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Phenology of autumn passage of Willow Warblers at Dungeness, 1960–2000

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EXECUTIVE SUMMARY

1 The Willow Warbler *Phylloscopus trochilus* is perhaps the commonest bird that is a summer visitor to Britain & Ireland. It nests in all regions except Shetland and in almost every 10 km square. In autumn, it is one of the earliest species to depart. Autumn passage birds are especially abundant on the southeast coasts of England, in East Sussex and Kent, and have been ringed there in large numbers at sites including Dungeness and Sandwich Bay.

2 The Common Birds Census has revealed a substantial decline in the UK breeding population of Willow Warblers, estimated at 40% for the 31-year period 1968–99. This decline has been strong in southern Britain and relatively minor in northern England and Scotland, and has been linked to a decrease in adult survival rates among birds breeding in southern Britain.

3 This study investigates daily counts of passage Willow Warblers at Dungeness Bird Observatory for autumns from 1960 to 2000, and draws upon data from the British & Irish Bird Ringing Scheme, held by the BTO. The national ring-recovery data set for Willow Warbler contained 2,856 records from birds ringed in Britain & Ireland at the time of this analysis, and 98 recoveries from birds ringed abroad. Only 284 recoveries, however, were from birds passing through coastal southeast England in autumn.

4 The phenology of the autumn passage of Willow Warblers at Dungeness shows a double or treble peak during August. The origin of this multi-modality is not clear but may relate to birds of different age-classes or breeding areas. Between the 1960s and 1990s there was a tendency for the passage peaks to fall later in the year.

5 Ring-recoveries of birds passing through southeast England in autumn show that birds on passage in July, when passage is beginning, are from breeding areas close to Dungeness. In early August, birds arrive from localities as distant as the north of Ireland and southern Scotland, whereas later in that month birds also arrive from central Ireland and from northern and central Scotland. Birds on passage in September are linked by recoveries to locations mainly in eastern Britain, suggesting that many such birds are of Continental origin.

6 The apparent shift towards later passage may stem from the decreases shown by CBC among southern breeding birds, since recoveries show that these are the birds that pass through Dungeness relatively early in the autumn. An alternative hypothesis, supported by the later timing of all three passage peaks in the 1990s compared with the 1960s, is that all elements of the population are passing through later in the autumn. The latter hypothesis may link to global warming, if warmer weather tends to delay departure – but evidence from observatory data from the Baltic region suggests that a warmer climate in the breeding areas might promote earlier rather than later autumn departure.

7 Some further work to help resolve these issues is suggested.

1 INTRODUCTION

1.1 Status and movements of Willow Warbler in Britain & Ireland

The Willow Warbler *Phylloscopus trochilus* is described as the commonest bird that is a summer visitor to Britain & Ireland, nesting in all regions except Shetland and in almost every 10 km square (Gibbons *et al* 1993). High breeding densities are found in widespread areas of Britain north to Easter Ross and in a large part of northern and central Ireland. These birds belong to the nominate race, *trochilus*, which is found widely in western Europe north to Scotland and southern Sweden and east to Poland and Rumania. After breeding, the whole population of nominate birds departs for its winter quarters in West Africa, where most are found around the Gulf of Guinea (Norman & Norman 1985, 2002).

Spring return is relatively early among long-distance migrant birds, allowing two broods to be raised before departure; data from the BTO's Nest Records Scheme suggest that few birds attempt a second brood, however, although there is probably some observer bias towards the under-recording of nests that are active relatively late in the breeding season (Crick & Baillie 1996). Adults have a complete moult, at or close to their breeding sites, in July–August, generally beginning southward migration only when their new flight feathers are fully grown. Juveniles moult to a first-winter body plumage in autumn; they disperse short distances during the second half of this moult but do not begin migration until it is complete (Lawn 1984).

In autumn, Willow Warbler is an abundant migrant at coastal bird observatories and is one of the earliest species to depart from Britain & Ireland (Riddiford & Findley 1981). First migrants are generally noted in the second half of July. At observatories on the south and west coasts of Britain, peak numbers occur in early or mid August, whereas at sites on the east coast the passage begins and ends later, peaking in late August. At most sites the bulk of passage is over by mid September, but at Fair Isle, the northernmost British observatory, Willow Warblers are commonly recorded into October. Riddiford & Findley (1981) suggest that this pattern arises because passage on the east coast includes migrants of Continental origin in progressively greater numbers at sites from Sandwich Bay northwards to Fair Isle. Southern Scandinavia seems the most likely origin for these birds; ring-recoveries link eastern England with March–May localities north to 62°N in southern Norway and east to the Gulf of Finland at 24°24'E (Norman & Norman 2002).

Willow Warblers are especially abundant in autumn on the southeasternmost coasts of England in East Sussex and Kent, and have been ringed there in large numbers at Beachy Head, Rye Bay (Icklesham), Dungeness and Sandwich Bay. Ring-recoveries demonstrate that this area receives migrants from almost all of Britain and from northern and central Ireland, as well as from the European Continent. It thus appears that there is a general southeasterly movement across Britain & Ireland in autumn, towards the shortest crossings of the English Channel from Kent and Sussex, and that this movement involves birds from all regions of Britain & Ireland except the southern third of Ireland and the English Southwest Peninsula (Norman & Norman 2002).

1.2 Occurrence of Continental races in Britain & Ireland

The northern and eastern European race *acredula* breeds from northern Scandinavia to western Siberia and winters to the east of nominate *trochilus* in eastern and southern Africa (Lindström *et al* 1996). There is a migratory divide across Scandinavia at 62°N, with *acredula* to the north migrating mainly southeast in autumn and nominate *trochilus* breeding at more southerly latitudes and migrating mainly southwest (Chamberlain *et al* 2000).

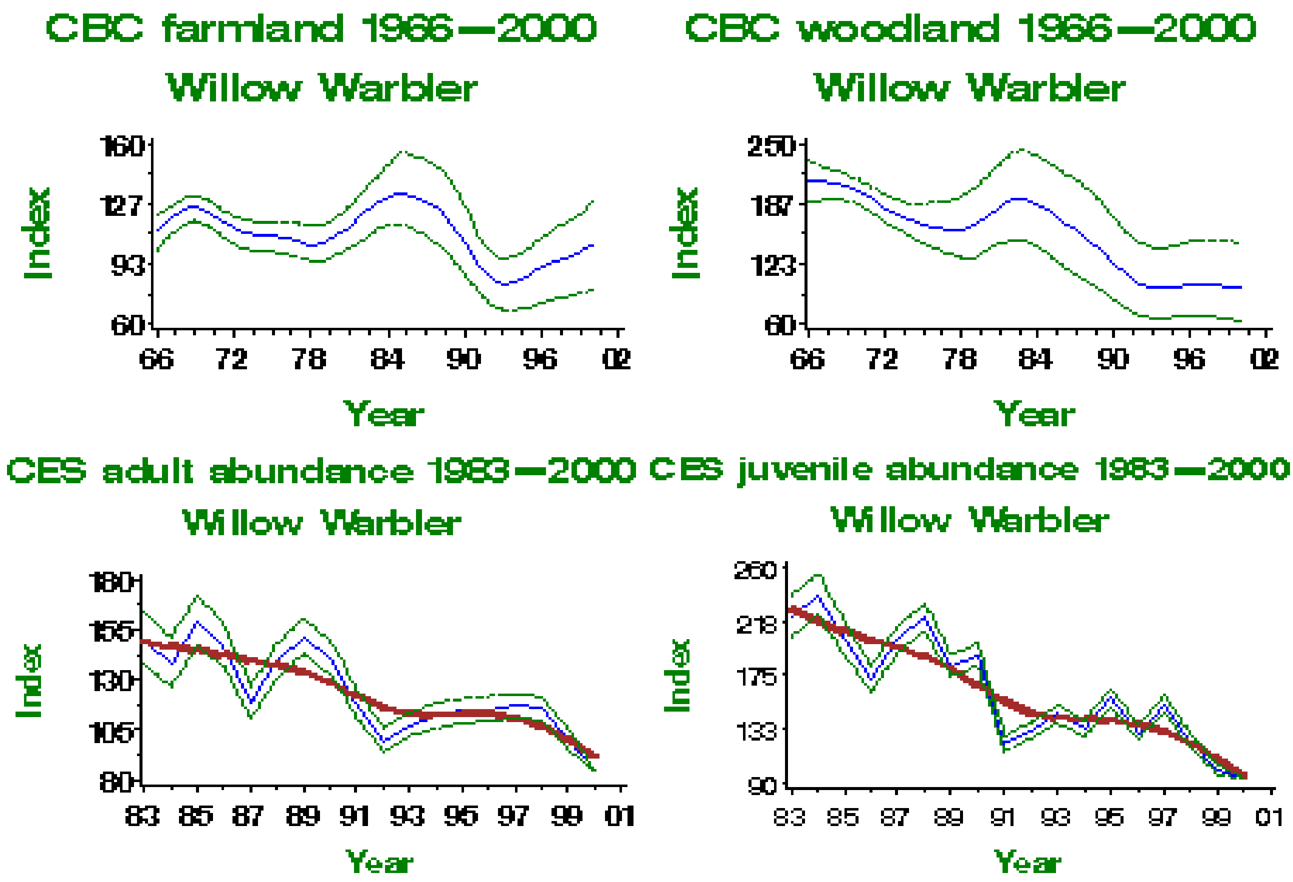
The BOU Records Committee lists *acredula* as a migrant and possible breeder in Britain (BOU 1992). Pale, greyish Willow Warblers, identified as *acredula*, have been found nesting in Scotland (Sharrock 1976), and occur in small numbers at many British coastal sites in spring and autumn. According to Riddiford (1991), *acredula* are regular at Dungeness in spring, especially in May when 80% of 41 spring captures were made, and may include some Scottish breeders. The precise status of *acredula* in Britain & Ireland is unclear, however, because there are no known characters by which individuals can be certainly identified (Svensson 1992) and because there is some dispute over the appropriate trinomial for the Willow Warblers that breed in southern Norway and migrate mainly southwest towards West Africa. They are sometimes treated as *acredula*, although use of this name is probably better restricted to those birds that breed to the north of the migratory divide. As yet, there is no evidence that birds originating north of 62°N reach Britain or Ireland but, in view of their large range so close to northern Britain, the occurrence of genuine *acredula* at least occasionally can hardly be doubted. The east Siberian race *yakutensis* also winters in Africa; it is not listed for Britain (BOU 1992), since there are no certain records, but this race too apparently occurs in late autumn (Cramp 1992).

1.3 Population changes of Willow Warblers breeding in Britain & Ireland

A number of census schemes have monitored Willow Warbler breeding numbers over recent decades. In the UK, a combination of ringing and census data suggests that the breeding population was remarkably stable during 1947–88 (Marchant *et al* 1990). Since then, however, the BTO's Common Birds Census (CBC) has revealed substantial decline in the UK breeding population of Willow Warblers, especially during 1986–93 (Figure 1). Across all CBC habitats, the decline has been estimated at 40% for the 31-year period 1968–99 and at 24% for the ten years 1989–99 (Baillie *et al* 2002). Some recovery has been noted in the CBC trend since 1993 but the population remains comparatively very low.

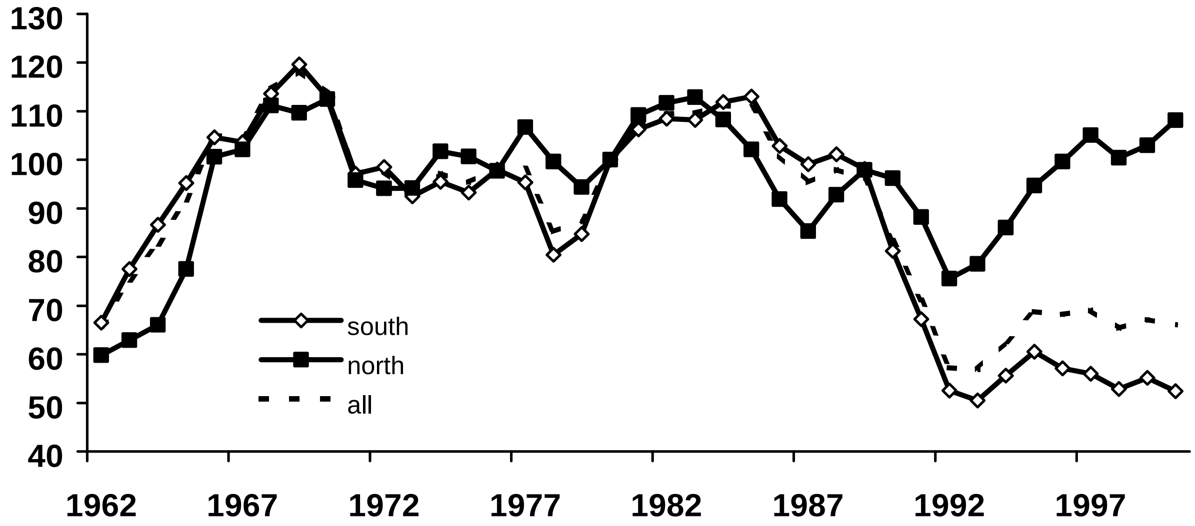
Standardised mist-netting for the Constant Effort Sites ringing programme (CES) has shown a similar decline, of 32%, in captures of adult Willow Warblers during breeding seasons 1983–2000 (Balmer *et al* 2001; Figure 1). A sharp fall was noted from 1989 to 1992, followed by a shallow recovery and then a further decline to new lows in 2000 and 2001 (Balmer *et al* 2001, Balmer & Milne 2002). The recent population decline is associated with a moderate decline in CES productivity (Figure 1) and an increase in nest failure rates at the chick stage (14 days) from 18% to 26% (Baillie *et al* 2002). Laying dates have become earlier, which may be a consequence of recent climate change (Crick & Sparks 1999). Constant-effort netting in France and the Netherlands has also revealed recent breeding declines, especially steep in France, which lies at the southern edge of the Willow Warbler's world breeding range (Balmer & Milne 2002).

Figure 1. **Trends for Willow Warbler from Common Birds Census (smoothed line only) and Constant Effort Sites, with their confidence intervals. (Source: Baillie *et al* 2002.)**



In an early analysis of Willow Warbler population trends, Marchant & Balmer (1993) noted that, while the downward trends derived from CBC plots in southeast and southwest Britain were similar in extent and timing, the trend from plots in the north of the UK was strikingly different, being more stable and showing little sign of decline. Their northern region comprised Scotland, Northern Ireland, and England north of grid northing 430 km, approximating to a line from Preston to Hull. Using the same north–south division, Peach *et al* (1995) estimated the trend in breeding population in the north at -7% overall during the seven years 1986–93, whereas numbers in the south had dropped by 47% over the same period. An updated analysis of regional CBC trends is presented in Figure 2.

Figure 2. CBC index trends in the north and south of Britain. The division between north and south is taken as National Grid northing 430 km, approximating to a line from Preston to Hull. Index trends are not smoothed and are drawn from all CBC habitats.



Peach *et al* (1995) were able to link population decline to a small but significant increase in nest failures at the nestling stage in southern Britain in 1989–92 compared to 1974–88, and to a significant drop in adult survival among breeders in the south of Britain, but not in the north, between 1987–88 and 1991–92. They concluded that declining survival rates of adult Willow Warblers breeding in southern Britain had been a major cause of the population decline observed there. The reason for the rise in mortality rates is unclear. It may be linked to deteriorating conditions for the species on its winter quarters in Africa; if birds from northern and southern Britain winter in different parts of the winter range, that might explain why survival rates have differed between these two regions.

1.4 Scope of this project

Concerns about declines in numbers of Willow Warblers on autumn passage at Dungeness Bird Observatory (DBO), culminating in a particularly poor season in 1999, prompted the present project. Its aims are:

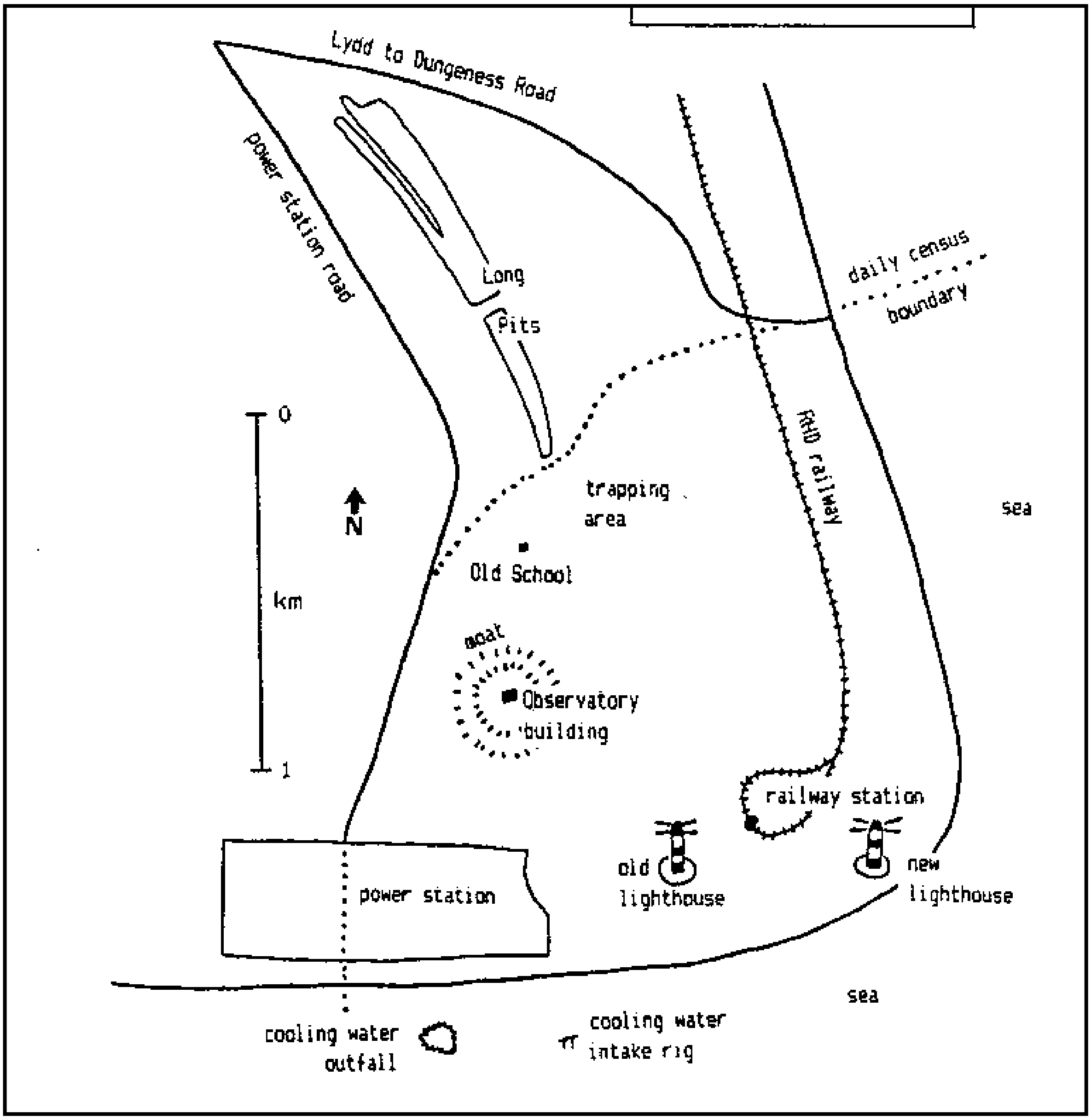
- *to analyse the patterns of temporal change in the numbers of birds counted at DBO on passage;* and
- *to look for links between Willow Warbler ring-recoveries and the DBO count data that might help to explain these patterns.*

2 MATERIAL AND METHODS

2.1 Dungeness Bird Observatory daily log

In common with other observatories, DBO has a clearly defined counting area for which daily estimates of all birds present are entered in a daily log-book. The DBO daily census area extends from the power station road eastwards to the eastern shore and northward towards the Pilot Inn; it does not include the Long Pits, although these do form part of the overall DBO study area of around 250 hectares (Riddiford 1991, D Walker pers comm). The whole of the trapping area is included in the daily census, together with the observatory moat and the old lighthouse garden (Figure 3).

Figure 3. Map of the Dungeness area showing the location of the daily census area at the tip of the Dungeness Peninsula. (Source: Riddiford 1991.)



The methodology of the daily census is probably not clearly defined at any observatory, being dependent on manpower and weather conditions, but has the overall aim of providing the best estimate that is available of numbers of each bird species present or passing through the site. Estimates are compiled from the observatory staff's observations, which tend to follow a daily pattern, supplemented by records provided by visitors. Often the starting point is the daily number of birds trapped, to which are added estimates of birds seen and considered to be additional. Where circumstances did not allow full coverage of the census area, or where conditions for observation or for trapping were poor, some allowance may be made for this in compiling the estimate, or a tick may be entered to indicate that a species was present but in unknown numbers. The observatory warden supervises log entries, thus minimising the subjective element in the data, at least within the tenure of each warden. Visitors provide relatively little information for common and regular species. Such data have been collected at DBO since at least 1953.

A number of short-term and long-term factors have affected the DBO daily log. Riddiford (1991) describes how, even though the boundaries of the census area have been constant, its character has changed over the years. The adjacent nuclear power station was built and commissioned during 1960–65. The new lighthouse, which replaced the old one in 1961, has shown a lesser tendency to attract night-migrating birds. The sallows in the observatory moat grew from a height of 1 m in the 1950s to 2 m by the 1970s. Those in the trapping area, which were below 1 m high in the 1950s, coalesced into thickets that by 1977 were 2.5 m high and had been invaded by aspen and birch; thus, by 1977, the trapping area had become low secondary woodland. A pair of Willow Warblers nested in the study area in 1969 and from 1972 onwards, with three pairs in 1977. Riddiford (1991) also states that coverage in July during 1953–77 was less comprehensive than that achieved later in the autumn. Coverage at weekends, when more visitors are present, is known to have been more thorough, at least for rare species (Scott 1969).

Weather is a major influence on the daily log counts, affecting the numbers of birds arriving or passing through Dungeness on any one day (Riddiford 1991). It may also affect the numbers remaining on site, having been counted already on previous days, and the ease with which the birds that are present can be detected. Interpretation of the daily log counts needs to take account of the influence of immediate weather conditions. Because the relationship of the numbers of grounded migrants to total passage numbers is unknown, the log data should be regarded as a measure of grounded birds and not necessarily of total through passage, including birds that do not stop, as might be detected by radar (*eg* Lack 1963).

A particular problem for estimating numbers of Willow Warblers in the field is their similarity to congeneric Chiffchaffs *Phylloscopus collybita*, which are also abundant autumn migrants at Dungeness; separating these species by observation requires care and can be time-consuming. Chiffchaff, however, does not appear commonly before September, when Willow Warbler migration is tailing off, and is still numerous in October (Riddiford 1991). Individuals observed that might be either of these two species, but cannot be specifically identified, are referred to as 'Willow–Chiffs'. On some days, especially when ringing data were lacking and observations sparse or inconclusive, log entries were made for 'Willow–Chiffs' in addition to or instead of entries for Willow Warbler.

The material supplied by DBO specifically for this study was an Excel spreadsheet containing all numerical daily log entries for Willow Warblers for the 41 years from 1960 to 2000, covering the 123 days from 1 July to 31 October. Ticks to indicate presence, if used in the original log, were not included in the spreadsheet, however, nor were any data for 'Willow–Chiffs'. The compiler of the spreadsheet drew attention to 1967 as a year when a large number of birds were recorded as 'Willow–Chiffs', but no data for 'Willow–Chiffs' were supplied.

2.1.1 Dealing with missing values

Of the 5,043 days covered by the daily log, spreadsheet cells were empty for 2,156 (43%). Counts entered in the remaining cells had values ranging from 1 to a maximum of 1,550 birds, which was the estimate for 16 August 1980. A problem for interpreting the spreadsheet was that empty cells may have represented either absence of Willow Warblers, or the presence of an unknown number (perhaps, but not necessarily, with an entry for 'Willow–Chiff' or a tick for Willow Warbler having been made in the original daily log-book). After consultation with DBO, no completely objective way to separate these two kinds of empty cells was identified.

Given that the number and distribution of missing values was likely to differ somewhat between years, analysis of the dataset without making some allowance for missing values would give potentially misleading results. Values were therefore imputed to replace all missing counts, according to the following procedure. Most missing counts lay either before the first or after the last known record of the autumn: these were treated as zeros. Others were imputed by taking the mean of the real count immediately preceding the missing value and the one following it. Where there was a run of consecutive days with missing values, the count was imputed in the same way and applied to all the days in that run. This procedure was believed to mimic the likely distribution of the real numbers, which are zero or low at the start of the autumn and return to zero in late September or in October. Imputed entries that were the mean of two values were not rounded and were recorded to the nearest 'half bird'.

2.1.2 Analysis of the daily log data

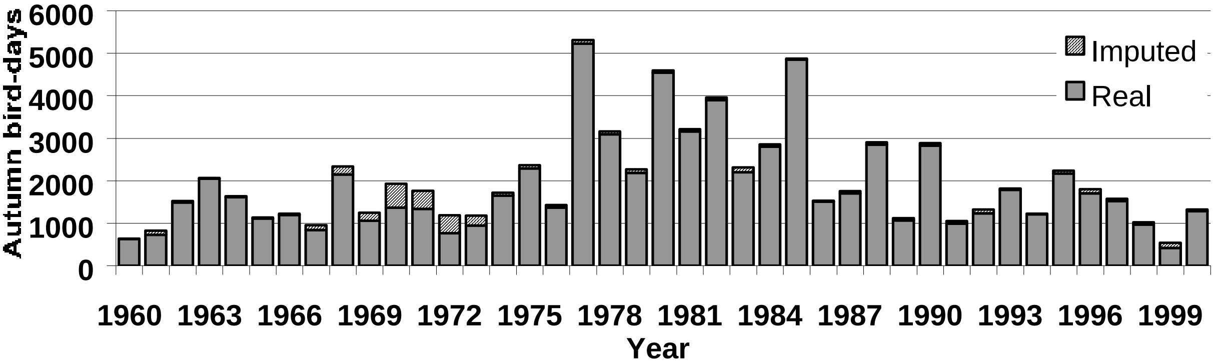
The analysis employed the concept of 'bird-days', with a bird-day defined as the recorded presence of one bird on one day. When counts are summed across days, the units are not 'birds' because an unknown proportion of individual birds were present on more than one day. Twenty birds, each present for two days, are thus equivalent in bird-days to counts of zero and 40 on successive days.

In an exploratory analysis, summing bird-days across the whole autumn for each of the study years did not produce a clear time-trend in total numbers over the whole period (Figure 4). Factors that may have influenced the counts recorded in the daily log, and hence bird-days and comparative bird-day totals, have already been noted. Observer effects could perhaps have been responsible for the run of much higher counts recorded during 1977–85, but there is some evidence that this is unlikely: in an analysis of 1985–94 data from 12 observatories, Woodbridge (1996) found that Willow Warbler totals for 1985 were exceptionally high not just at Dungeness but also at Sandwich Bay, Spurn Point and the Isle of May. Other short-term time-trends are difficult to discern but there was a notable run of four successive declines during 1995–99 that took bird-day totals to the lowest point in the whole 41-year period.

The values of imputed daily counts were mostly zero or very small. Such data formed only 4.9% of the overall total bird-days, and only in 1969–73 and 1999 did they form more than

12% of the yearly bird-day total (Figure 4). In practice, therefore, the effect of imputed data on the results will have been small.

Figure 4. Total autumn bird-days for Willow Warblers in the Dungeness Bird Observatory daily census area during 1960–2000. Imputed counts (see text) are shown separately. The figures for 1967, when many 'Willow–Chiffs' were recorded, may be too low.



Median and quartile dates of passage were calculated for each year individually, by treating each daily count as an independent weighting variable; this procedure ignored any odd 'half birds' in the imputed daily counts. As already noted, however, counts were not independent, because of the overlap of individual birds between days. The assumption is made that change in the pattern of turnover is not a major factor in determining the apparent timing of passage, and therefore that medians and quartiles can validly be compared between years. Overall medians and quartiles were compiled from the mean values of the counts for each day, across all years.

As a further step in the analysis, designed to investigate changes in phenology in more detail, additional comparisons were made of the seasonal distribution of mean daily counts between groups of years. By combining years, it was hoped that the effects of immediate weather conditions would be less dominant. Because of the obviously non-normal distribution of counts through the season, non-parametric statistical tests were used.

Groups of years were defined as objectively as possible, by using the CBC all-habitats index. Siriwardena *et al* (1998) have shown the value of identifying turning points in a smoothed index trend and, using an objective method, located turning points in the farmland CBC trend for Willow Warblers alongside other farmland species. These points can also be derived by eye from the smoothed trend. Visual scrutiny of the smoothed all-habitats CBC index for Willow Warbler (Baillie *et al* 2002, extended by unsmoothed results for 1962–65 from Marchant *et al* 1990) suggested five distinctive periods: 1962–68, in which the population was rising; 1969–79, falling; 1980–85, rising; 1986-93, falling sharply; and 1994-2000, stable. The last of these periods stands out as the one in which the index of breeding population size of Willow Warblers in the UK was consistently the lowest.

Further statistics, covering these groups of years, were computed as follows. First, the daily counts for each year were combined into five-day periods, starting at day 1 (1 July), by taking the mean of the five counts; imputed counts were included in this calculation. Second, the mean values for each five-day period were averaged across the years in each group.

2.2 Ringing data

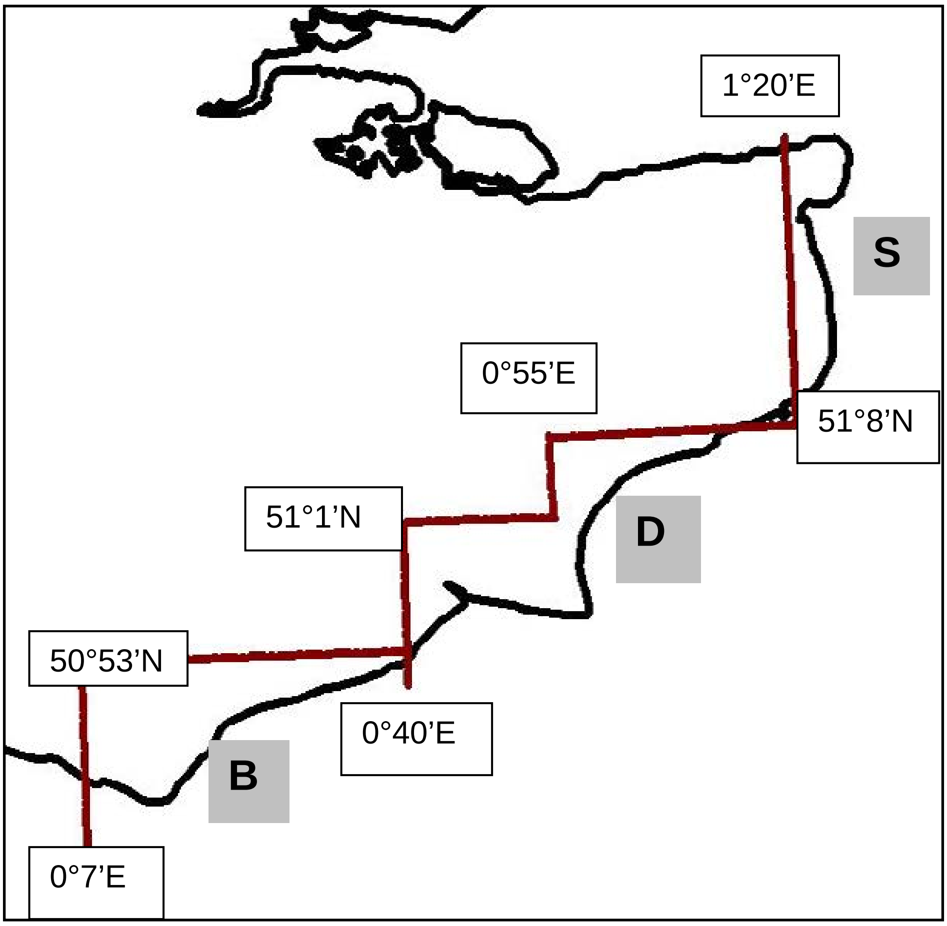
The ringing data that were available for this study consisted of the national collection of ring-recoveries. These give information for the initial capture of a bird and a subsequent finding, generally either as a dead bird or as a recapture, and further release, by a ringer. For long-distance migrants such as Willow Warbler, records that indicate site-fidelity are sometimes included in the national archive but, in general, live recaptures within 5 km are part of this data set only in special circumstances. These data concentrate, therefore, on findings of dead birds and on movements between sites.

The national ring-recovery data set for Willow Warbler that was available for this analysis contained 2,856 records from birds ringed in Britain & Ireland during the period from 1909 to 30 April 2001, and 98 recoveries post-1979 in Britain & Ireland of birds ringed abroad. These small numbers, relative to the totals of birds ringed, reflects the very low recovery rates of this and other small birds, especially those that spend much of the year in parts of the world with a sparse or poorly educated human population.

The ring-recoveries relevant to the present study were defined as those indicating presence in the Dungeness area or nearby during the autumn period, beginning 1 July. Given that the ring-recovery samples were small, analysis was not confined to DBO itself. Three separate areas of Kent and Sussex were defined as being of interest, using lines of latitude and longitude (Figure 5). These were centred on Beachy Head (zone B), Dungeness (zone D) and Sandwich Bay (zone S), at each of which very large numbers of Willow Warblers have been ringed annually since the 1960s. The more recently established major site at Icklesham (Rye Bay) was included in zone D.

Even with such a wide geographical catchment for ring-recoveries, just 360 were from birds recorded within the three study zones, and only 284 of these were recorded there on dates after 1 July. Each of these 284 birds was assigned a ‘passage day’, being the date on which it was recorded in autumn in one of the zones of interest in southeast England. This could be the date of ringing, for a bird ringed on autumn passage in one of the study zones and recorded later elsewhere, or the finding date, for a bird found in the study zones already carrying a ring from elsewhere. If there were two autumn dates within the zones for any individual, the earlier date was taken.

Figure 5. **The study zones, centred on Beachy Head (B), Dungeness (D) and Sandwich Bay (S). All ring-recoveries for which there were autumn dates in zones B, D, or S were included in the analysis.**



Eight individual birds were each recorded on a third occasion in the ring-recoveries database. One, ringed as a juvenile in Cambridgeshire on 3 August, was retrapped at Rye Bay five days later and again in North Yorkshire the following May. A second bird, also ringed in Cambridgeshire as a juvenile, on 31 July 1994, was trapped at Beachy Head on 13 August the following year and in Northamptonshire in April 1998. A further six birds were caught twice at the same finding location. Second recaptures of all of these birds were omitted from the analysis.

The 284 relevant records were examined for evidence indicating their age and breeding origin (Table 1). The best such evidence came from birds ringed as pulli, whose natal origin was known precisely. There were 19 such birds, and a further 20 that were ringed as fully grown juveniles between their fledging dates and mid July. The latter group may have included birds that had begun post-juvenile dispersal although, since there was ringing evidence of long-distance dispersal and migratory movements only after mid July (see Figure 8), it is likely that all such birds were at or close to their natal sites.

Table 1. **Breakdown of relevant ring-recoveries. Columns indicate the age of the bird when recorded in autumn in the study zones (i.e. on the 'passage day'), and rows the nature of evidence (if any) for its breeding origin. The breeding season is defined as 1 April to 15 July. The age codes used by the ringers are given in brackets.**

Class of evidence to indicate breeding area	**First-autumn (3J, 3)**			**Adult (4) (i.e. not first-autumn)**	**Age not known (2)**	**Total (n = 284)**
	Beachy Head area (zone B)	**Dungeness area (zone D)**	**Sandwich Bay area (zone S)**			
Ringed as pullus (1, 1J)	3	9	5	2		19
Ringed as juv (3J, 3) in breeding range in breeding season	7	11	1	1		20
Recorded as adult (4) in breeding range in breeding season	34	47	9	5		95
Recorded as of unknown age (2) in breeding range in breeding season					1	1
Ringing and finding both at passage times and locations	25	63	12	15	4	119
Recovery location south of Kent/Sussex	12	8		2	8	30

A large group of birds (95) were recorded as adult birds in the breeding season. Many of these would have been caught on their breeding territories but others would not have been breeding and were probably still on passage towards their breeding areas, which are likely to have lain further north. These two groups were indistinguishable. Most such birds had been ringed as juveniles in an earlier autumn, although five were adult when recorded in the study zones. These birds provide good evidence of breeding location although, through natal dispersal, not necessarily of natal origin.

The largest number of birds (119) were recorded only after mid July, so that both ringing and finding records indicate passage localities. These birds give very limited information on the breeding areas of the birds concerned although, assuming that northward movements in autumn, such as pre-migratory dispersal of juvenile birds, are likely to be relatively short, breeding areas will usually lie to the north of the passage localities. Except in the case of two birds with links with southern Norway, these were treated as being of unknown country of origin. A further 30 ring-recoveries linked the zones of interest with locations further south along the migratory route and so provided no information about autumn migration through Britain & Ireland.

3 RESULTS

3.1 Phenology of passage from DBO log data

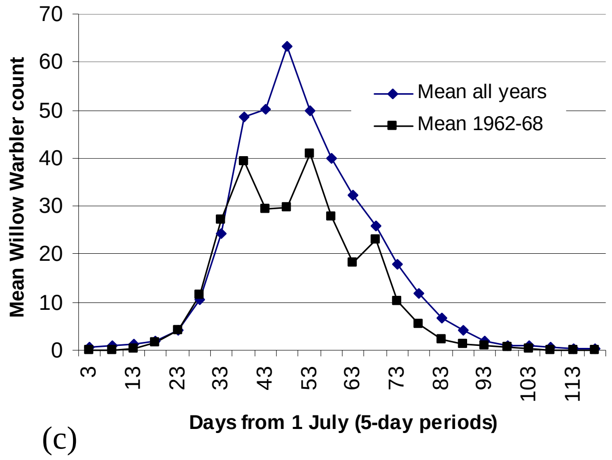
The distribution of mean count against date, across all years 1960–2000, shows a sharp rise in daily counts of Willow Warblers at Dungeness in late July and early August, a high plateau or possibly a double peak in mid August, and a shallower dropping away from late August through September (days 63–92) and into October (Figure 6a–e). Splitting these data into five shorter periods of years, based on the CBC trend, reveals apparent differences in the phenology of passage during this period. These were plotted alongside the all-years index, for direct comparison. Scales on the y-axis vary, to show passage phenology in each period as clearly as possible within the format of this Figure.

Each of the five periods of years shows a double or treble peak in Willow Warbler numbers during the autumn (Figure 6a–e). The three middle periods, from 1969 to 1993, each show seasonal distributions that closely match the long-term average. The all-years average is influenced most heavily by the data for 1980–85, when counts were unusually high throughout the autumn (Figure 6c). During 1962–68, however, the daily distribution was clearly earlier than the long-term average, and for 1994–2000 it was obviously later (Figure 6a, e). Comparing these two periods directly (Figure 6f) shows that each has three peaks but that those for 1994–2000 were one or two five-day periods later in the year.

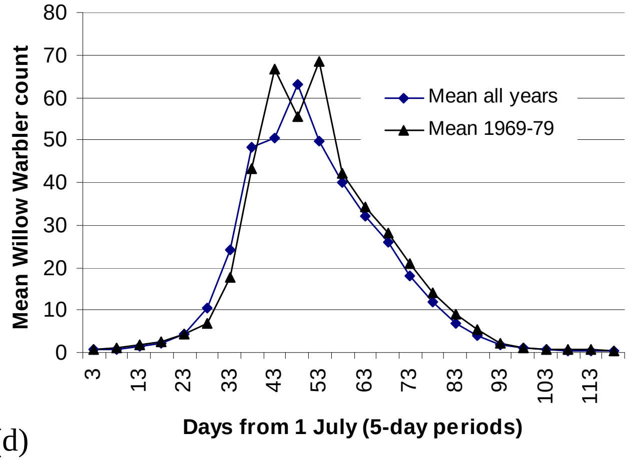
A more detailed summary, of each autumn independently, also indicates that the timing of passage has tended to become later during the study period (Figure 7). The annual median and quartile dates of autumn Willow Warbler passage derived from the DBO log are strongly variable but appear to show a shallow overall trend over time towards the dates, especially the last quartile, becoming later in the year (Spearman rank correlation of last quartile with year is $P<0.05$, $n=41$).

Figure 6. **Mean daily counts of Willow Warblers at Dungeness during 1960–2000 and in five shorter periods defined on the basis of the CBC trend: (a) 1962–68 (CBC index rising); (b) 1969–79 (falling); (c) 1980–85 (rising); (d) 1986–93 (falling sharply); and (e) 1994–2000 (stable). The sixth graph (f) compares the data for the first and last of the five periods.**

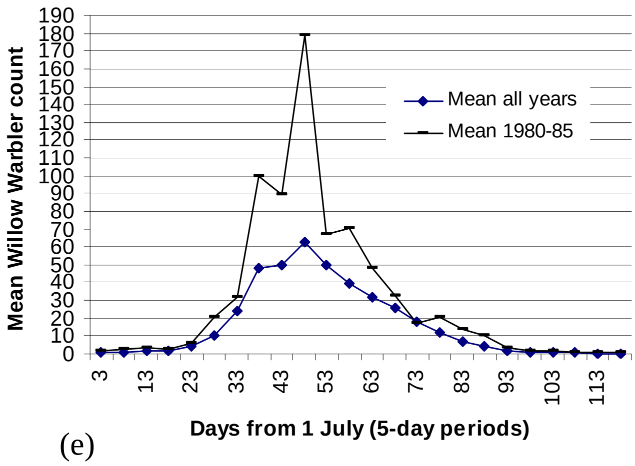
(a)



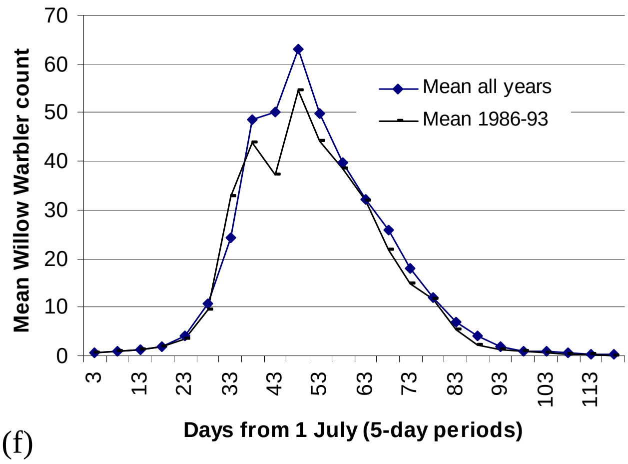
(b)



(c)



(d)



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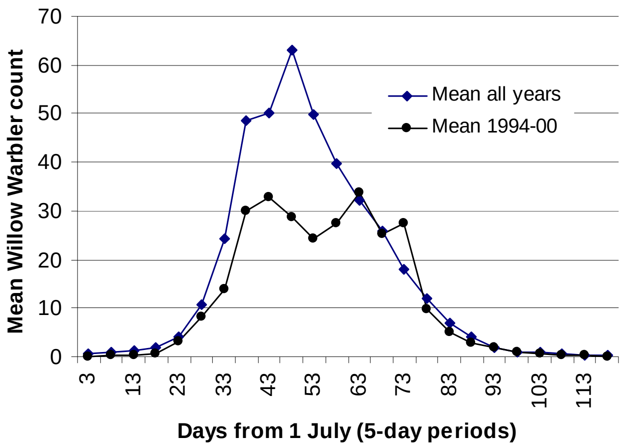

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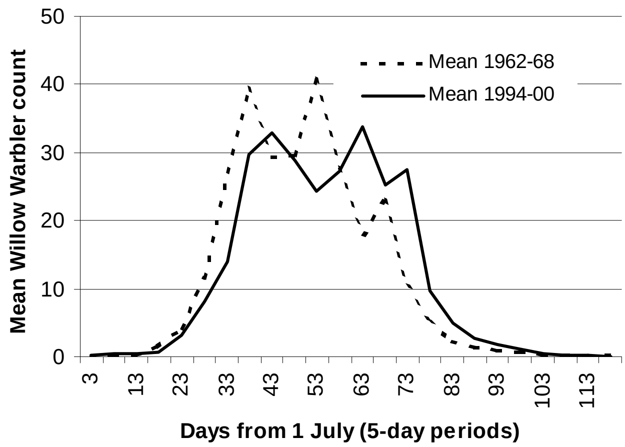
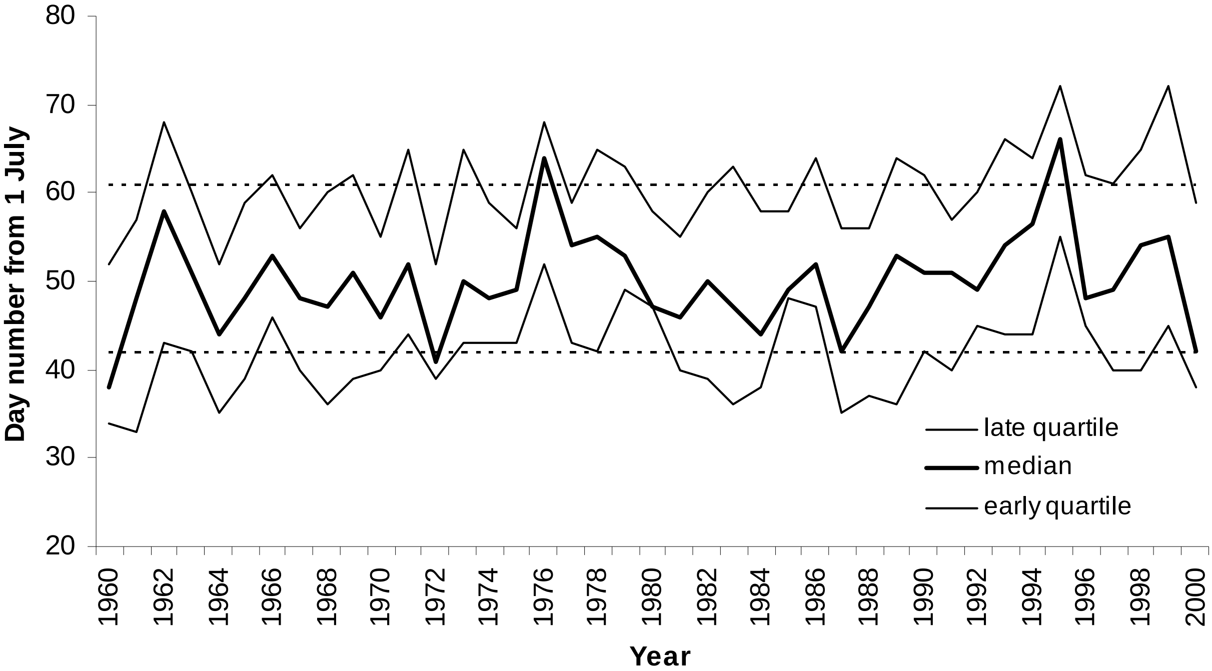


Figure 7. Median and quartile dates of Willow Warbler passage at Dungeness in each autumn 1960–2000. The overall median date was day 50 (19 August). Overall quartiles, at days 42 (11 August) and 61 (30 August), are also plotted.



3.2 Results from ring-recoveries

Ringers can often identify birds that are not in their first autumn, with care, by plumage characteristics. Birds aged as autumn adults when passing through the study zones, together with those ringed elsewhere and known from their ringing date not to be in their first autumn, were classified as 'adult', known first-autumn birds as 'juvenile' and others as 'unknown age'. For each of these three groups, the recovery distance (the distance between ringing and recovery locations) was plotted against the date of autumn passage through the study zones (Figure 8).

Adults were recorded in the ring-recovery data for zones B, D and S from days 24 (24 July) to 86 (24 September), with a median of day 47 (16 August; n=25). The latest date for an adult bird clearly of British origin passing through the study zones was 1 September. Juveniles were present both earlier and later than known adults and were abundant during early August, when adults were scarce.

For both adult and juvenile birds, a clear positive relationship was found between recovery distance and passage day (Spearman rank correlations for adults $P<0.01$, n=25, and for juveniles $P<0.0001$, n=241). Birds recorded early in the season showed no evidence of long-distance movement, while the range of distances from which birds arrived increased progressively during late July and early August for juveniles and during mid August for adults. The latest recoveries from individuals passing through the study zones both showed evidence of Scandinavian origin: these were a juvenile ringed at Dungeness on 26 September 1977 that was recovered in Norway on 13 September 1980, and a bird ringed in Norway as a juvenile on 21 August 1994 that was trapped at Rye Bay on 24 September 1996.

Figure 8. **Recovery distance (distance between ringing and recovery locations) in relation to passage day (date of autumn passage through the study zones) for three age-groups of birds. Evidence of British or Irish origin includes capture on British or Irish breeding grounds (as pullus, adult or juvenile) between spring arrival and 15 July.**

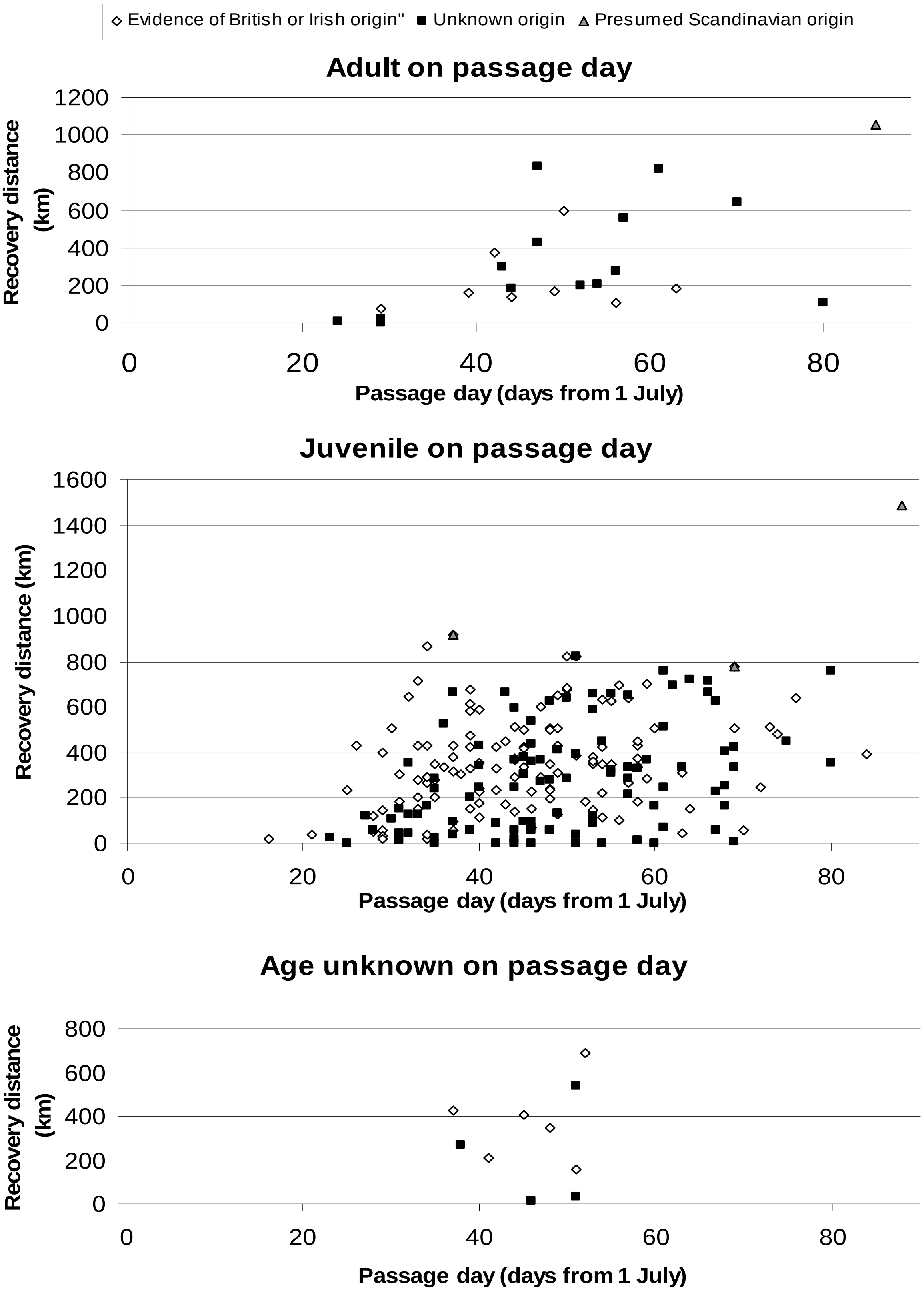
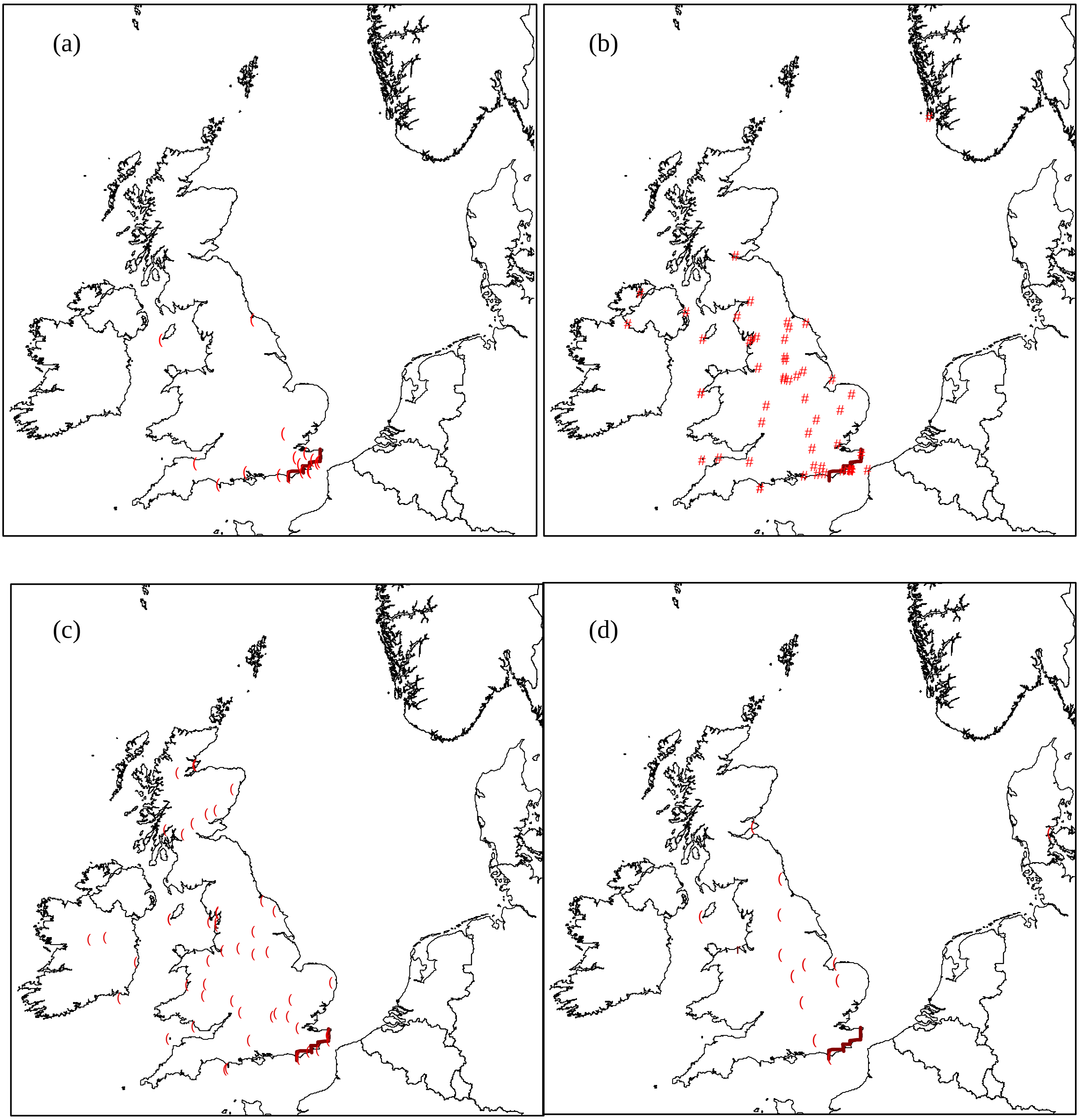


Figure 9. Maps of localities linked to the study zones by ring-recoveries, with passage days in the study zones of (a) 16-31 July, (b) 1-15 August, (c) 16-31 August and (d) spots 1-15 September, star 22 September.



Birds recorded passing through the study zones in July were mostly from southeast England, although three were linked by ring-recoveries to the Calf of Man (Figure 9). Localities for birds in the study zones in August were much more widespread, with concentrations in northern England and later in the month in central and northern Scotland. These maps suggest a sequential passage of birds from breeding grounds progressively more distant from Kent and Sussex as the autumn progresses.

Finding or ringing locations of birds passing through Kent and Sussex in September have a strikingly easterly distribution, suggesting that a large proportion may be of Continental origin.

4 DISCUSSION

4.1 Effect of changes in habitat and coverage at DBO

There has been a long-term change in the vegetation structure in parts of the DBO counting and trapping areas, towards the development of patches of increasingly varied scrubby woodland. This change may be an important influence on the numbers of birds recorded, perhaps by increasing the proportion of passing birds that alight at DBO or the average length of stay, but is one that cannot be assessed. It is unlikely that habitat change at DBO itself should influence the arrival dates of birds on passage. Probably, any influences of habitat change are small by comparison with those affecting the numbers of birds on passage.

4.2 Multi-modality in the DBO log counts

Analysing DBO data from 1953–77, Riddiford (1991) considered that there were two overlapping waves of autumn movement, resulting in peaks in early and late August. He considered that these peaks were due not to the passage of birds from different parts of the catchment area but to age-class differences within the overall catchment. Birds in early August were mainly first-brood juveniles. These were followed later in the month by second-brood juveniles, adults having completed their wing-moult, and possibly by a small number of migrants from the Continent. Since the second peak at Dungeness is higher than the first one, this theory would require either that second broods are more common than is indicated by the nest record cards, or that Continental migrants are more numerous and more regular in their occurrence than previously suspected. He considered that it was less likely that the second wave represented the passage of birds from northern and western parts of Britain & Ireland, because there is no discontinuity in the breeding range that would separate the two waves. Ring-recoveries indicated that birds from Yorkshire were at Dungeness as early as 4 August.

The shorter periods of years investigated in the present study suggest that there are indeed two or sometimes three passage peaks during the autumn. While Riddiford's interpretation that these are primarily due to differential timing of passage between age-classes seems plausible, we present no data to support his interpretation. The pattern of peaks and troughs is not evident when all years 1960–2000 are combined, because their timing has been different in different groups of years within this period. In particular, the three peaks recorded during 1994–2000 are 5–10 days later than those for 1962–68. The present analysis of ring-recoveries shows that there are clear tendencies for birds from parts of the breeding grounds close to Kent and Sussex to pass through a week or two earlier than birds of the same age-classes from more distant parts of Britain & Ireland. A similar result was found for juvenile birds by Norman & Norman (1985). It suggests that peaks representing different age-classes would be expected to be broad, rather than sharp spikes.

The influence of immediate weather conditions on the timing and strength of passage peaks has not been investigated in detail.

A discontinuity in the British & Irish breeding range that was not considered by Riddiford (1991) is the Irish Sea. The recovery data show that birds from the north of Ireland pass through southeast England in early August, alongside birds from southern Scotland and from large areas of England and Wales, whereas birds from central Ireland pass later, as do those from central and northern Scotland (Figure 9).

At present, therefore, it is still uncertain why the autumn passage of Willow Warblers at Dungeness is multi-modal. There might be a hiatus between the passages of birds from Wales and the English Midlands and those that come from Ireland and Scotland, because the intervening distance band contains relatively little land. Continental arrivals tend to be late in the autumn. Overlain on these patterns are the earlier start to the passage of juveniles and the likely differences between early and late broods.

4.3 Why are passage dates apparently getting later?

Autumn passage of Willow Warblers through Dungeness has been later than the long-term average for 1960–2000 in most years since 1993, whereas in most years in the 1960s it was earlier than this 1960–2000 average. Since the time-scale is still relatively short, it is not clear whether this trend towards later passage is likely to continue, or if it may be part of some long-term fluctuation. Any interpretation that is applied to the present results must be tentative and should be followed up by further work designed to remove some of the uncertainties (see Table 2).

Provisionally, we suggest two possible mechanisms that could be behind this change.

First, there may have been a general shift of passage dates to later in the season, such that birds of all age-classes and breeding origins are remaining longer on or near the breeding grounds. Such a change might be expected as a consequence of global warming, if there is an evolutionary advantage to birds staying longer, for example being able to raise a second brood of young, or if the cues that stimulate the onset of autumn passage are now occurring later in the year.

There is an alternative scenario, however, in which climatic warming might result in an earlier autumn departure rather than a later one. In an examination of autumn passage phenology on the southeast shore of the Baltic, Sokolov *et al* (1999) found that in many species the mean date of autumn passage tended to vary in parallel, becoming earlier in warm years when the birds had arrived and bred relatively early in the year. It is possible that whether birds depart earlier or later in response to climatic warming might depend on whether, as may be the case in more temperate parts of Europe than Sokolov *et al* were studying, an early spring arrival might increase the proportion of pairs attempting a second brood.

If there are indeed more second broods being raised, a corollary of this hypothesis would be that there should be more young birds per adult recorded on passage and that, since second-brood young would be expected to migrate later than those from first broods, there should be more young birds in more recent years in the later stages of the passage season.

It seems unlikely that an increase in the number of second-brood young is responsible for the shift towards a later passage through DBO, since breeding productivity as a whole has concurrently been in sharp decline, according to CES data (Figure 1). There is the possibility, however, that we have not investigated, that an increasing proportion of surviving young have been from late broods.

Second, the pattern may be a reflection of the major decrease in breeding Willow Warblers that has occurred in southern Britain since 1983. Ring-recoveries show (in this analysis) that birds originating close to the Dungeness area are the first to pass in autumn, followed by birds from progressively greater distances. It would be expected, therefore, that a reduction in the breeding population in southern Britain would result in many fewer birds passing in the early part of the autumn, while numbers later in the season would be relatively little changed.

This second hypothesis rests on the assumption that the numbers of birds recorded on autumn passage reflect the number of breeding territories of the species that were established earlier in the year. There is limited evidence to support this assumption, although it is widely held. Migration counts are used to monitor breeding populations of birds where relevant breeding census data are lacking, for example for Canadian passerines and for raptors in both Eurasia and North America. In Britain, where census programmes during the breeding season are practical and well developed, some observatory count data have been shown to broadly reflect the known major changes in population level of species such as Sparrowhawk, Corncrake and Whitethroat (Woodbridge 1996). Where migration counts have been compared in detail with census data, however, results have been mixed, even when results from 12 observatories were combined (Woodbridge 1996).

There are several reasons why autumn numbers might not reflect the UK census data. An important one is that the proportion of total passage that is actually detected at ground level by the observatories is unknown and probably variable: Lack (1963) concluded that migration visible at ground level bore little relation to the passage detectable by radar. Another is that the catchment area from which birds are drawn is incompletely known, because of geographical variations in ringing effort and in the probability of reporting a recovery. For many cases, such as for Willow Warbler at Dungeness where suitable weather may bring falls of Continental migrants, the effective area of the catchment is variable from year to year. This becomes important where population trends vary in different parts of the range, as has been demonstrated for Willow Warblers within the UK (Marchant & Balmer 1993, Peach *et al* 1995). Further, autumn migrants include a high proportion of juvenile birds, so that migrant numbers reflect not only breeding numbers but also breeding productivity.

Despite these difficulties, Woodbridge (1996) found a correlation during 1985–94 between the Willow Warbler CBC index and a migration index derived from counts at 12 observatories. Annual patterns differed between sites; at both Fair Isle and North Ronaldsay, 1993 was the year of highest numbers despite the CBC index reaching its lowest point in that year.

4.4 Further investigation

The two hypotheses described above are not mutually exclusive and it is possible that both mechanisms are operating together or that others not formulated here, such as the direct effects of changing weather patterns, are more important. If one or other of the suggested mechanisms is operating in isolation, further work could help to distinguish between them.

Further investigation of the present data set could address, for example:

- investigation of whole ring-recovery dataset for evidence of phenology of autumn movement from different areas of origin, in Britain, Ireland and elsewhere in Europe

- inter-relationships of passage day, age, latitude and longitude, by means of a generalised linear model or regression analysis

- relationships between phenology and annual climatic data for source areas.

If the whole passage is shifting to later in the season, there should be trends for ring-recoveries from each specific part of the catchment area to be occurring progressively later in the season. The pattern of ring-recoveries from different areas of Britain & Ireland could be compared with the numbers of adults and juveniles ringed in each area, derived from the age-specific totals lists held at BTO HQ. It might be expected that more second-brood pulli are being ringed or nest-recorded. This hypothesis would explain the similar, but time-shifted, pattern of peaks and troughs between data from the 1960s and 1990s.

If on the other hand the apparent shift is due to the population decline in the birds that formerly passed through early in the season, no change in the timing of passage of birds from northern Britain should be detectable. It would also be expected that the annual changes in autumn numbers would decline alongside the CBC index. This is not the case for total numbers each autumn, which did not decrease during 1986–93, the main period of CBC decline. Since the median and quartile dates of passage shifted later during this period, however, there may be a correlation between the Willow Warbler CBC index for southern Britain and Dungeness passage numbers up to a certain cut-off date – say 1 August, after which movements from more than 600-km distance are recorded. A long-term correlation of this kind would indicate that population decline in the south is likely to have influenced the apparent timing of passage.

Conclusions could be verified by comparison with similar daily log data from Sandwich Bay Bird Observatory and with the counts on ringing days made by the Beachy Head Ringing Station for each autumn since the 1960s. Observatories have a particularly important part to play in monitoring the effects on bird migration patterns (Marchant 2002).

A complete ringing capture data set for Willow Warbler from Dungeness and the other sites nearby, for a substantial part of the period of this study, would enable the passage to be described more precisely in terms of the age, sex, weight and winglength of grounded birds day by day. By analysis of retraps, it would also allow the estimation of rates of turnover of individuals and this could improve the estimates of the total number of birds using the site each autumn. Riddiford & Auger (1983) have also conducted an analysis of this kind for spring Willow Warbler passage at Dungeness. We would encourage those who hold such data to aim for complete computerization as soon as is practicable.

Table 2. Summary of suggestions for future research on autumn passage phenology.

Suggested further work	**Comments**	**Relevance to the aims of the present project**
Computerization and analysis of the complete ringing and recapture data sets for DBO	This work is in progress	Capture samples throughout the autumn and for a long period of years would, in particular, provide information on age and sex ratios through the autumn, and help to estimate rates of turnover
Investigation of similar Willow Warbler data sets from other bird observatories and ringing stations	Sandwich Bay and Beachy Head are the most relevant sites	Verification and elaboration of conclusions from DBO data alone
Broadening analyses to include other species abundant on autumn migration	Chiffchaff and Whitethroat would provide good comparative data	If trends are similar in other long-distance migrants, as found by Sokolov *et al* (1999), this may strengthen the evidence for climate change as a major driving factor
Further investigation of Willow Warbler population trends elsewhere in western Europe	Census and/or CES data are available from Sweden, Finland, Denmark, the Netherlands and France	May help to determine whether the third peak at DBO, not evident in every autumn, is related to population trends of Continental populations
Further investigation of the effects of weather conditions on daily bird counts	Weather data sets are increasingly available via the Internet	May allow the effects of short-term weather to be eliminated, clarifying the influence of longer-term factors such as climate change

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