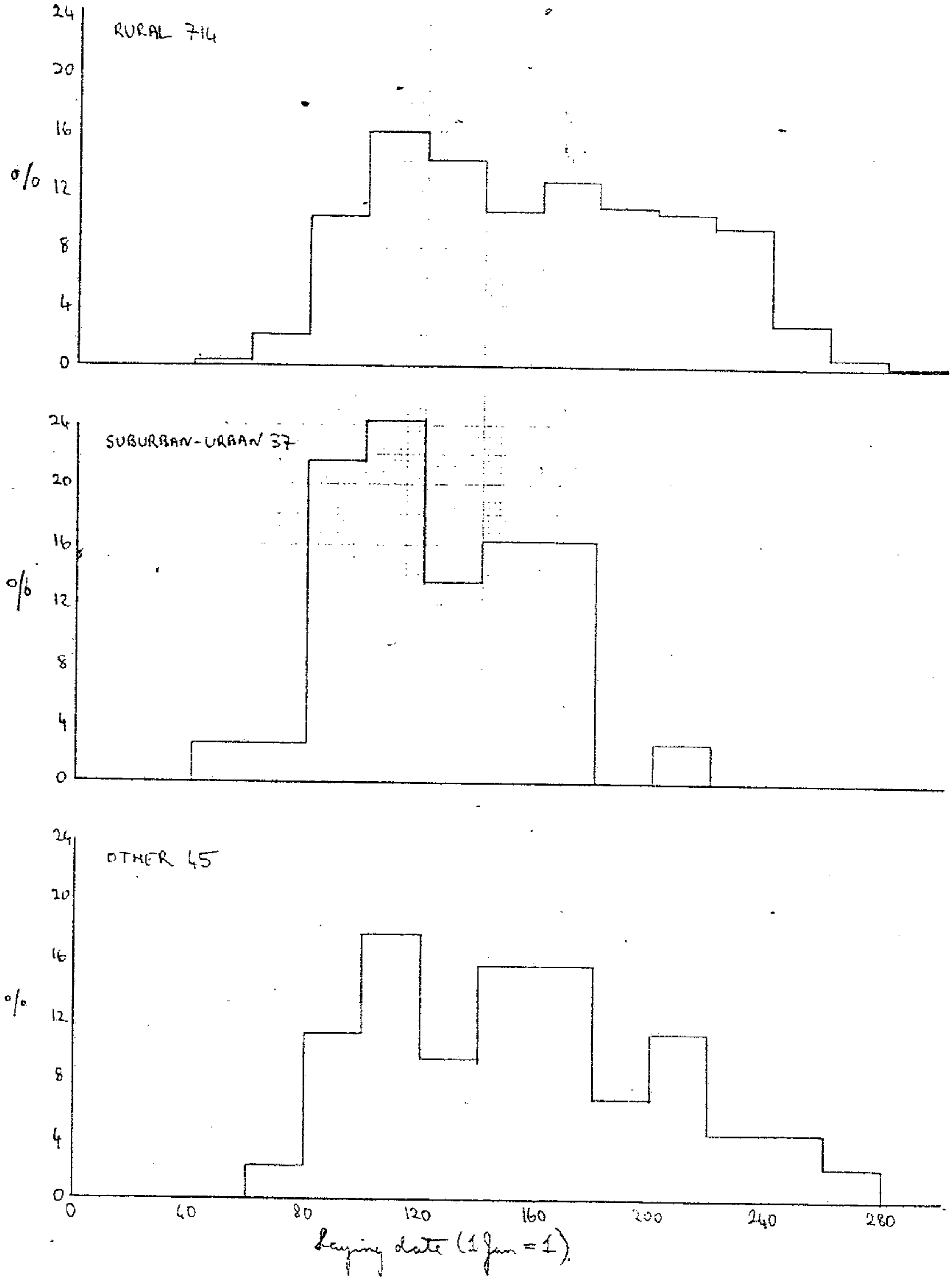
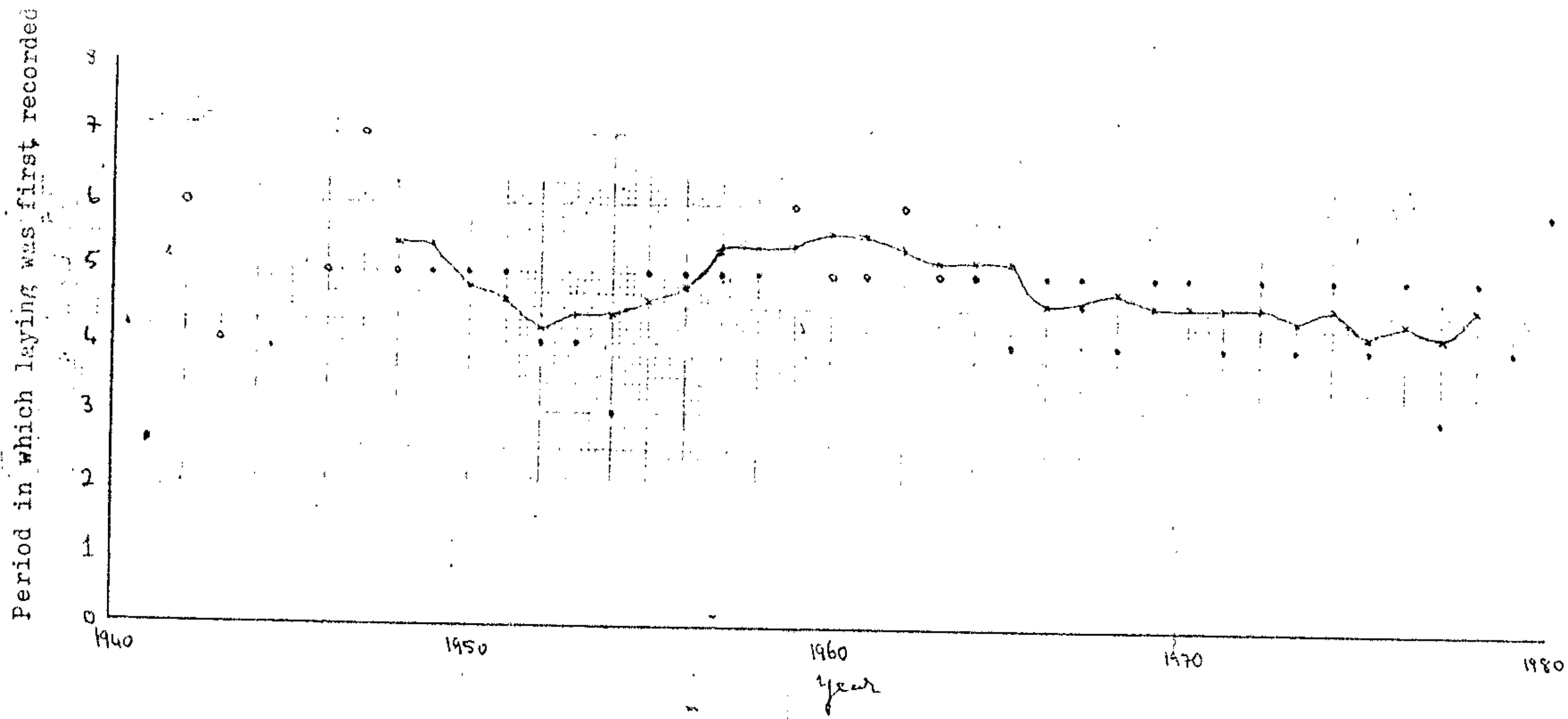

RURAL 714
SUBURBAN-URBAN 37
OTHER 45
%
0
4
8
12
16
20
24
0
40
80
120
160
200
240
280
laying date (1 Jan = 1)

Fig. 17

o Fewer than 10 nests with first egg date established for that year

x Five year moving average



ıre 18 **Ringing date of Stock Doves marked as nestlings and later found: plotted as three-day periods within groups of five years.**

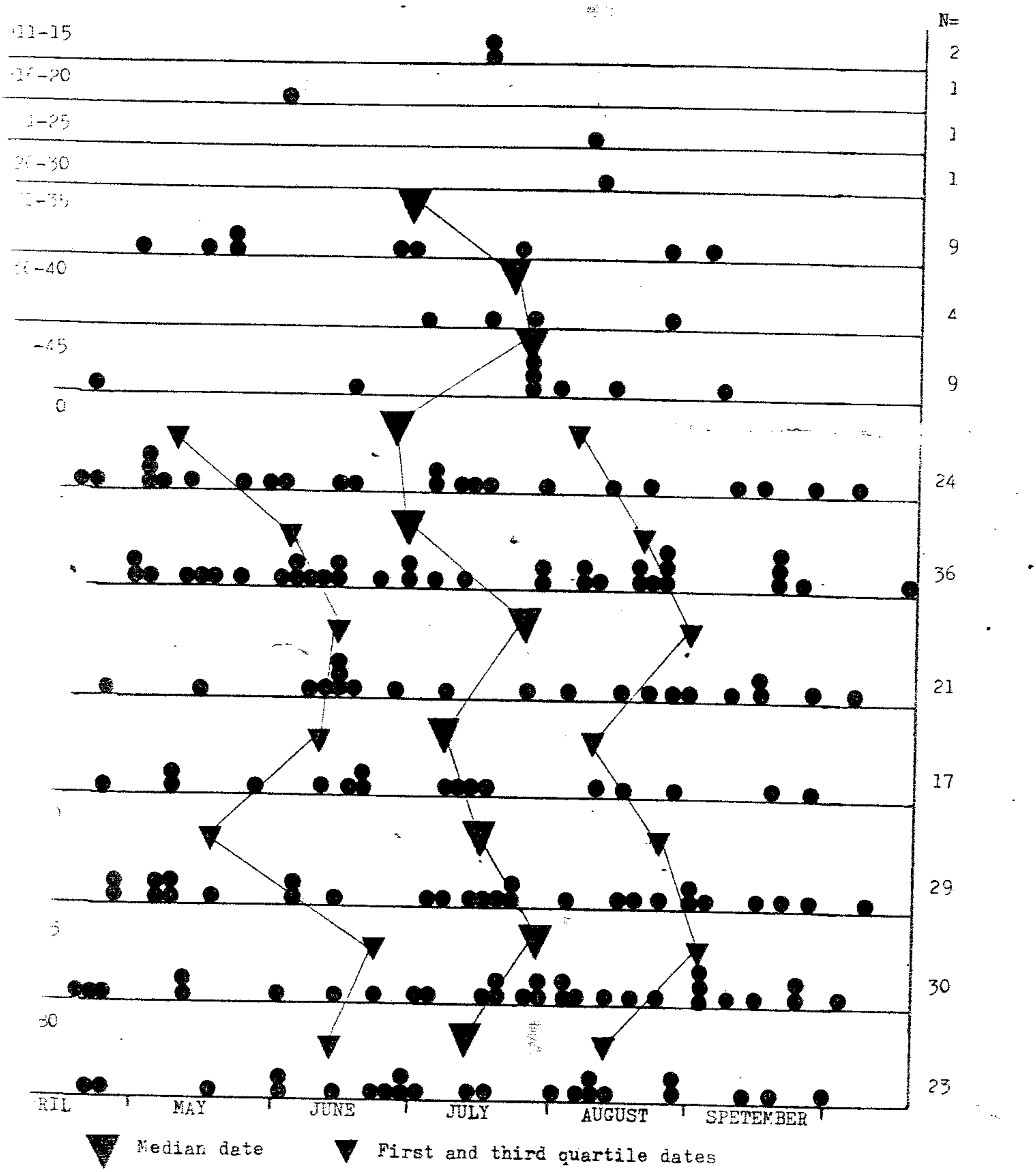


fig. 17

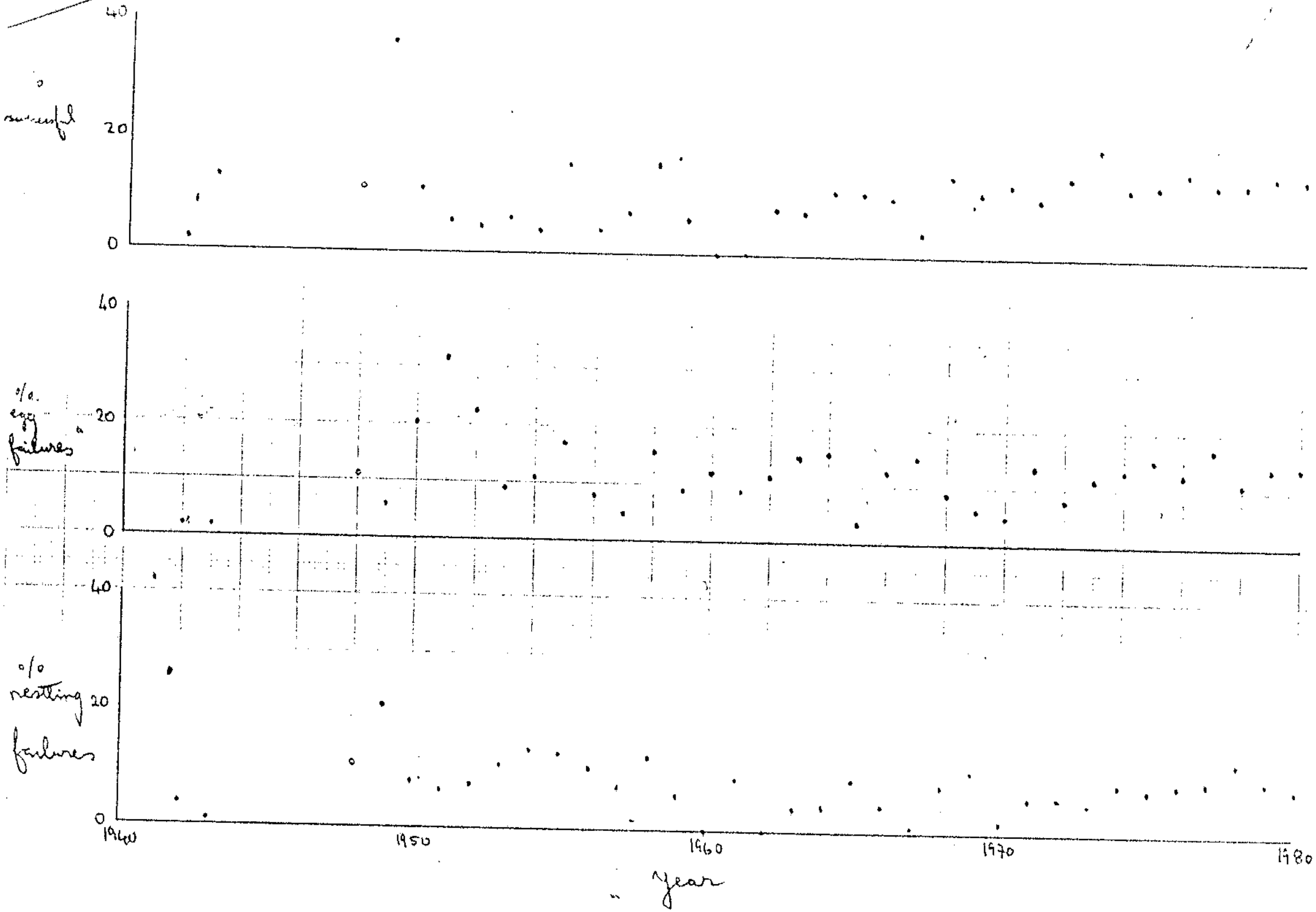

successful
40
20
0
%
egg
failures
40
20
0
40
%
nestling
failures
20
0
1940
1950
1960
1970
1980
Year

Fig. 20

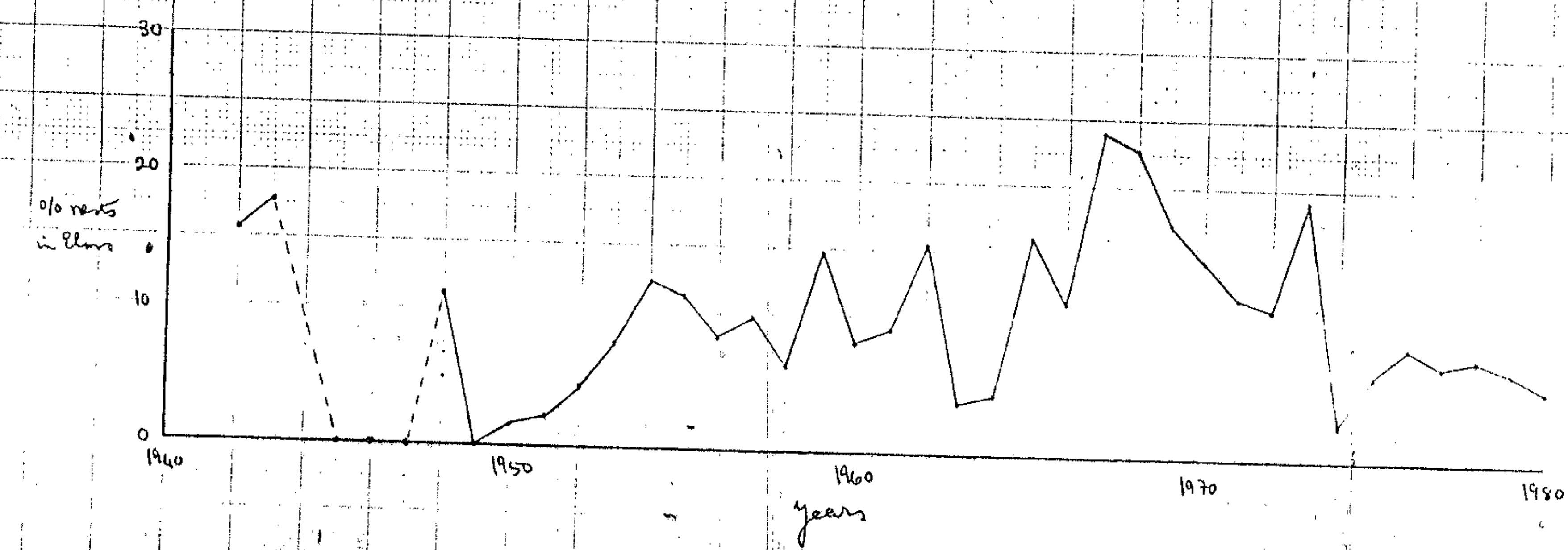
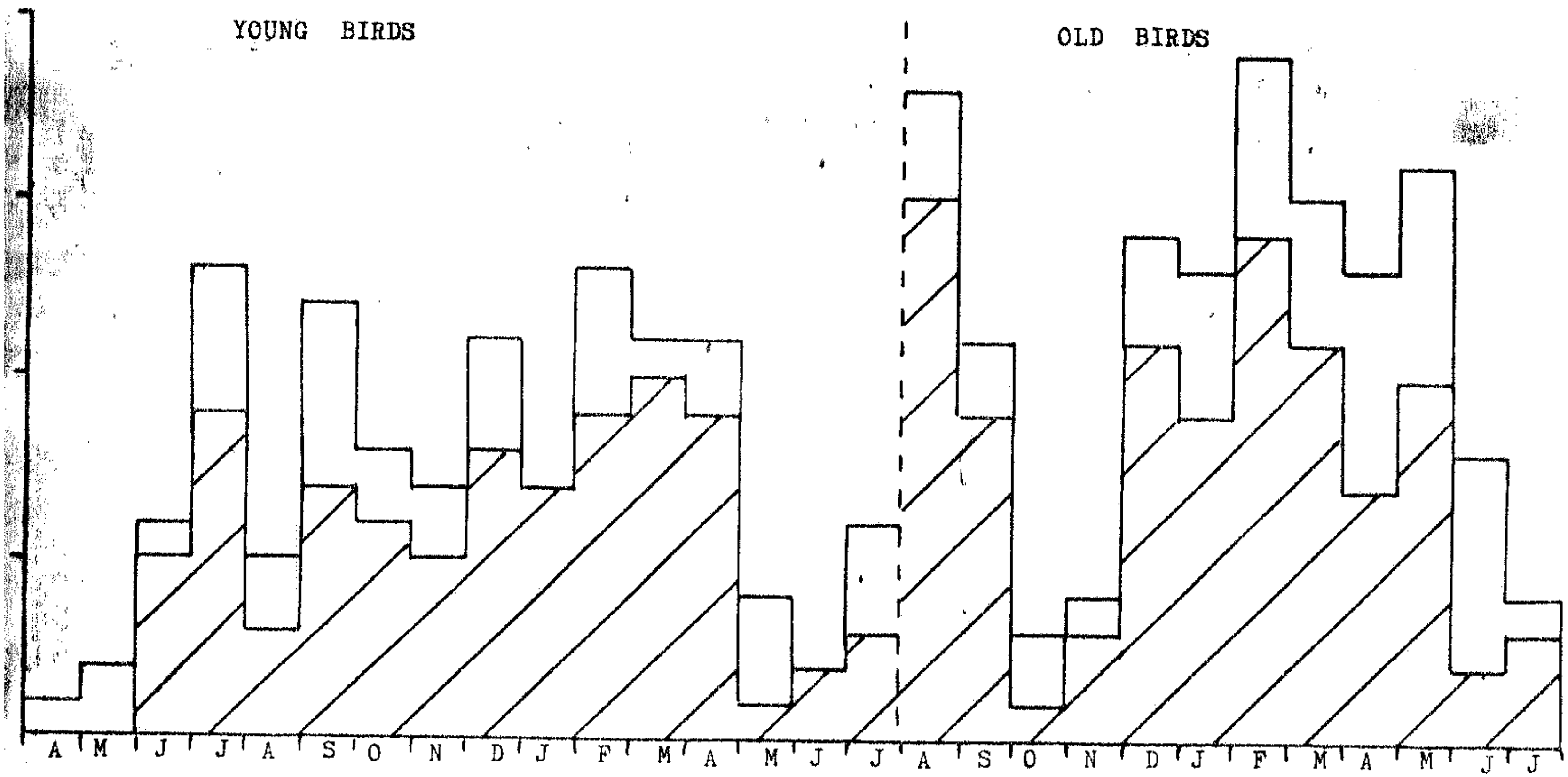
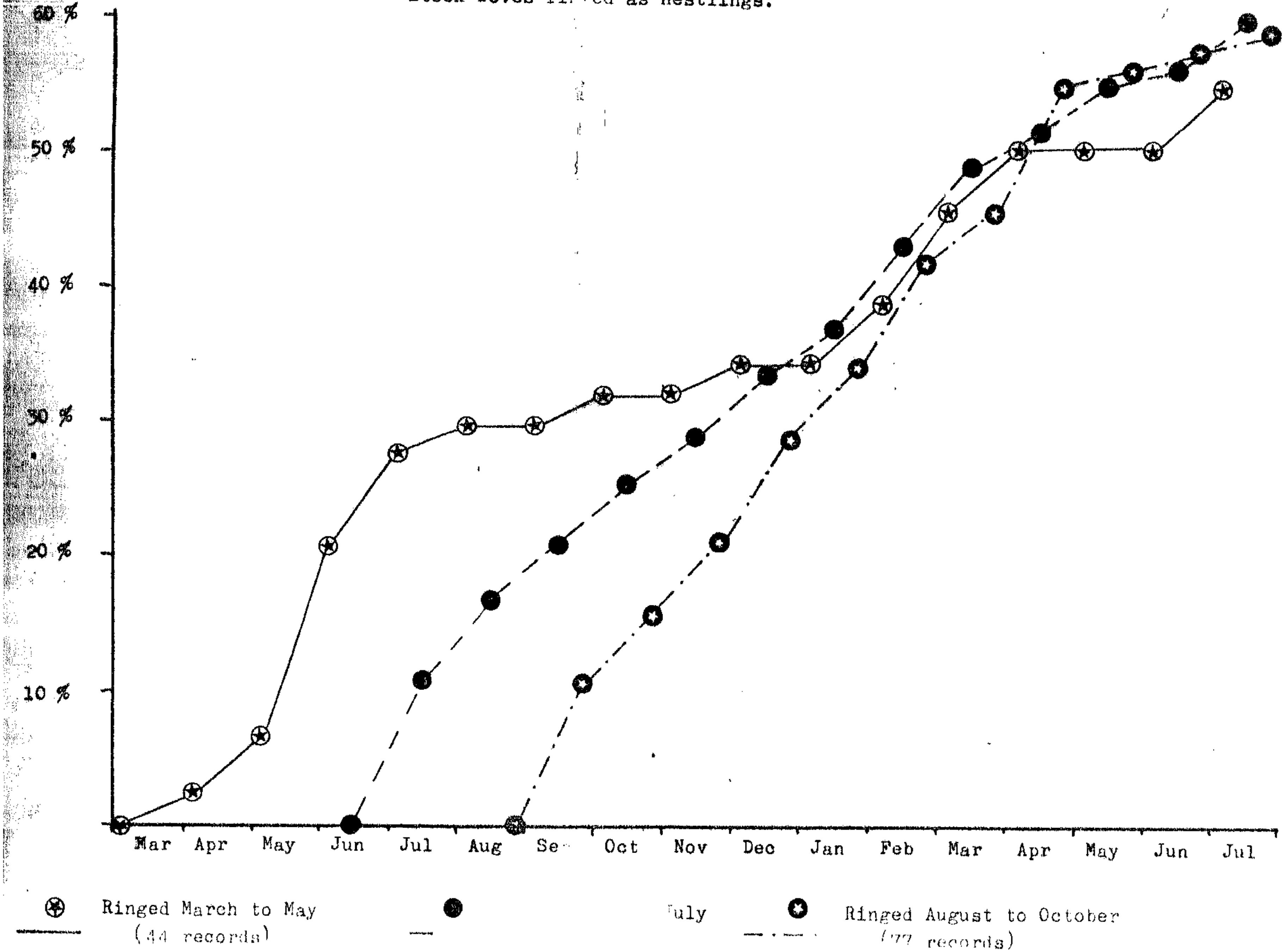


Figure 21. Monthly recovery totals of Stock Doves from all causes and shot birds only.



The hatched area rer[illegible] birds which wer[illegible] [illegible]ported as shot.

Figure 22. Cumulative frequency diagram of months of mortality to the end of July in their second year of Stock Doves ringed as nestlings.



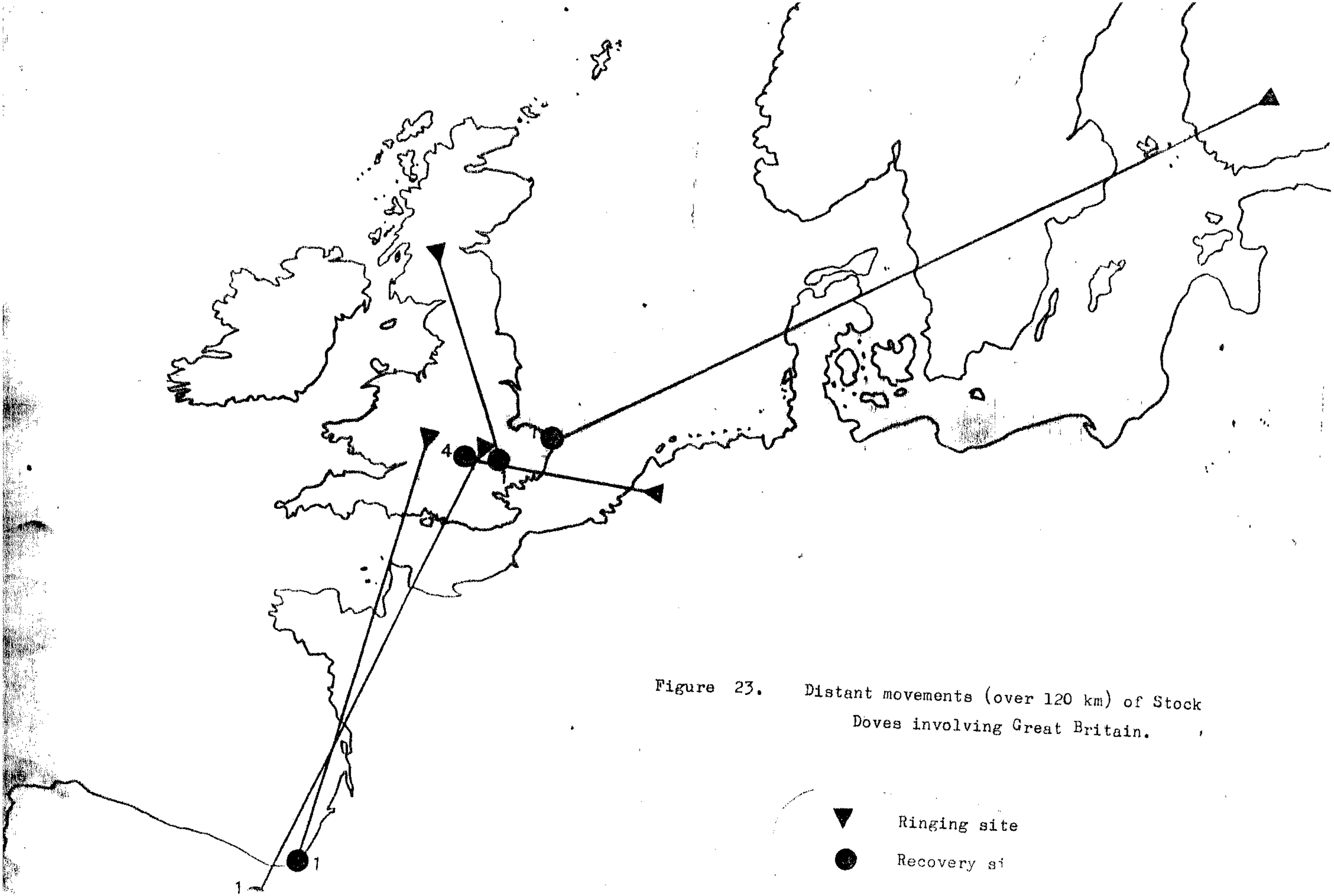
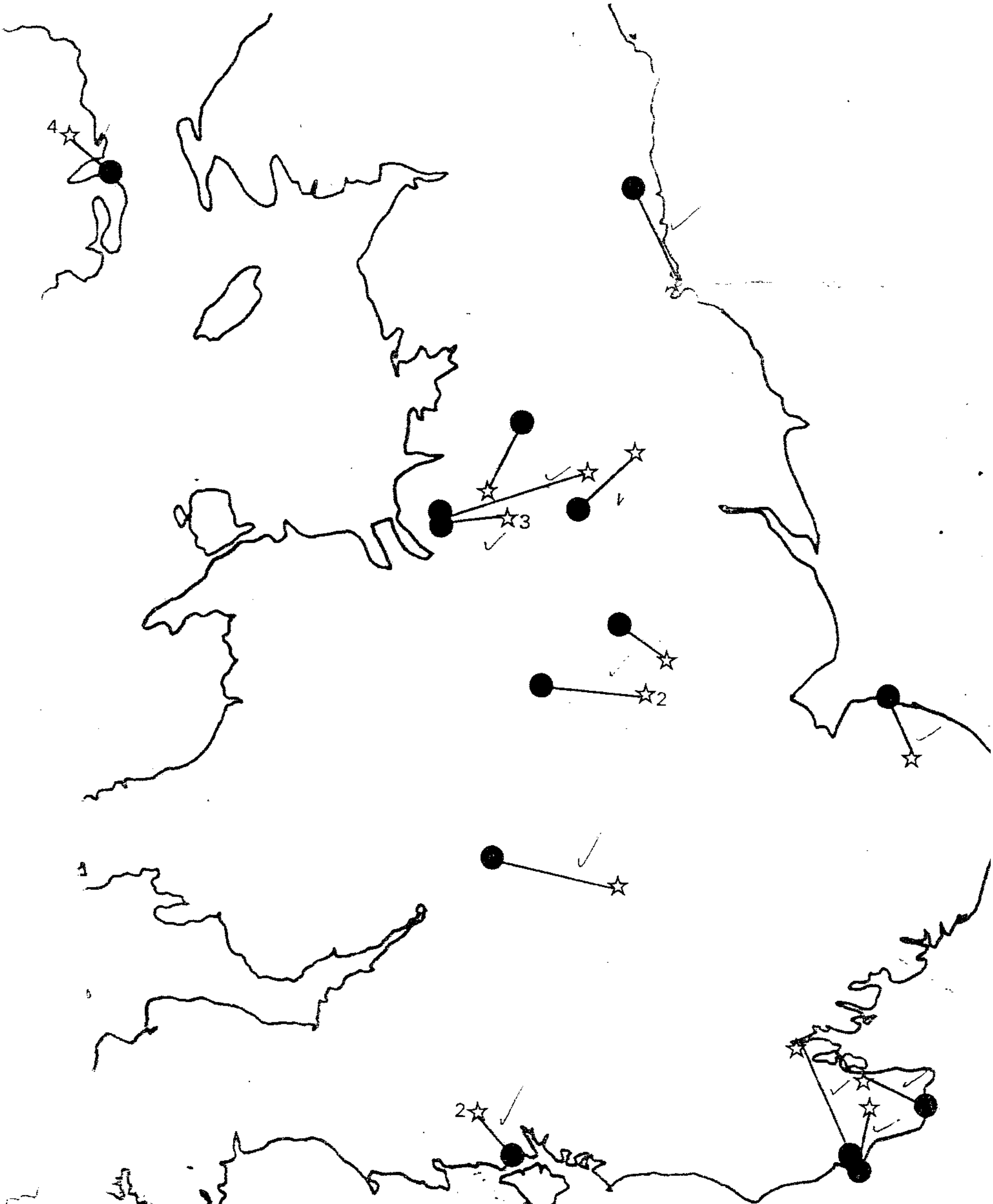


Figure 23. Distant movements (over 120 km) of Stock Doves involving Great Britain.

Figure 24. Movements of Stock Doves ringed as fully-grown birds between 25 and 250 kilometres within Britain & Ireland.

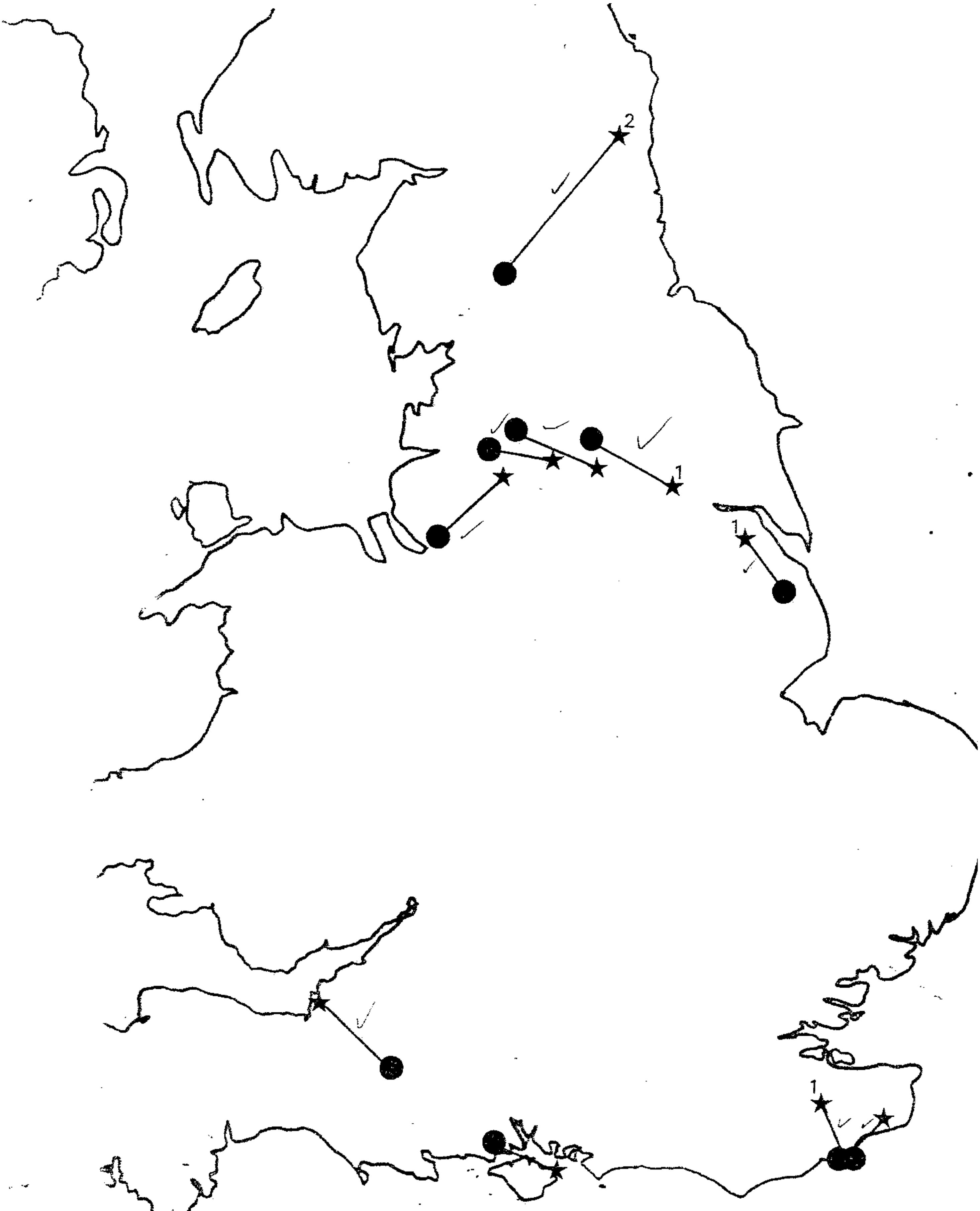
Figure 25. Movements of young Stock Doves (ringed as nestlings or juveniles) between 25 and 250 kilometres within Britain & Ireland, recoveries made during winter (October - March).



● Summer ringing site

☆ Winter recovery site - first winter unless figure given

Figure 26 Movements of young Stock Doves (ringed as nestlings or juveniles) between 25 and 250 kilometres within Britain & Ireland; recoveries made during summer (April – September).



● Summer ringing site

★ Summer recovery site – same summer unless figure given