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# A report on long-term UK population trends in the pied flycatcher (*Ficedula hypoleuca*)

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## Summary

The pied flycatcher (*Ficedula hypoleuca*) enjoys favourable conservation status throughout most of its European range, but recent reports describe dramatic local declines in certain UK breeding populations in the last 10 years. Using all available nest data, supplied by the British Trust for Ornithology (BTO), we show that UK pied flycatcher breeding populations more than doubled at sites between 1974 and 1988, associated with increasing nest box provision. However, since 1988 the number of breeding pied flycatchers has declined just as dramatically in sites across Wales, England and Scotland, with much local variation in the rate of decline but no obvious trends in geographical variation. Local populations of blue tits (*Parus caeruleus*) and great tits (*Parus major*) remained largely stable or increased during this same period, and variation in nest box number and the quality of woodland habitat (e.g. woodland type, size, degree of isolation, etc.) were not implicated in rates of pied flycatcher population decline. Pied flycatcher (and blue and great tit) per capita clutch size, brood size and nestling mortality were relatively constant after 1988. Site-specific variation in the reproductive variables of all three species were correlated, but unrelated to habitat variables or rates of pied flycatcher population decline. During 1974 to 2001, there was a gradual advancement in pied flycatcher lay-dates across the UK, linked to general increases in spring temperatures, but this appeared unrelated to changes in pied flycatcher numbers. The decline in pied flycatchers therefore appears to be unrelated to ecological conditions at breeding sites within the UK. Instead, the declines may be due to the loss of over-wintering habitat in Africa or the more likely loss of key pied flycatcher migration stopover sites since 1988. Further investigation is now required to link local European pied flycatcher population declines with specific migration routes and/or over-wintering sites. Such effects might be especially associated with reduced recruitment of first year birds, because adults (by definition) will have already established viable personal migration routes and over-winter sites.

## Introduction

There are approximately 50 species of passerines breeding in northern Europe which migrate and winter in Africa, south of the Sahara (Moreau 1972; Bertold 1993). Many of these species have suffered population declines during the last 20 years, both in the UK and in Europe, such as the swallow (*Hirundo rustica*), tree pipit (*Anthus trivialis*), marsh warbler (*Acrocephalus palustris*), lesser whitethroat (*Sylvia curruca*) whitethroat (*Sylvia communis*) and spotted flycatcher (*Muscicapa striata*) (Marchant et al. 1990; Marchant 1992; Bertold 1993; Bertold et al. 1998). However, census data between 1976 and 1989 from five northern European countries have indicated that the number of trans-Saharan migrant species whose populations were increasing may be similar to, and possibly greater than, the number that are declining (Marchant 1992). Despite the importance of such cases, not least as indicators of larger scale ecological change, there are relatively few long-term studies of trans-Saharan migratory bird populations (but see Virolainen 1984; Järvinen 1987; Stennning et al. 1988; Møller 1989; Both et al. 2002).

The pied flycatcher (*Ficedula hypoleuca*) was scarce in the UK during the early part of the 19th century, being common only in North Wales and Cumbria, before undergoing a range expansion during the 1940's (Holloway 1996). Between 1965 and 1988, the UK population was considered stable, with only local increases due to the provision of nest boxes (Marchant et al. 1990). The 1968-1972 UK bird breeding atlas estimated the pied flycatcher population at 20,000 pairs (Sharrock 1976), with further increases to 35-40,000 pairs being recorded in the 1988-1991 atlas (Lundberg 1993). Therefore, the pied flycatcher is neither a red nor an amber data species, and of little conservation concern within the UK (Batten et al. 1990). Furthermore, the pied flycatcher is a 'category 4 species of European concern', meaning that it is a species with a global population that is concentrated in Europe, but which has a favourable conservation status and is considered 'secure' (Tucker & Heath 1994).

Despite its favourable conservation status as a species, local breeding populations of the pied flycatcher have declined by up to 50% since 1990 in Gloucestershire (Lande 1999), as well as in Shropshire/Powys, County Durham and Strathclyde (Anon 2001). In North Wales, occupancy rates have fallen just as dramatically at Abergwygregyn (J. Wright pers. obs.), but with no apparent declines in mid-Wales (R. Cowie pers. comm.). This phenomenon may also be occurring across Europe, with declines being reported in some Dutch populations, but not in one of the main study populations in Hoge Veluwe (C. Both, pers. comm.). Without a full analysis of all existing data, it is difficult to say exactly where the declines in pied flycatcher breeding populations are occurring, what the scale of any decline is, if they are limited to only a few isolated sites, regions or habitats, and what the possible cause of any decline might be.

Here we present the first comprehensive survey of UK-wide pied flycatcher breeding populations, using long-term data sets collated by the British Trust for Ornithology (BTO). As well as the number of breeding pairs of pied flycatchers, we examine the per capita breeding performance of these birds, along with similar data for associated populations of blue tits (*Parus caeruleus*) and great tits (*Parus major*). In this way, we aim to quantify long-term population changes in the pied flycatcher in the UK, assess any geographical variation in the decline in the number of breeding pairs and link it to local changes in breeding performance (clutch size, brood size and lay-date), habitat characteristics of the different woodlands and climatological variables.

# Methods

## The study species

The pied flycatcher is a small trans-Saharan migratory passerine bird which breeds in many forested areas of the Palaearctic region, and migrates to over-winter in tropical West Africa between the Sahara desert and the Gulf of Guinea (Lundberg & Alatalo 1992; Cramp & Perrins 1993). While relatively little is known about pied flycatcher wintering grounds and migration, the propensity for this species to breed in nest boxes in the Palaearctic has made it a very popular species for breeding studies in Western Europe (Lundberg & Alatalo 1992).

Pied flycatcher breeding populations are compared throughout this study with those of resident blue tit and great tit populations. Both these tit species breed in woodland habitats throughout forested areas of the Western Palaearctic region, often competing for available nest boxes with pied flycatchers (Cramp & Perrins 1993), and they have also been the subject of extensive academic study (Perrins 1979).

## The study areas

Data concerning the breeding ecology of pied flycatchers were collected throughout its range in mainland UK. Long term data sets included in the analyses range from Devon to Argyll, and from Gwynedd to North Yorkshire. However, the geographical spread of the data sets generally reflects the range and abundance of pied flycatchers, which inhabit the more westerly and often upland forested areas of the UK (Cramp & Perrins 1993). A list of sites included in the analyses can be found in Appendix 1.

**Data collection**

Data on populations of small hole-nesting passerines breeding in nest boxes have been collected by ornithologists for many years, under licence from either the Countryside Council for Wales, English Nature or Scottish Natural Heritage. Consequently, the British Trust for Ornithology (BTO) has a main list of 52 ornithologists who submit more than 4 nest record cards and/or ring more than 20 pied flycatcher pulli per year. For ecological comparison, data were also provided concerning blue tit and great tit nest records at these same sites whenever possible.

In all, data were collated for 89 pied flycatcher sites, of which 69 contained data on blue tits and 52 on great tits. Of these, we used only those sites where the reliable data covered more than 5 years in duration and where there were no gaps of greater than 5 years. The data set presented here therefore consists of 63 pied flycatcher sites (mean ± S.E. duration = 14.98 ± 0.854 years), including data for 46 blue tit sites (16.22 ± 1.024 years) and 36 great tit sites (16.47 ± 1.277) between 1974 and 2001. Further details regarding the duration of data from each site are provided in Appendix 1.

For each year at each site, data were collated concerning the number of nest boxes available, the number of breeding pairs of all three species, as well as the clutch size and brood size per pair. Not all of these data were available in every instance, and a summary of the sample sizes for each variable is provided in Table 1.

A minority of male pied flycatchers tend to be polygynous in any population (Lundberg & Alatalo 1992), but the data here record only the number of broods. Therefore, our measure of 'number of breeding pairs' more accurately reflects the number of breeding females at each site in each year. Unfortunately, clutch size was not recorded in every case, due either to a lack of time or fear of disturbance by the observer. Repeat (re-laid) clutches were often problematic to identify unequivocally, and so all breeding attempts were included when calculating average clutch and brood sizes. Failed nests that were known to contain a complete clutch of eggs, but no nestlings at 7 days old (i.e. due to abandonment and/or predation), were still included in clutch size estimates.

**Table 1.** Summary of breeding population sample sizes available for each variable (PF = pied flycatcher; BT = blue tits; and GT = great tits).

| Variable | Min Sample Size | Max Sample Size | Mean (± SE) | No. of Sites |
|---|---|---|---|---|
| Nest box Number | 10 | 350 | 66.06 (7.71) | 59 |
| Number PF Pairs | 2 | 67 | 16.36 (1.85) | 63 |
| Number BT Pairs | 1 | 141 | 15.58 (3.31) | 46 |
| Number GT Pairs | 1 | 47 | 9.40 (1.67) | 36 |
| PF Clutch Sizes | 3 | 66 | 15.52 (1.73) | 61 |
| BT Clutch Sizes | 2 | 142 | 16.48 (4.01) | 38 |
| GT Clutch Sizes | 2 | 47 | 9.34 (1.90) | 30 |
| PF Brood Sizes | 3 | 66 | 15.12 (1.67) | 62 |
| BT Brood Sizes | 2 | 142 | 15.97 (3.89) | 39 |
| GT Brood Sizes | 2 | 47 | 9.72 (1.89) | 31 |

Brood size was defined at 7 days old or when the chicks were ringed, because chick mortality in the nest after either of these points is uncommon (Lundberg & Alatalo 1992). Data on 19,189 young from 12 of the sites used here showed that an average of 81% of pied flycatcher pulli ringed subsequently fledged successfully. Comparable figures for blue tits and great tits were 93% (n = 18,671) and 94% (n = 7,359) respectively. In each case, the number of young at 7 days old and the number of young ringed does appear to give a reasonable indication of the final number of young fledged. Chick mortality from hatching failure and/or starvation in the nest was quantified as the difference between recorded clutch sizes and brood sizes.

Lay-date was estimated for each of the three species as the mean date of initiation of the first five clutches per year. Although not a perfect measure, especially for populations that are changing in size, this measure did help reduce the data collation for our individual observers and avoided the accidental inclusion of re-laid clutches in the estimate. Pied flycatcher, blue tit and great tit lay-dates were available for only 19, 8 and 6 sites respectively, due to observers rarely being able to visit nest boxes frequently enough to obtain reasonable lay-date estimates (i.e. to reliably record the timing of clutch initiation prior to incubation, or to record precise hatch dates to allow lay-date to be back calculated based upon the species and clutch size involved). Whenever there were fewer than 5 lay-dates in any given year, the lay-date data for this species were considered unreliable and were not used.

The precise location of each site was ascertained in most cases with a grid reference, longitude and latitude, and classified by country into six regions of the UK: 1=Wales; 2=Midlands; 3=South West; 4=North West; 5=North East; and 6=Scotland (see Appendix 1). Each site was classified as either 'deciduous' or 'coniferous' (depending upon the woodland type that occupied the larger proportion of the woodland) or 'mixed woodland' (if patches of deciduous and coniferous trees were interspersed throughout), and as 'plantation' (trees of similar age) or 'mixed aged' (trees of a variety of ages). The size of the nest box area within each wood was defined as 1, 2, 5 or '10 or more' $km^2$, and the distance calculated to the nearest suitable patch of woodland for pied flycatchers, again defined as 1, 2, 5 or '10 or more' kilometres.

Temperature data were obtained from the UK Meteorological Office via the Historical Central England Temperature Data (www.badc.rl.ac.uk). The nationwide data include temperatures that are representative of a roughly triangular region of the UK enclosed within lines between Preston, London and Bristol. Daily maximum temperatures between 16 April and 15 May inclusive from 1974 to 2001 were used to indicate relevant spring temperature, because this represents the average time of pied flycatcher arrival on the breeding grounds and the start of breeding (Both & Visser 2001).

**Statistical analysis**

Data for each site in each year were treated as independent units of analysis in statistical tests. However, we might expect population sizes in adjacent years to be auto-correlated (see below), and therefore in some way non-independent, at least biologically. Therefore, data were also converted to year on year changes and average rates of population change per site. Therefore, initial tests quantified changes in the absolute number of breeding pairs of pied flycatchers, whilst the main analyses examined possible explanations for difference in year-to-year changes in pied flycatcher numbers between sites.

Although no populations went extinct, changes (usually increases) over time in the number of sites and the number of nest boxes per site were assessed and, where possible, controlled for in tests concerning population changes. Given the non-linear nature of population trends, all tests included an assessment of non-linear components (e.g. year, $year^2$, $year^3$, etc.) and the results presented represent those that provided the best fit to the data. All analyses were weighted to account for the varying number of nest boxes and/or the varying number of years of data at each site, because larger sites monitored over more years were more likely to yield more reliable estimates of population change. All models were full factorial in design, but non-significant interaction terms are not always presented here for reasons of brevity. All tests are two-tailed and a critical P-value of 0.05 applied throughout.

# Results

## General population trends

Over the whole 28 years (1974-2001) for which we have reliable data for the UK, the number of pied flycatcher pairs per site initially more than doubled, reaching a maximum around 1988, but then decreased by almost the same amount again before 2001 (Fig.1). Regression analysis over the whole period revealed a monotonic curvilinear relationship between year and the number of pied flycatcher pairs, with a quadratic function peaking at 1988 providing the best fit ($r^2$=0.27, $F_{2,929}$=12.84, P<0.001; no. pairs = 20.49 + year0.12 + year$^2$-0.06).

However, it appears from Fig.1 that both the increase up until 1988 and the decrease after that were in themselves linear. This was tested for by performing pairs of linear regressions, with the break point between the two being moved up and down for the different years either side of 1988. The results are shown in Table 2 in the form of the total mean residual sum of squares from both regressions combined, which demonstrates that a split linear regression centred on 1988 provides the best fit to these data (Fig.1: pre-1988: $r^2$=0.07, $F_{1,249}$=18.85, P<0.001; no. pairs = 2042.92 + year1.04; post-1988: $r^2$=0.02, $F_{1,679}$=12.62, P<0.001; no. pairs = 1334.76 + year-0.66). Indeed, at 254152, these two linear regressions provide a lower combined mean residual sum of squares than the 255083 value derived from the overall non-linear (quadratic) regression described above. Reassuringly, all of these results also hold when the data are expressed as percentage nest box occupancy (e.g. Table 2b). Incidentally, the low $r^2$ values described in Table 2 are almost entirely due to variation in flycatcher numbers between sites. Linear regressions on just the mean values per year yield much more convincing $r^2$ values (Fig.1: pre-1988: $r^2$=0.94, $F_{1,13}$=217.20, P<0.001; post-1988: $r^2$=0.85, $F_{1,11}$=64.43, P<0.001).

**Figure 1.** Mean (±SE) number of pied flycatchers pairs per site 1974-2001. Best-fit lines are shown for linear regressions either side of 1988 - see text for details.

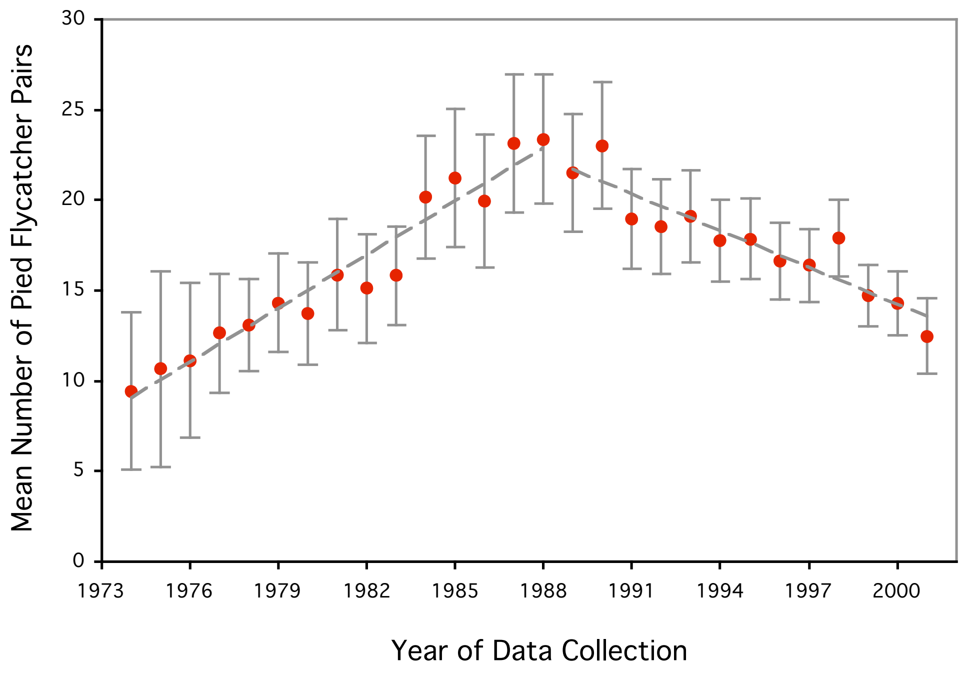



**Table 2.** Total mean residual sum of squares from pairs of linear regressions for **(a)** the number of pairs and **(b)** the percentage nest box occupancy of pied flycatchers, against the year at which the two regression lines were split (see Fig.1 and text for details). The lowest values are highlighted in bold, because these represent the best fit to the data.

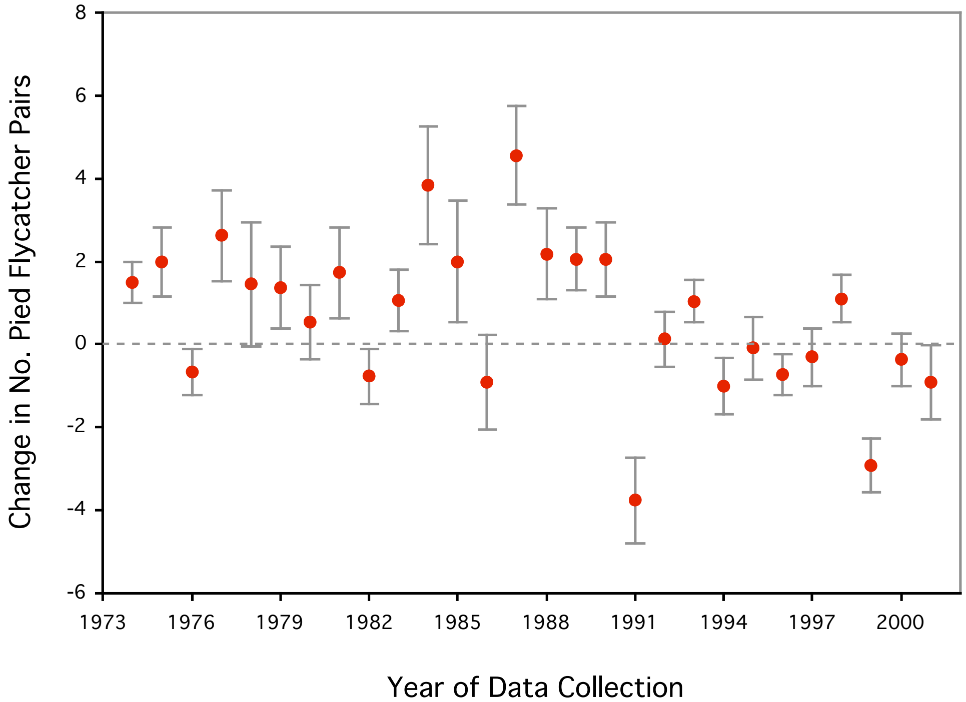
| **Variable** | **1985** | **1986** | **1987** | **1988** | **1989** | **1990** | **1991** |
|---|---|---|---|---|---|---|---|
| **(a)** Number of pairs | 254419 | 254134 | 254181 | **254152** | 254336 | 254521 | 255184 |
| **(b)** % Occupancy | 260029 | 255685 | 258524 | **258510** | 259000 | 258919 | 260685 |

This split in the data at 1988 suggests that different factors may have been influencing pied flycatcher populations before and after this date. Therefore, subsequent analyses have mostly been carried out on the two halves of the data separately, from 1974 up to and including 1988, and from 1989 to 2001 inclusive.

**Autocorrelation in population sizes between years**

As expected, the number of pied flycatcher pairs in any one year was significantly positively autocorrelated with the numbers in preceding and subsequent years (Fig.1: pre-1988: r=0.76, n=15 P=0.001; post-1988: r=0.59, n=13, P=0.001), although partial autocorrelations revealed no significant effects lasting beyond one year (all P-values <0.05). Therefore, when population values were expressed as the year-to-year change in the number of pied flycatcher pairs, there were no significant autocorrelations (Fig. 2: pre-1988: r=-0.28, n=15, P=0.230; post-1988: r=-0.23, n=13, P=0.348).

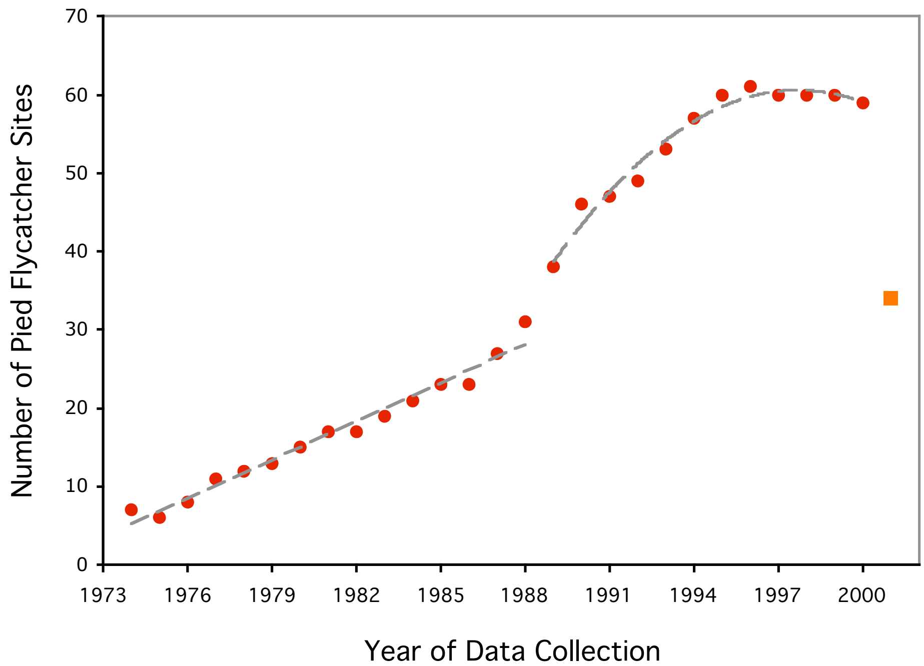
**Figure 2.** Mean (±SE) year-to-year changes in the number of pied flycatchers pairs per site 1974-2001.



**Changes in the number of sites and the number of boxes per site**

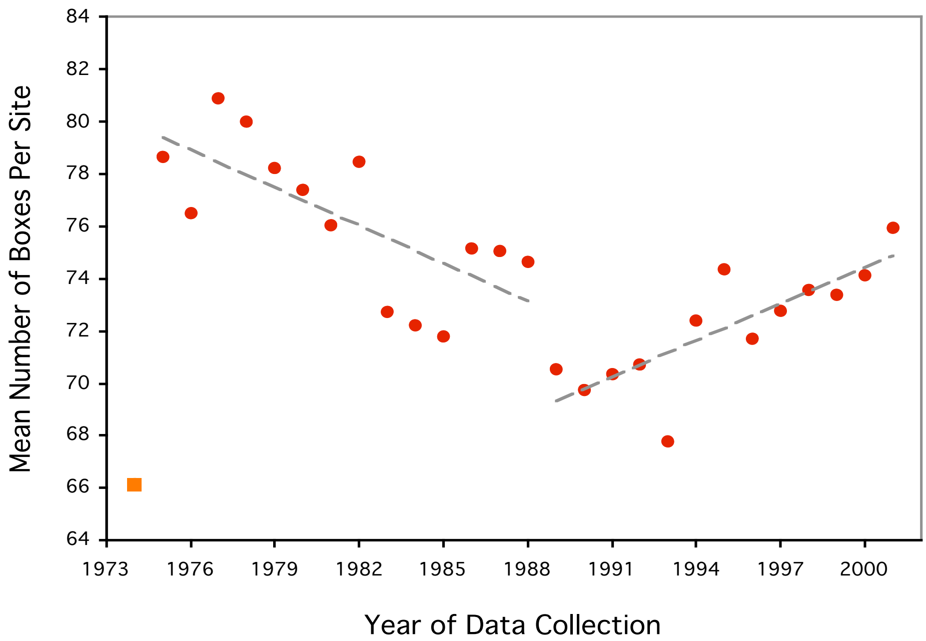
There was a gradual increase in the number of sites recording pied flycatcher numbers throughout the whole period (Fig.3). Incomplete records from 2001 make this year an exception, and it has therefore been excluded from these particular analyses. The increase in the number of sites for which data were available was linear between 1974 and 1988: (Fig.3: $r^2$=0.97, n=15 P<0.001; no. sites = 28.12 + year1.64), but after 1988 this increase was significantly non-linear (quadratic regression) and reached an asymptote by 1996 (Fig.3: $r^2$=0.97, n=12, P<0.001; no. sites = 33.86 + year5.35 + year$^2$-0.27). This gradual addition of new sites suggests that changes in the mean population sizes per site shown in Fig.1 were not simply the result of different sites being included or excluded according to their availability in different years.

**Figure 3.** Number of UK pied flycatcher sites 1974-2001. Best-fit lines are shown for linear regression (pre-1988) and quadratic regression (post-1988), with one excluded data point for 2001 – see text for details.



Patterns in the mean number of nest boxes per site were also complex (Fig.4). The first year 1974 contained only a few sites with very few boxes in each, and it has therefore been excluded from these particular analyses. There was a linear decrease in the number of boxes per site between 1974 and 1988 (Fig. 4: $r^2$=0.50, n=14 P=0.005; no. boxes per site = 73.15 + year-0.48), probably as a result of an increasing number of relatively smaller sites being set-up each year (see Fig.3 above).

**Figure 4.** Mean number of pied flycatcher nest boxes per site 1974-2001. Best-fit lines are shown either side of 1988, with an excluded data point for 1974 - see text for details.




However, after 1988 there was a significant linear increase in the mean number of boxes per site (Fig. 4: $r^2$=0.65, n=12, P=0.001; no. boxes per site = 68.86 + year0.46). This may have been due to new larger sites containing more nest boxes being set up after 1988. However, the addition of extra boxes to existing sites must have been important, not least as a cause of the increase in the number of boxes per site after 1996 (Fig.4), because after this date there were few new sites with larger numbers of boxes being added (see Fig.3 above).

More detailed ANCOVA analyses showed that when controlling for the significant difference in the number of boxes at the different sites (pre-1988: $F_{29,143}$=211.87, P<0.001; post-1988: $F_{58,481}$=67.03, P<0.001), there were no significant or consistent year to year changes in the number of boxes per site (pre-1988: $F_{1,143}$=1.28, P=0.260; post-1988: $F_{1,413}$=3.78, P=0.053). Thus, the trends in the mean number of boxes per site in Fig.4 were, as suspected, largely the result of new sites of different sizes being added, which changed the mean number of boxes per site in the dataset in different years. However, this same ANOVA model revealed key interaction terms describing contrasting changes in the number of boxes within different sites. At some sites nest box numbers remained more or less constant (i.e. no effect of year), whilst at many other sites nest box number increased in a non-linear (cubic) function with year, as evidenced by significant interaction terms between site and all measures of year, both before 1988 (year*site: $F_{1,143}$=2.18, P=0.003; $year^2$*site: $F_{1,143}$=4.21, P<0.001; $year^3$*site: $F1_{,143}$=5.09, P<0.001) and after 1988 (year*site: $F_{1,413}$=4.37, P<0.001; $year^2$*site: $F_{1,413}$=3.53, P<0.001; $year^3$*site: $F_{1,413}$=3.35, P<0.001). Therefore, box numbers increased in a step-like manner at some sites but not others at various times throughout the dataset, even before 1988 when the mean number of boxes per site was decreasing overall.

Therefore, changes in the number of sites and the number of boxes per site had to be carefully considered in subsequent analyses concerning changes in the number of breeding pairs of pied flycatchers. The number of nest boxes available for pied flycatchers in any one year at a site will also depend upon the number of nesting great tits and blue tits, and so this variation must also be considered.

**Examining population change per site**

ANCOVA on absolute pied flycatcher numbers before 1988 confirmed that there was a significant linear increase in the number of breeding pairs per year (Fig.1: $F_{1,166}$=7.04, P=0.009), with no significant curvilinear terms (quadratic year$^2$: $F_{1,166}$=0.38, P=0.540). This result persisted whilst controlling for the expected significant effect of site on pied flycatcher numbers ($F_{29,166}$=68.16, P<0.001), but it did involve significant interactions between site and year ($F_{23,166}$=11.01, P<0.001), and between site and year$^2$ ($F_{23,166}$=6.15, P<0.001). Thus, the increase in pied flycatcher numbers prior to 1988 was linear, and the rate of increase was somewhat dependent on the particular site involved, with the additional effect that some sites showed a slowing of the rate of increase in the years leading up to 1988.

These changes in pied flycatcher numbers at each site before 1988 can be seen in Appendix 1, which demonstrates the significantly positive nature of the population changes, as well as illustrating the variation that existed between sites. There were significant increases in 11 of the 21 sites for which sufficient (>4 years) data were available. For 5 of these 11 sites, the increase in pied flycatcher numbers was also significantly associated with an increase in nest box number, and this association was significantly positive overall (Appendix 1). There was little change in this result when using box availability to account for blue tit and great tit box use (Appendix 1). Therefore, increases in nest box availability pre-1988 may well have been one of the causes of the early increase in UK pied flycatcher populations, but it also represents a potentially confounding effect for any subsequent analyses of the pre-1988 data. This is because changes in nest box number effectively represent variation in sampling effort per site. As a result, additional exploration of factors affecting population increases in pied flycatchers before 1988 will not be carried out here. Some limited analyses could perhaps be performed on the small sub-set of <10 sites showing little or no changes in box number, although it is not clear how representative these might be. Either way, it is really the pied flycatcher declines after 1988 that are of interest here and that require explanation, and so it is these that will form the majority of the remainder of these analyses.

The ANCOVA for the data after 1988 showed the expected significant linear decrease in the number of breeding pairs per year (Fig.1: $F_{1,528}$=17.59, P<0.001), with no significant curvilinear terms (all P-values <0.05). Again, this result held whilst controlling for the highly significant effect of site ($F_{58,528}$=72.81, P<0.001), as well as a significant interaction between site and year ($F_{58,528}$=11.01, P<0.001). So, the post-1988 decrease in pied flycatchers was not simply a function of additional (and perhaps more poorly occupied) sites being included in the data set, plus the rate of decline varied according to the particular woodland site.

The details for each site after 1988 confirm these conclusions, with 45 out of 62 sites showing a decline in pied flycatcher numbers, 16 of which were significant in themselves (see Appendix 1). Despite the significant decline on average, variation between sites was apparent, with 16 of the 62 sites actually showing increases in pied flycatcher numbers, 2 of which were significant. In contrast to the pre-1988 results, very few of these changes were confounded by changes in nest box number, or nest box availability (which includes blue tit and great tit settlement), with no significant overall associations between either variable and pied flycatcher numbers (see Appendix 1). It is therefore apparent that decreases occurred in the number of nesting pairs of pied flycatchers in the majority of monitored nest box study sites in the UK since 1988, some of which were substantial (i.e. 7.5% mean loss per year for the 16 sites with significant declines). Sufficient variation is also present in the extent of these declines per site, which should make it possible to identify any causal factors that might exist in the breeding and habitat variables being analysed here.

**Habitat effects since 1988**

As Appendix 1 shows, the decline in pied flycatcher numbers since 1988 was widespread throughout the UK, occurring at many different sites in Wales, all parts of England and in Scotland. The percentage rate of decline in pied flycatchers per site was not significantly affected by region within the UK ($F_{5,56}$=1.32, P=0.268), and in a separate analyses there were no significant effects of geographical position (latitude: $F_{1,31}$=1.56, P=0.221; longitude: $F_{1,31}$=0.63, P=0.435). Qualitatively similar results were obtained for percentage changes in numbers of blue tits and great tits per site.

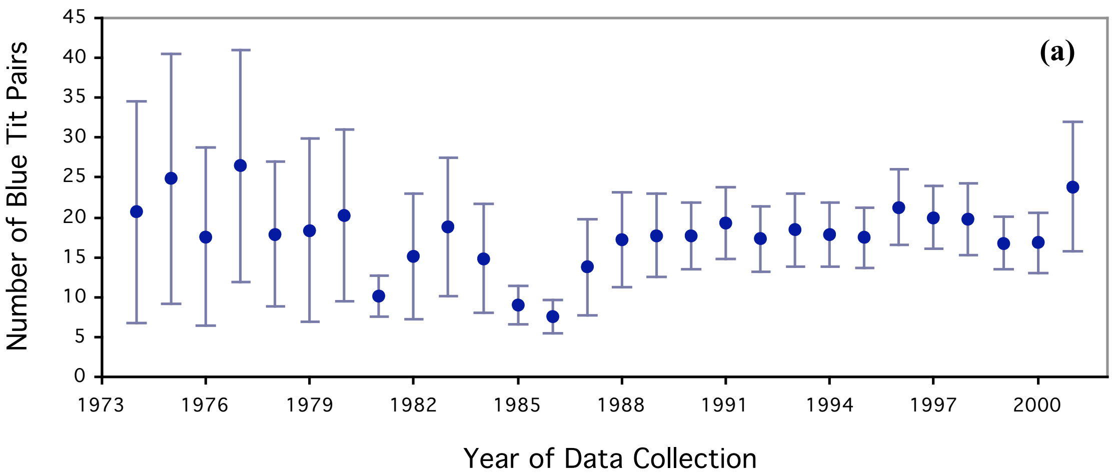
There were 32 pied flycatcher woodlands in the UK 1989-2001 for which we have some ecological data. Most are 'mixed aged' stands of 'deciduous' trees, with only 3 'mixed species woodlands' and 6 'plantation' sites (all of these plantations being 'deciduous'). This severely limits our ability to critically assess the effect of woodland type on pied flycatcher population change (i.e. analyses were restricted to separate t-tests that do not assume equal variances). However, there were no significant effects of woodland type ($t_{30}$=0.52, P=0.653) or tree age structure ($t_{29}$=0.66, P=0.520) on the percentage changes in pied flycatcher populations per site pre-1988. There were also no significant effects of woodland area ($F_{1,28}$=0.00, P=0.971) or distance to the next suitable woodland site ($F_{1,28}$=2.33, P=0.138). Again, qualitatively similar results were obtained for percentage changes in the numbers of blue tits and great tits per site. All of which suggests no obvious role here for variation in the woodland habitats.

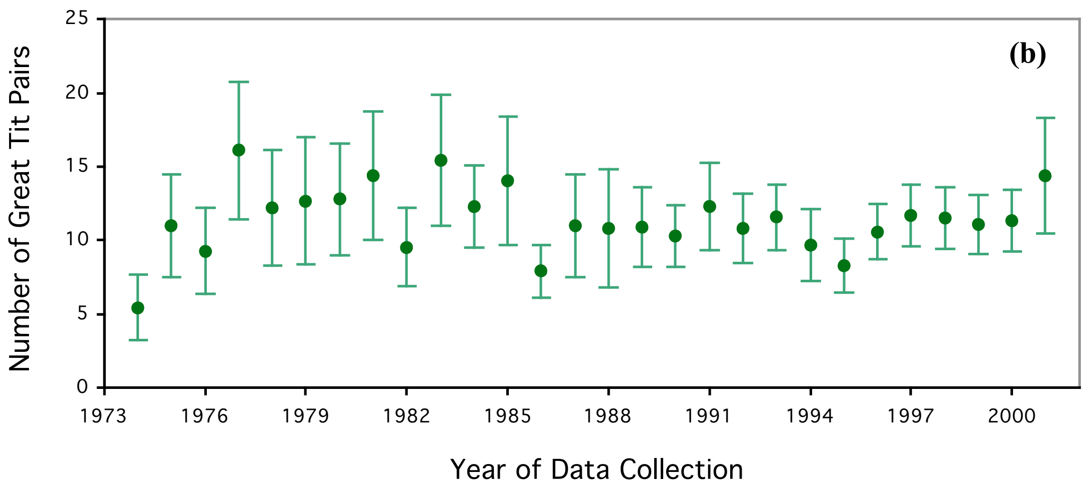
**Blue tit and great tit population effects since 1988**

Unlike the pied flycatchers, data on blue tit and great tit populations after 1988 showed no evidence for any decline in the number of breeding pairs per year (Fig.5: ANCOVA: blue tits:

$F_{1,385}$=1.04 P=0.308; great tits: $F_{1,316}$=4.09 P=0.044). Indeed the marginally significant result for great tits actually describes a moderate increase in numbers since 1988 (Fig.5b, Appendix 2). For both tit species there were the usual highly significant effects of site on the number of breeding pairs (blue tits: $F_{41,385}$=51.14, P<0.001; great tits: $F_{34,316}$=17.30, P<0.001), but no significant interactions between site and year (blue tits: $F_{41,385}$=1.01, P=0.547; great tits: $F_{34,316}$=1.42, P=0.068). So, the post-1988 declines in pied flycatchers were not accompanied by similar declines in blue tits or great tits. Rather, tit populations were constant, and even increased in numbers, which may reflect the stability of UK woodland breeding habitats for these species since 1988.

**Figure 5.** Mean (±SE) number of **(a)** blue tit and **(b)** great tit pairs per site 1974-2001.



The analysis above on nest box number suggested that blue tit and great tit numbers had little effect on pied flycatcher populations by limiting nest box availability (see Appendix 1). In agreement with this, there was no correlation between the rate of decline in pied flycatcher numbers per site post-1988 and changes in blue tits numbers at those sites during the same period ($r=-0.17$, $n=45$, $P=0.265$). However, there was a weak positive correlation between changes in pied flycatcher numbers and changes in great tit numbers at sites since 1988 (Appendix 2: $r=-0.34$, $n=35$, $P=0.049$), and a similar positive but marginally non-significant correlation between changes in blue tit and great tit numbers per site ($r=-0.35$, $n=35$, $P=0.066$). These positive correlations perhaps reflect a correspondence in the ecological conditions that favour breeding populations of the three species. Site-specific changes since 1988 in insect food abundances and predation levels perhaps provide a weak link in the general population dynamics between species.

In order to further explore any interspecific interactions, more detailed ANCOVA were carried out, but they revealed no evidence that the pied flycatcher numbers after 1988 were directly affected by blue tit numbers ($F_{1,278}=0.03$, $P=0.872$) or great tit numbers ($F_{1,278}=0.07$, $P=0.797$). There was the usual highly significant effect of site on pied flycatcher numbers ($F_{34,278}=2.32$, $P<0.001$), but no interactions between the effects of site and blue tit numbers ($F_{34,278}=0.84$, $P=0.723$) or between site and great tit numbers ($F_{34,278}=0.61$, $P=0.960$). Analyses of the variation (and the percentage variation) in year-to-year changes in pied flycatcher numbers revealed similar non-significant affects of any year-to-year changes in blue tit and great tit numbers (all P-values >0.05). Therefore, the declines in pied flycatchers after 1988 do not appear to have been directly associated with any changes in blue tit and great tit populations during this period.

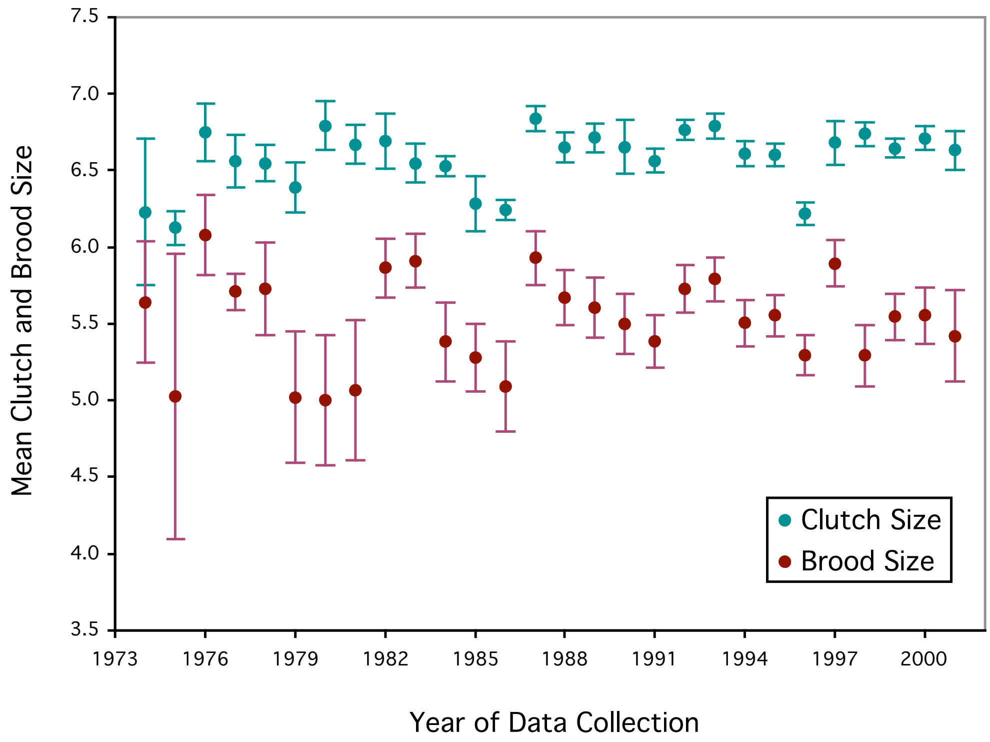
**Breeding productivity effects since 1988**

Table 2 shows that there were no significant overall changes with year since 1988 in either clutch size, brood size or chick mortality in the nest in pied flycatchers (Fig.6), or in blue tits or great tits at these same sites. There were, however, significant differences between sites in these breeding parameters, especially in the levels of chick mortality and the resultant brood sizes (Table 2; Appendix 3). There were also significant year by site interactions for pied flycatcher brood size and chick mortality, and for great tit brood sizes. These suggest some population variation in changes in breeding productivity 1988-2001, however the P-values in all these cases are not very convincing given the number of tests involved.

**Table 2.** Results of ANCOVAs showing the effects of year 1988-2001, population site and the interaction (year*site) on average breeding parameters: clutch size, brood size, and chick mortality in the nest for all three species. F-ratios with degrees of freedom and P-values are given, and significant results are underlined.

| Variable | Year | | Site | | Year*Site | |
|---|---|---|---|---|---|---|
| **Pied Flycatcher** | $F_{1,513}$ | **P** | $F_{59,513}$ | **P** | $F_{59,513}$ | **P** |
| Clutch Size | 0.05 | 0.831 | 1.32 | 0.063 | 1.02 | 0.432 |
| Brood Size | 0.97 | 0.326 | 1.93 | <0.001 | 1.50 | 0.012 |
| Chick Mortality | 2.21 | 0.138 | 2.28 | <0.001 | 1.46 | 0.018 |
| **Blue Tit** | $F_{1,310}$ | **P** | $F_{36,310}$ | **P** | $F_{36,310}$ | **P** |
| Clutch Size | 1.68 | 0.196 | 1.36 | 0.089 | 0.65 | 0.941 |
| Brood Size | 0.33 | 0.565 | 2.34 | <0.001 | 0.86 | 0.702 |
| Chick Mortality | 0.40 | 0.525 | 2.17 | <0.001 | 0.98 | 0.503 |
| **Great Tit** | $F_{1,233}$ | **P** | $F_{29,233}$ | **P** | $F_{29,233}$ | **P** |
| Clutch Size | 1.11 | 0.292 | 1.64 | 0.025 | 0.85 | 0.690 |
| Brood Size | 0.62 | 0.432 | 1.95 | 0.003 | 1.51 | 0.049 |
| Chick Mortality | 2.02 | 0.157 | 2.32 | <0.001 | 1.41 | 0.089 |

**Figure 6.** Mean (±SE) pied flycatcher clutch size and brood size values 1974-2001.




Consistent with the strong effects of site in Table 2, there were significant positive correlations between the species in mean clutch size per site (PF-BT: r=0.34, n=37, P=0.040; PF-GT: r=0.38, n=30, P=0.037) and mean brood size per site (PF-BT: r=0.78, n=38, P<0.001; PF-GT: r=0.34, n=31, P<0.001), as well as mean levels of chick mortality per site (PF-BT: r=0.83, n=37, P<0.001; PF-GT: r=0.69, n=30, P<0.001). There were even significant positive correlations between the mean year-to-year changes in these breeding variables per site, involving changes in clutch size (PF-BT: r=0.34, n=37, P=0.039; PF-GT: r=0.49, n=30, P=0.006) and brood size (PF-BT: r=0.43, n=38, P=0.007; PF-GT: r=0.44, n=31, P=0.012), but not in changes in chick mortality (PF-BT: r=0.26, n=37, P=0.118; PF-GT: r=0.16, n=30, P=0.414). So, as Appendix 3 illustrates, there was variation between sites in all three pied flycatcher breeding parameters since 1988, and average yearly changes were often associated with parallel changes in the breeding parameters of blue tits and great tits at those sites.

It is, however, unlikely that the between population differences in pied flycatcher breeding variables were due to any obvious differences in habitat between these sites. This is because there were no significant effects of region, latitude, longitude, woodland type or age structure, area or distance to the next nearest wood on mean pied flycatcher brood sizes and chick mortality (all P-values <0.05). There were also no significant effects of these habitat variables on the mean annual rates of change in pied flycatcher clutch sizes, brood sizes and chick mortality since 1988 (all P-values <0.05).

In ANCOVA, the number of pied flycatcher pairs at sites since 1988 was unrelated to any of the breeding parameters (clutch size: $F_{1,493}$=0.64 P=0.419; brood size: $F_{1,502}$=0.02, P=0.894; chick mortality: $F_{1,486}$=0.01 P=0.918). There were some of the usual significant effects of site on the number of breeding pairs (ANCOVA on clutch size: $F_{56,493}$=0.40 P=0.999; brood size: $F_{57,502}$=1.54, P=0.009; chick mortality: $F_{56,486}$=11.58 P<0.001), but no significant interactions between site and any breeding parameter (ANCOVA on clutch size: $F_{56,493}$=0.54 P=0.998; brood size: $F_{57,502}$=0.59, P=0.992; chick mortality: $F_{56,486}$=0.68 P=0.964). So, variation in the size of different pied flycatcher populations was not directly linked with variation in breeding productivity between sites.

The slopes of the change in pied flycatcher population sizes since 1988 were positively associated with mean brood sizes at those sites (r=0.28, n=61, P=0.030), probably as a result of significantly greater chick mortality at those sites with the greater levels of population decline (Fig.7; r=-0.36, n=60, P=0.009). However, there is an outlier (see bottom of Fig.7), which is the large site at Nagshead (Gloustershire) containing >400 boxes. Its removal for this analysis is justified because it is *four* full standard deviations from the mean, and in which case the association between mean chick mortality and rates of pied flycatcher population decline is reduced to a marginally non-significant one (Fig.7; r=-0.25, n=59, P=0.056).

**Figure 7.** Mean pied flycatcher chick mortality in the nest against mean yearly change in pied flycatcher numbers per site 1988-2001. Best-fit line is shown (y=0.11+-0.61x) for regression *including* the Nagshead (Gloustershire) outlier data point at bottom – see text for details.

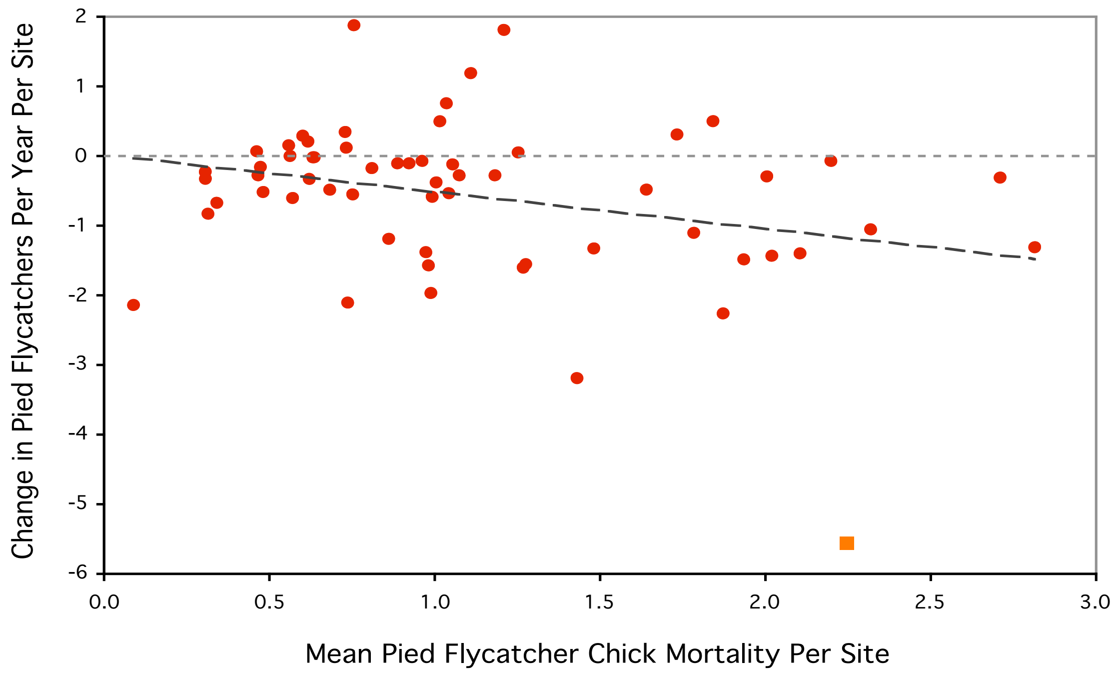
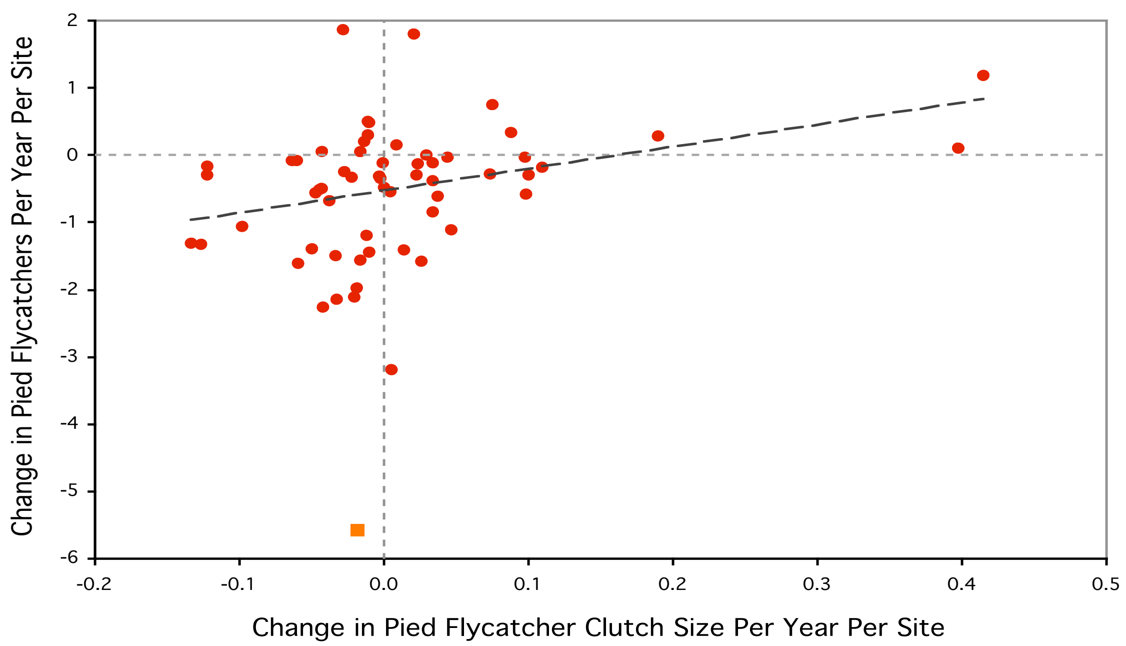



**Figure 8.** Mean yearly change in pied flycatcher clutch size against mean yearly change in pied flycatchers per site 1988-2001. Best-fit line (y = -0.5263 +0.2914x) is shown for the regression *excluding* the Nagshead (Gloustershire) outlier at the bottom – see text for details.



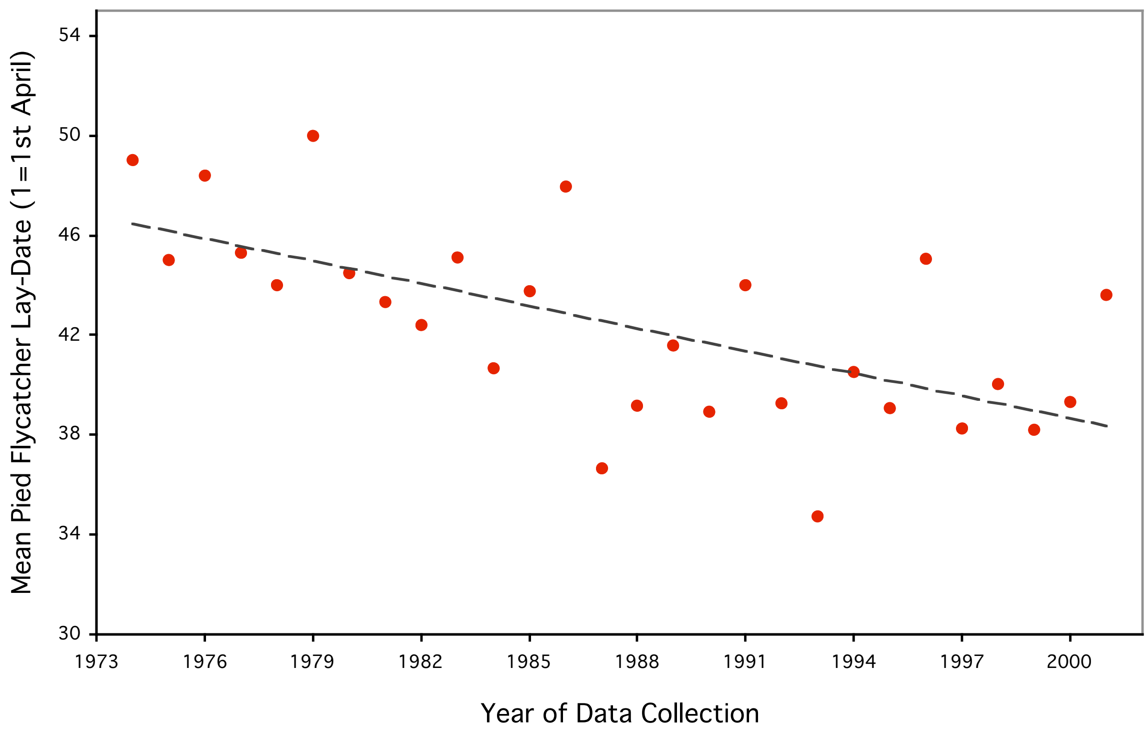
There was also a positive association between the mean change in pied flycatcher numbers per site since 1988 and the change in clutch size per site (Fig.8; r =0.30, n=60, P=0.021). Although not too convincing in itself, this result becomes much stronger following the removal above of the Nagshead (Gloucestershire) site as a possible outlier concerning rates of population change and such breeding variables (Fig.8; r=0.34, n=59, P=0.009).

Therefore, a couple of possible links do appear between local breeding parameters and UK pied flycatcher population declines since 1988. Population declines may have been greatest at sites that recorded the highest chick mortality in the nest. Declines may also have been more severe at sites that also experienced declines in mean clutch size during the period 1989-2001. However, both these results depend heavily upon the inclusion/exclusion of certain key data points. They also follow a large number of exploratory tests across a range of breeding and habitat variables. Given the lack of supporting evidence in other parameters, they should perhaps be viewed with some degree of caution at this stage.

**Variation in the timing of breeding**

The timing of breeding in UK pied flycatchers, as measured by average lay-date of the first five clutches, became significantly earlier during the period 1974 to 2001 (Fig.9; $r^2$=0.41, n=27, P<0.001). There were no obvious changes in lay-dates either side of the usual 1988 breakpoint used above. There was a very strong effect of population site on pied flycatcher lay-dates (Fig.10; $F_{1,21}$=7.52 P<0.001). However, variation in mean lay-dates, and even the rate of change in lay-date per year (1974-2001), were not significantly related to longitude or latitude, or geographical region of pied flycatcher population sites, with the same also being true for blue tits and great tits lay-date data at the same sites (all P-values >0.05).

**Figure 9.** Mean pied flycatcher lay-dates 1974 to 2001 for the 23 UK sites for which data were available. Best-fit regression line is shown (y = 640.59 + -0.301x).




Over the period 1974 to 2001, there was a linear increase in mean daily spring temperatures equivalent to 0.065°C per year (16$^{th}$ April to 15$^{th}$ May; $r^2$=0.28, n=25, P=0.005), but not in mean daily summer temperatures (16$^{th}$ May to 15$^{th}$ June; $r^2$=0.00, n=25, P=0.950). This suggests a likely cause of the advancement in pied flycatcher lay-dates shown in Fig.9, and regressions of lay-date against spring temperature performed on data for each site separately (to control for the strong effects of site, see above), were significantly negative overall (Fig.10; mean slope = –1.23 ± 0.35; t=-3.56, n=23, P=0.002).

Despite local variation between sites in the rate of advancement in pied flycatcher lay-dates 1974-2001 (see Fig.10), there was no significant effect of local changes in spring temperatures between sites (Fig.11; $r^2$=0.07, n=22, P=0.223). Unfortunately, however, there were only 6 different meteorological stations providing the 'local' temperature data for the 23 sites for which pied flycatcher lay-date data were available.

**Figure 10.** The effect of local spring temperatures (16th April to 15th May) on local pied flycatcher lay-dates for the 23 UK sites for which data were available 1974 to 2001. Best-fit regression lines are shown for each site separately – see text for details.

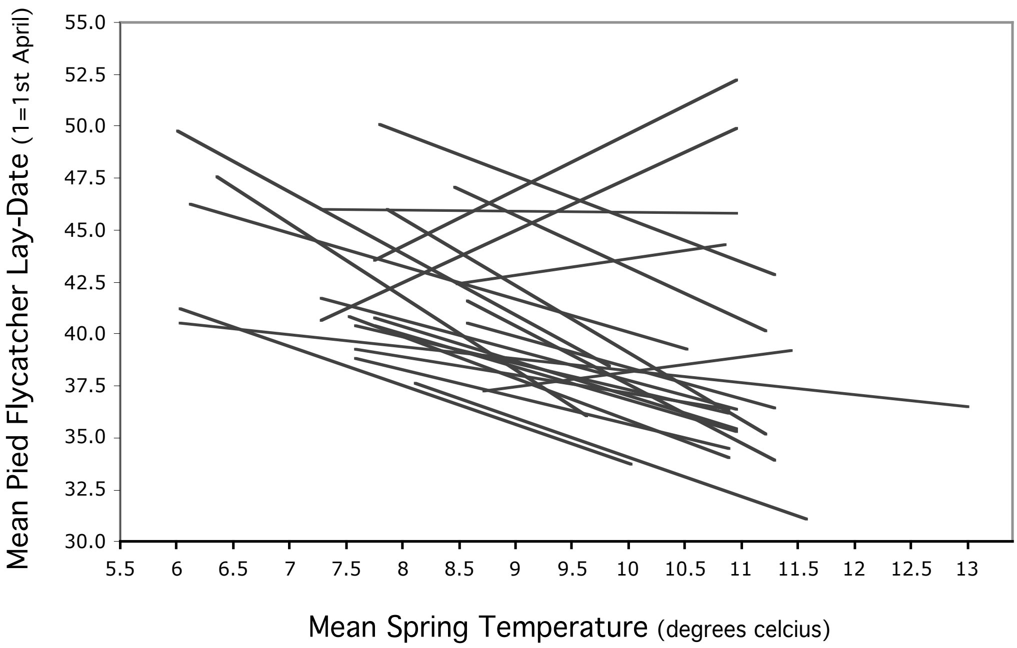
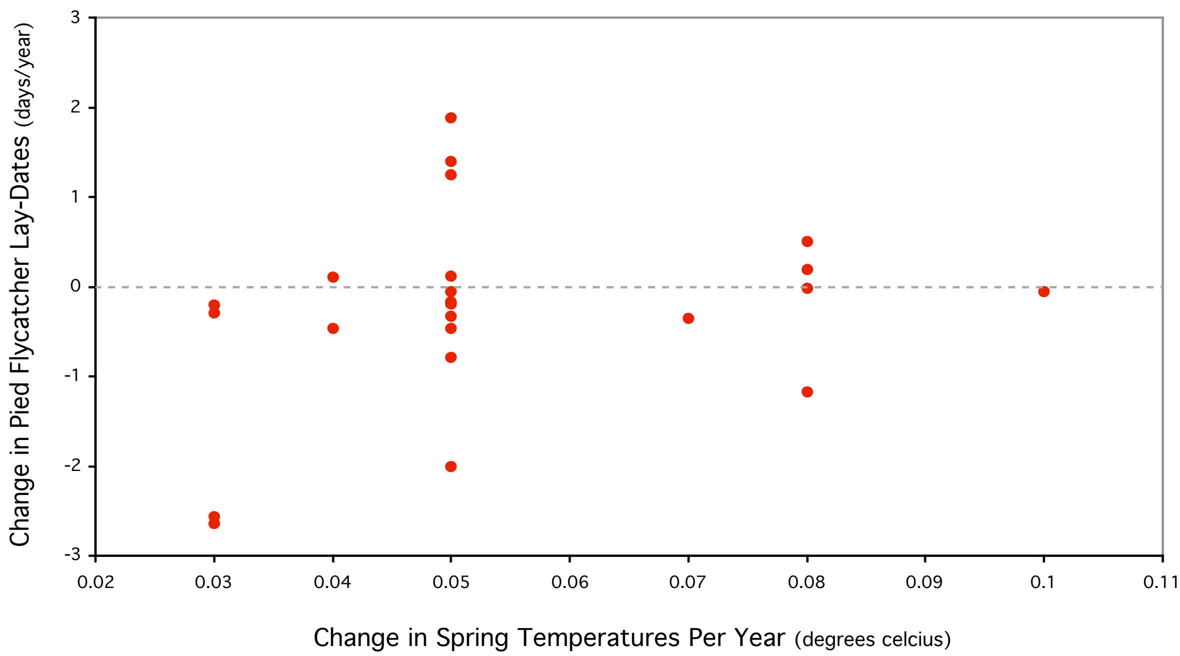



**Figure 11.** No effect of local changes in mean spring temperatures on local changes in pied flycatcher lay-dates 1974 to 2001 for the 23 UK sites for which data were available.



Variation in lay-dates had no significant effect on the number of pied flycatcher pairs per site since 1988, and this held for lay-dates from all three species (pied flycatcher: $F_{1,148}$=0.15 P=0.699; blue tit: $F_{1,75}$=0.03, P=0.958; great tit: $F_{1,63}$=0.00 P=0.987). The usual effects of site were not significant (pied flycatcher: $F_{22,148}$=0.85 P=0.662; blue tit: $F_{9,75}$=0.1.29, P=0.256; great tit: $F_{8,63}$=0.38 P=0.927), probably as a result of the strong correspondence between site and lay-date itself (see above), which may itself reveal additional statistical problems here concerning co-variation. There were also no significant interactions between site and lay-date (pied flycatcher: $F_{22,148}$=0.57 P=0.938; blue tit: $F_{9,75}$=0.93, P=0.507; great tit: $F_{8,63}$=0.13 P=0.998). So, variation in pied flycatcher numbers was not directly linked to differences in lay-date for any of the three species, although the small number of sites for which there were blue tit and great tit lay-date data severely limits the power of some of these tests.

Since 1988, there were no correlations between mean number of pied flycatchers (or the mean yearly rate of change in those numbers) per site and mean lay-dates, or the mean yearly rates of change of those lay-dates. These results held for pied flycatchers, as well as for lay-date data from blue tits or great tits at those same sites (all P-values <0.05). Therefore, local variation in lay-dates was not associated with local declines in pied flycatcher populations.

There were also no correlations between mean pied flycatcher lay-dates (or the mean yearly rates of change in those lay-dates per site) since 1988 and any other breeding parameters (e.g. clutch size, brood size and chick mortality), or the mean yearly rates of change in those breeding parameters. Again, these results held for data from pied flycatchers, as well as for data from blue tits and great tits at those same sites (all P-values <0.05). Despite the small samples sizes involved for some of these tests, these null results suggest no obvious population consequences, as yet, from the advancement of pied flycatcher (or tit) lay-dates, with no associated decrease in breeding productivity or population sizes.

## Discussion

### Nest box provision and pied flycatcher population trends

The willingness of the pied flycatcher to breed in nest boxes has been extensively demonstrated by the numerous scientific studies on this species (e.g. Alatalo et al. 1985; Gustafsson & Nilsson 1985; Lundberg & Alatalo 1992). With an ever increasing number of nest boxes being erected in woodlands during the last few decades, it is not surprising that the results presented here show a link with pied flycatcher populations that have been increasing rapidly throughout the UK between 1974 and 1988. The provision of nest boxes has previously been shown to increase breeding density in this species (Alatalo & Lundberg 1984; Alatalo et al. 1985; Fuller & Crick 1992), as well as increasing individual breeding success when compared to natural cavities (Nilsson 1984; Alatalo et al. 1985; Lindberg & Alatalo 1992). The provision of nest boxes in suitable breeding habitat has also been shown to expand this species' range (Lundberg & Alatalo 1992; Lundberg 1993, 1997; Both et al. 2002). The increasing number of nest box sites in the UK may therefore have opened up new breeding habitats to pied flycatchers previously limited by the number of natural nest holes. However, to properly assess the scale of such population increases we need to know the number of breeding pairs that were resident in natural cavities at these sites before and after nest box introduction and population monitoring occurred (Nilsson 1984).

The apparent importance of nest box provision suggests that pied flycatcher populations in the UK are not limited by food availability, which is often the most important factor determining breeding success (Lundberg & Alatalo 1992). The fact that pied flycatcher clutch and brood sizes did not substantially influence population growth (1974-1988) or decrease (1988-2001) again indicates that food availability was not a limiting factor to population density in this case, as it is for many other hole-nesting passerines (Perrins 1979; Newton 1998). Therefore, unlike some of the well-studied Scandinavian populations (see Alatalo & Lundberg 1984), there appears to be little evidence that UK pied flycatchers are anywhere close to their population carrying capacity and subject to density dependent changes in per capita breeding success.

**Pied flycatcher population declines, habitat type and breeding success**

The large declines in pied flycatcher nest box occupancy between 1988 and 2001 (2.66% per year on average, and 7.25% per year for the 16 worst affected sites) were almost on the same scale as the increases in numbers prior to 1988. Changes in nest box number per site did not appear have any influence on these declines, nor was there any reduction in the number of nest box sites available to pied flycatchers. Whilst pied flycatcher populations were changing so dramatically, there were no such changes mirrored in blue and great tit populations. If limited food availability were the cause of the reduction in pied flycatcher numbers, then we might have expected a similar decrease in tit numbers, which raise young on a similar diet of lepidopteran larvae for the most part. In addition, there were no obvious links between the declines in the number of pied flycatchers and changes in breeding parameters of pied flycatchers, blue tits or great tits. Some weak statistical evidence was discovered for links between pied flycatcher nestling mortality and population declines, and for rates of decline in pied flycatcher clutch sizes and population declines, but these were unduly influenced by the inclusion/exclusion of single outlying data values from the large Nagshead site in Gloucestershire. Either way, strong statistical links were lacking between breeding productivity and rates of decline in pied flycatcher nest box populations. In a short-lived species such as the pied flycatcher, the time delay between a decline in population productivity and a reduction in the numbers of breeding adults would have been short enough to be detected here (Bibby 1992; Lundberg & Alatalo 1992; Newton 1998). All of this implies that there was a simply decline in the number of young pied flycatchers being recruited into these breeding populations, whilst the potential for reproduction per pair on the breeding grounds probably remained undiminished.

Pied flycatcher population changes also appeared to be largely unaffected by geographical location, perhaps because this would require a larger sampling area than mainland Britain (Jävinen 1989; Lundberg & Alatalo 1992). There was also no evidence of any obvious ecological factors being associated with differences in pied flycatcher population sizes or rates of decline (or with breeding parameter data on pied flycatchers, blue tits or great tits). It is possible that any statistical tests concerning links with woodland type were limited because there were so few coniferous, or even mixed species, woodland sites in this UK data set. It is well known that pied flycatchers prefer deciduous over coniferous woodland (Lundberg et al. 1981; Gezedins et al. 1984; Alatalo et al. 1985), and experience higher reproductive success in continuous areas of deciduous woodland, rather than fragmented and coniferous woodlands (Alatalo et al. 1985; Huhta et al. 1998; Lundberg & Alatalo 1992). Nevertheless, there was also no clear link between the rates of population decline per site and tree age structure, area and degree of isolation of each woodland site. The lack of any such habitat effects on pied flycatcher numbers and breeding parameters is perhaps unsurprising, due to the limited ecological variance represented by the sites included here. This is because woodlands containing nest boxes, and especially those being regularly monitored by observers, were probably chosen because they contained a certain number of breeding pied flycatchers, and therefore represented some of the most suitable and unvarying breeding habitat available in the UK for this species. In addition, it is very unlikely that these particular areas of breeding habitat have changed in any way during the period of this study, and especially not in any dramatic fashion either side of 1988 (see Fuller 1995; Forestry Commission 2001).

The lack of evidence here for linkss between UK pied flycatcher population declines and changes in breeding productivity could be claimed to be the result of a lack of statistical power, given that data on clutch and brood sizes were available from only a minority of sites. Even smaller data sets for blue tit and great tit nests at the same sites could make those comparisons even weaker. However, it was clear that despite these much reduced data sets, and the possible homogeneity of pied flycatcher UK nest box habitats (see above), subtle variation was detected in many of the breeding variables. Correlations were apparent between pied flycatchers and blue tits and great tits in their productivity per nest between sites, and in year-to-year variation in nest productivity within sites. So, the data presented here were sensitive enough to reflect the site-specific effects of certain unrecorded ecological factors that must be important for the breeding productivity of these types of small woodland bird species. Obvious possibilities that suggest themselves here include factors influencing the local abundance of prey species (e.g. tree leaf density/quality and winter moth productivity), the density of predators (e.g. weasel or sparrowhawk numbers), or even the size and type of nest box used. Systematic changes over time in these types of ecological influences were detected, because they must have affected productivity of pied flycatcher, blue tit and great tit populations in parallel. Given such empirical sensitivity, we are perhaps justified in our conclusion that little evidence exits to suggest that the serious decline in UK pied flycatcher is the result of changes in breeding habitat or per capita reproductive success.

**Changes in spring temperatures and pied flycatcher lay-dates**

The advancement of pied flycatcher lay-dates as a result of global warming has been shown in populations all across Europe (e.g. Winkel & Hudde 1997; Sokolov, 2000; Both & Visser, 2001; but see Sanz et al., 2003). Previous studies of this type have involved only a limited number of pied flycatcher populations in the UK (see Both et al. In Review), with exception of a number of sites in Wales (Slater, 1999; Sparks et al. In Review). The present study adds to this evidence, with the advancement in pied flycatcher lay-dates 1974-2001 being demonstrated for populations across the whole of the UK, with a clear causal link to global warming via spring (but not summer) temperatures. Despite a lack of any systematic geographical variation in changes in the of timing pied flycatcher breeding, there was still much local variation in the rate of lay-date advancement. However, it was not possible to replicate the Europe-wide result of Both et al. (In Review), showing that local variation in rates of change of spring temperatures can explain local variation in rates of changes in pied flycatcher lay-dates. It is probable that the small geographical distances involved, and perhaps a lack of variation in local climate change at this spatial scale, limits the magnitude of any such variation in lay-date change within the UK. This was not helped, however, by the relative geographical grouping of the 23 pied flycatcher sites with sufficient lay-date data, which meant that the 'local' temperature data was obtained from only 6 different meteorological stations.

The advancement of pied flycatcher lay-dates showed no obvious link with breeding productivity or rates of population decline, either within or between sites or years (nor in any association with data from blue tit or great tit populations at the same sites). Therefore, changes in mean lay-dates were not implicated in the UK pied flycatcher populations declines since 1988. Nevertheless, it has been suggested that this continued advancement of lay-dates is, at some point in the near future, going to come into conflict with the fixed timing of migration of pied flycatchers, which is less labile and based upon day length (Both & Visser 2001). We might therefore expect to see detrimental effects on the breeding of late arriving birds, which miss the peak of food abundance in woodlands, thereby leading to an evolutionary shift in the timing of migration in this species. The data here suggest that this hypothesised effect is not yet happening within UK pied flycatcher populations, assuming of course that subtle changes in pied flycatcher arrival dates have not already started to occur (see discussion in Sparks et al. In Review). Clearly, all these effects are open to more thorough testing using the long-term UK data sets (held and/or managed by the BTO), including more complete and accurate information (than that used here) concerning changes in individual lay-dates and nest productivity throughout the whole pied flycatchers season.

**Alternative causes of the decline in pied flycatchers**

The number of breeding pairs of pied flycatchers has clearly been declining in the UK since 1988, and despite variation in this decline between breeding sites there does not appear to be any obvious explanation based upon changes in the breeding habitat or any density dependent phenomena concerning reproductive contributions to the population. It therefore seems appropriate here to speculate upon some of the possible alternative causes of this decline, both on the over wintering grounds and during migration to and from the UK (Bibby 1992; Lundberg & Alatalo 1992).

Pied flycatcher over-wintering habitat in tropical West Africa has been studied very little, although this species is known to inhabit a vast area and range of woodland types, from forest canopy to savannah woodland, and even gardens around Freetown, Sierra Leone (Lundberg & Alatalo 1992; Cramp & Perrins 1993). The quantity and quality of these habitats may have suffered in recent decades, due to deforestation, hydrological schemes, coastal development and the use of pesticides (Kelsey 1992; Jones et al. 1996). Indeed, over-winter mortality as a result of such habitat loss being implicated in the decline of at least four warbler species (Baillie & Peach 1992). The overall rate of deforestation in Africa has been estimated at around five million acres per year during the 1980's, but this dropped to four million acres per year in the 1990's, although it may now have risen again since then (Chew 1995). Despite their frighteningly large-scale, these habitat changes are not, as far as we know, centred upon any specific over-wintering woodland habitats of the pied flycatcher in West Africa. In addition, there are no obvious sudden changes in these figures that match the time-scale of the changes from 1988 onwards reported here for UK flycatcher breeding populations. Therefore, on the basis of currently available evidence, it seems unlikely that over-winter mortality is particularly responsible for the recent rapid decline in UK pied flycatcher populations.

UK pied flycatchers migrate in the spring and early autumn to and from West Africa, via the Iberian Peninsula, the Sahara and the Atlas Mountains (Hope Jones et al. 1977; Lundberg & Alatalo 1992; Pilastro et al. 1998; Hope Jones 2002). Birds migrating south each autumn make a dog-leg journey to Iberia, instead of migrating immediately south (Lundberg & Alatalo 1992; Hope Jones 2002), probably to exploit favourable feeding areas in the woodlands of Portugal at this time of year (Lundberg & Alatalo 1992; Cramp & Perrins 1993). Given the importance of migratory stopover sites for refuelling (Bibby & Green 1980), the decline in UK pied flycatchers may well be due to the removal or alteration of small areas of key habitat *en route*. Unfortunately, we know relatively little about migratory habitat use by pied flycatchers (Cramp & Perrins 1993). However, pied flycatchers are known to associate with woodland trees in Iberia and oases across the Saharan desert (Lundberg & Alatalo 1992; Cramp & Perrins 1993). The similarly migrant southwestern willow flycatcher (*Empidonax trailli extimus*) often seeks out water sources during migration (Finch et al. 2000), which may also provide an important resource for pied flycatchers and be associated with potential prey in the absence of trees.

Data do exist showing that the wetlands of Morocco have been reduced by 25% between 1978 and 1999 (Morgan 1982; Green et al. 2002), with 98% of this loss being concentrated in the crucial wetland types of low salinity, 48% being mountain lakes and 33% being *Phragmites* /

*Scripus lacustris* marshes. Although there have been no losses recorded in any other wetland types, degradation has occurred at all sites due to hydrological impacts, overgrazing and/or excessive reed cutting, sedimentation, urban development, pollution and other causes. Unfortunately, of the 47 wetlands studied, only 10 have any kind of protection status. It is also these types of freshwater wetlands that hold the majority of invertebrate species, with man-made channels and reservoirs having limited value as migratory stop-over sites for many birds, and presumably also for pied flycatchers (Green et al. 2002). The use of Saharan oases by migrant birds has been described by Schaub & Jenni (2001) and by Schaub et al. (2001), and these oases can be especially important at the northerly and southerly margins as they effectively increase the width of the desert (Bairlein 1992). Therefore, key North African stopover sites for pied flycatchers might have been lost during the period after 1988, which may explain the dramatic changes in UK breeding populations.

Unfortunately, we do not have similar figures relating to the loss of woodland in southern Portugal and Spain, although the destruction of vast areas of cork oak and other woodland during the last decade deserves further study. The economic downturn in the market for real cork, and the now regular occurrence of large summer fires in Portugal, would certainly appear to fit the 1988 breakpoint identified in the present study. Furthermore, juvenile pied flycatchers undertaking their first migration appear to target key stop-over sites on the Iberian peninsula less accurately than older birds that have previously made at least one migratory journey (Rabøl 1978; Lundberg & Alatalo 1992). Ringing recoveries and autumn release experiments showed that these inexperienced first year birds had less accurate angular dispersions upon release, and therefore end up taking more southerly routes, missing key stop-over sites for fattening in Iberia (Sandberg et al. 1991). Therefore, any habitat changes may well be expected to differentially affect young first year birds, because they will be more likely to miss the limited remaining areas. Adult birds, by definition, will include those birds with a proven level of accuracy and/or experience to have survived during their first migration. Therefore, we suggest that site-specific declines in the number of breeding pairs of pied flycatchers in the UK might be associated with variation in relative rates of first year recruitment, as opposed to adult return rates. This hypothesis is clearly open to testing using existing UK ringing return records held by the BTO.

**Conclusions**

The post-war increase in UK pied flycatcher numbers has clearly continued up until 1988 and seems linked to the provision of nest boxes, mostly at new woodland sites, but also through the expansion of existing sites. Of more interest is the dramatic and rapid reversal of this trend on or around 1988, and the subsequent decline which appears to be relatively site specific and is continuing until the present day. A range of ecological factors was investigated, but failed to show evidence that population declines were a result of differences in pied flycatcher breeding habitat. The lack of degradation in these prime UK woodland habitats was also evidenced here by the consistency in blue tit and great tit populations and per capita breeding performance of the pied flycatchers themselves. The previously noted advancement of pied flycatcher lay-dates was identified for populations across the UK, as was the causal link to global warming via spring temperatures. However, the limited local variation in data available concerning UK spring temperatures meant that there were no site-specific effects on local changes in lay-date. It was also clear that local variation in advancement of pied flycatcher lay-dates was having no effect on breeding productivity, as yet, and that it was not implicated in the pied flycatcher populations declines since 1988. We have therefore come to the conclusion that the cause of the recent decline UK pied flycatcher numbers is probably the result of habitat degradation of over-wintering sites in west Africa, or the more likely loss of migratory refuelling stop-over sites in Iberian woodlands and/or north Africa oases.

**Suggestions for future work**

This study has been confined to pied flycatcher nest box population sites in mainland Britain, mostly because the BTO provides one of the most detailed and complete data sets worldwide. However, the UK does not necessarily constitute a geographically distinct pied flycatcher population separate from the rest of Europe, because there will be a certain degree of mixing upon migration and especially at the over-wintering grounds. Indeed, a wider analysis across Europe might provide some useful insight as regards the geographical extent of the recent pied flycatcher population declines and their possible cause. The contrasting migration routes taken by different breeding populations might also provide a fruitful direction of future study, if as we suspect it is the loss of key refuelling stopover sites that is the cause of the decline, perhaps by preventing first year recruitment in some but not all populations. Studies of migrating bird populations can now be much more effective through the additional use of genetic analyses (e.g. mitochondrial DNA or nuclear microsatellite primers) and the more recent use of geographic variation in isotope frequencies within feathers grown either following summer or winter moults. Therefore, the continuation of this work into the causes and consequences of UK pied flycatcher population declines would necessarily involve a Europe-wide approach and substantial financial investment. As such, it could provide an excellent model system with which to develop these future methods and techniques in global avian conservation.

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