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The decline of the Bullfinch *Pyrrhula pyrrhula* in Britain: is the mechanism known?

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Abstract. The Bullfinch has declined in Britain and elsewhere in Europe, but definitive evidence about the cause and demographic mechanism has yet to be published. We review current knowledge, concentrating on analyses of demography, and present new integrated population modelling analyses designed to reveal the demographic changes most important in the decline. It is likely that changes in brood size and clutch size have not been important and our models suggest that the decline can be explained without invoking variation in numbers of breeding attempts or post-fledging survival rates. However, although changes in the egg period daily nest failure rate provide the best explanation for population change during the years of steepest decline, nestling period failures, adult survival and first-year survival could all have been equally important. Egg period nest failure rates have been higher in the preferred habitat, woodland, than in farmland and have fallen over time in farmland, where a larger decline has occurred (65% versus 28%), arguing against a causal link with abundance. Despite evidence for a negative effect of agricultural intensification on Bullfinch presence, little evidence exists clearly linking any demographic rate to environmental change and agricultural land-use has had little effect on nest failure rates. Predation appears to have had no significant impact. Future work should focus on contemporary investigations of the importance of hedgerow structure and woodland understorey vegetation.

Key words: Bullfinch, *Pyrrhula pyrrhula*, demography, population models, bird conservation, granivorous birds

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INTRODUCTION

The Bullfinch is one of several predominantly granivorous birds that were identified by Marchant et al. (1990) as having undergone severe declines in abundance in Britain. Declines have also been reported in 14 other European countries, with eight of the declines being measured as greater than 50%. The species is not included in the list of Species of European Conservation Concern only because its range extends far eastward into Asia (Tucker & Heath 1994). Unlike many declining granivorous species, Bullfinches make little direct use of open field habitats (crops or their associated weeds) at any time of year. They are also unique in having been regarded as a pest species in Britain, because of their liking for the buds of fruit trees in orchards, and have there-

fore been controlled in key population centres such as Kent and Worcestershire. Different ecological or environmental factors may well therefore underlie this species' decline and the conservation measures necessary to reverse it may be different to those that would help other seed-eating birds. Reversing the decline has been made a key aim of the Bullfinch's Species Action Plan, proposed as part of the response of the UK government to the UN Convention on Biodiversity of 1992. Completing analyses of the demography of the population was stipulated in the Action Plan, with the aim of improving understanding of Bullfinch population change and aiding the design of conservation prescriptions (UK Biodiversity Group 1998). In this paper, we review research into the potential mechanisms for the decline, concentrating on investigations into

demography, and present new models synthesizing the available demographic information.

The best records of historical variation in the abundance and demography of the Bullfinch in Britain are to be found in the long-term databases of the British Trust for Ornithology (BTO). The BTO's Common Bird Census (CBC), which first identified a decline, monitors abundance (Marchant et al. 1990), the Nest Record Scheme provides historical data on Bullfinch breeding success (Crick & Baillie 1996), recoveries of dead birds ringed under the Ringing Scheme supply information on survival rates (e.g., Greenwood et al. 1993) and the Breeding Bird Atlases tell us about geographical distribution (Sharrock 1976, Gibbons et al. 1993).

POPULATION TRENDS AND HABITATS

Re-analysis of Bullfinch CBC data, using more reliable statistical techniques, has confirmed that statistically significant declines have occurred in both farmland and woodland (Siriwardena et al. 1998a, Baillie et al. 2001). The shape of the species' long-term trend on farmland has been most similar to the trends shown by Grey Partridge *Perdix perdix* and Lapwing *Vanellus vanellus*, rather than those shown by other seed-eating passerines (Siriwardena et al. 1998a). These three species are very different ecologically, so probably have similar trends only by coincidence and not because of a shared mechanism for population change. This tends to support the idea that unique factors might underlie the Bullfinch's decline.

We have taken the analysis of CBC data further by testing habitat and regional differences formally, using generalized linear models (McCullagh & Nelder 1989) in which counts are modelled as a function of CBC plot and year (as categorical variables) with a logarithmic link function and a Poisson error distribution. When the year-effects estimated by the models are back-transformed, an index of abundance is produced which is relative to a value of one in the first year: the "CBC index". Analyses were conducted using the GENMOD procedure of SAS (SAS Institute, Inc. 1996). Habitat, i.e. farmland versus woodland and, within farmland, arable versus mixed (both arable and pastoral) versus pastoral, and regional differences were tested by comparing models with interactions between year and the appropriate additional categorical effect against the basic model, using likelihood ratio tests. We used three

regions in Britain (see Gregory & Marchant 1996 for details of the sub-regions):

- 1) South East (South East England, East Anglia and East Midlands);
- 2) South West (South West England, West Midlands and Wales);
- 3) North (northern England and Scotland).

For each analysis, there was no evidence of overdispersion because the deviance and Pearson Chi-Square statistics took values considerably lower than their degrees of freedom (Crawley 1993). The population trends derived from all CBC plots and from each of farmland and woodland plots alone separately show pronounced declines between 1977 and 1982, preceded and followed by relative stability (Fig. 1). A larger decline is apparent on farmland CBC plots (65%, overall) than on woodland ones (28%), which is reflected in a significant interaction between year and habitat type ($\chi^2_{32} = 81.93$, $p < 0.001$). Note, however, that there was no evidence of any difference in population trends between geographical regions ($\chi^2_{64} = 59.59$, ns) and no evidence of any difference, within farmland CBC sites, between arable, mixed and pastoral regimes ($\chi^2_{64} = 42.01$, ns). The greater declines on farmland are suggestive of problems associated with changes in agriculture, as have been linked with the declines of other species (e.g. Baillie et al. 1997, Chamberlain et al. 1999, Krebs et al. 1999), but there are also clearly negative influences on Bullfinch abundance in the habitats found on woodland CBC plots. Although the significant interaction between annual farmland and woodland CBC counts shows that trends in the two habitats have not been parallel, the differences between them primarily show the effects of only few year-to-year changes, such as 1975–1976, 1978–1979 and 1990–1991; the overall trends and majority of the year-to-year changes are similar (Fig. 1). This is reflected in a very high correlation between the annual indices for the two habitats (0.906) and the level of statistical confidence in each annual index (error bars in Fig. 1) suggests that small individual differences in year-to-year trend direction may well not be real. The overall similarity between the trends in farmland and in woodland suggests that a common cause and demographic mechanism underlie the major population changes; the greater decline in the less preferred habitat (farmland) could indicate that adverse environmental change has had a more severe impact there or, perhaps, that it is a population sink (Pulliam 1988).

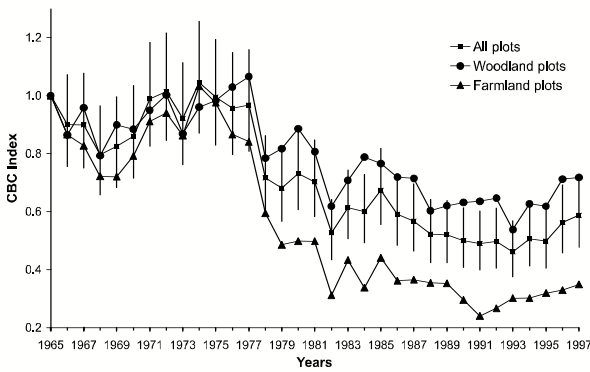


Fig. 1. Bullfinch CBC index series for all CBC plots and each of farmland and woodland plots only, produced using the log-linear Poisson regression method. The bars show 95% confidence intervals for the all plots index.

There was a small, but notable, contraction in the range of the Bullfinch in Britain (-6.5% , in terms of occupied 10×10 km squares) between the 1968–1972 Breeding Atlas survey and the 1988–1991 Atlas (Gibbons et al. 1993), i.e. accompanying the decline in abundance shown in Fig. 1. The squares from which local populations disappeared during such range contractions are most likely to be those where density was low before the decline (and perhaps supported by source populations elsewhere: Pulliam 1988), so conditions in these squares are unlikely to be good indicators of the causes of the decline (Chamberlain et al. 1999). Local variations in patterns of distribution can, however, be related to local land use to identify the environmental features that characterize “hotspots” for Bullfinches. The dependence of Bullfinch distribution on agricultural land-use at the 10×10 km square scale has

been investigated using “Frequency Index” data from the New Breeding Atlas (Siriwardena et al. 2000a). Frequency Index was defined as the proportion of the 25×2 km tetrads within each 10×10 km square in the British National grid in which a species was found (Siriwardena et al. 2000a). When considering key results it should be noted that all effects, except that of area of fallow land, were robust to controls for latitude, longitude and altitude (Table 1).

A more direct approach to investigating habitat preferences is provided by data on variations in density and habitat from the BTO/RSPB/JNCC Breeding Bird Survey (BBS). Gregory & Baillie (1998) analysed these data and found significant preferences of Bullfinches for deciduous woodland, mixed woodland and scrub, as well as for rural human sites, but significant avoidance of heathland, water habitats, urban and suburban areas and, notably, arable land and semi-natural grassland. Notwithstanding these preferences, equally large proportions (each around 40%) of the British Bullfinch population were found in woodland and farmland habitats, reflecting the dominance of the latter in terms of area in Britain (Gregory & Baillie 1998).

The data on the influences of habitat on Bullfinch distribution and density therefore suggest that deterioration (from a Bullfinch’s point of view) of agricultural habitats, perhaps as a result of agricultural intensification, could well have helped drive a national decline. However, the species’ core, preferred habitat is deciduous or mixed woodland, and the evidence for a similar pattern of decline in woodland as well as farmland (Fig. 1) means that other environmental causes may have been more important.

Table 1. Agricultural variables found to be significant predictors of Bullfinch frequency index, the direction of each effect (signs in parentheses) and our interpretation of each pattern.

Significant agricultural variables	Possible interpretation of patterns
Area of woods within farms (+)	Positive effect of area of preferred habitats in farmland
Areas of beet, potato, peas, wheat, rape and stockfeed crops (all -)	Negative effect of intensive arable farming with few hedgerows or copses
Area of young grassland (-), areas of old grassland, oats and fallow (+), Shannon index of agricultural diversity (+)	Positive effect of more extensive management of farmland in general and pastoral agriculture in particular; positive effect of more diverse, mixed farming
Number of sheep (-)	Negative effect of high stocking density: low weed (and therefore seed) density, replacement of hedgerows with fences
Heterogeneity in land-use (extent of mixing of arable and pastoral agriculture) (-)	Negative effect of variation in agriculture, but likely to have been an artefact of the scale of measurement (Siriwardena et al. 2000a)

DEMOGRAPHY AND POPULATION CHANGE

The demography of the decline of the Bullfinch on British farmland has been investigated by combining data within periods with consistent CBC trends and then comparing these blocks of years (Siriwardena et al. 1999, 2000b), and by using a simple population model in which annual estimates of survival rates were used to generate a long-term trend in abundance while other demographic variation was suppressed (Siriwardena et al. 1999). These analyses showed:

- 1) the variation in first-year and adult survival between 1962 and 1995 (as revealed by ring-recoveries) was a poor predictor of the long-term population trend (Siriwardena et al. 1999);
- 2) no variation was found between survival rates in periods of population increase, decline and stability, suggesting that changes in survival did not underlie these changes in trend direction (Siriwardena et al. 1998b, 1999);
- 3) although fledgling production (per breeding attempt, derived from nest records) varied between periods with different population trends, there was no correlation with the period-specific trend slopes (Siriwardena et al. 2000b).

The variation in fledgling production was due to variation in two of its four components, the egg period daily nest failure rate and chick: egg ratio, neither of which was correlated with CBC trend slope (Siriwardena et al. 2000b). Taking these results together, no clear demographic mechanism for the decline of the Bullfinch suggested itself, in contrast to the results from the same studies for other related species such as Linnet *Carduelis cannabina* and Goldfinch *C. carduelis* (Siriwardena et al. 1998b, 1999, 2000b). However, the lack of a clear relationship between survival and the long-term population trend does suggest that culling

has not had an important influence. Although the long-term trend in abundance was not clearly driven by survival, a significant, positive correlation was found between survival and inter-annual changes in abundance (perhaps including effects of culling), suggesting that it has had a role in causing fluctuations around the long-term trend (Siriwardena et al. 1999). The concentration on farmland habitats may also have obscured relationships that have been important across the full range of habitats occupied by the species. In addition, all the analyses described above examined demographic changes from 1962 onwards, rather than concentrating on the period of decline, and it is possible that different demographic regimes have governed Bullfinch population change during different phases of the long-term trend.

The best way to investigate the relative importance of the variation in each demographic rate is to combine them all in a single model of population dynamics. Such an approach also facilitates the exploration of variation in the demographic parameters that cannot be estimated directly through the BTO's historical data sets, i.e. survival rates immediately post-fledgling and the number of breeding attempts made in a season (Siriwardena et al. 2000b).

We fitted an integrated population model to the Bullfinch CBC index using available abundance, breeding success and survival data from all habitats. Combining habitats in this way was appropriate because the demographic changes are likely to have been broadly consistent across habitats (see above). The model (Table 2) used the following demographic equation:

$$N_{t+1} = (N_t \times S(ad)_t) + (N_t \times S(1^{st})_t \times q \times F_{pBat})$$

where

$$F_{pBat} = CS_t \times CER_t \times (1-EFR_t)^{EP} \times (1-NFR_t)^{NP}$$

Table 2. Notation for demographic equations.

Symbol	Definition
N_t	National, all plots index of abundance in year t (from the CBC).
$S(ad)_t$	Annual adult survival rates in year t
$S(1^{st})_t$	Annual first-year survival rates in year t
F_{pBat}	Number of fledglings produced per breeding attempt in year t (from Nest Records)
CS_t	Clutch size in year t
CER_t	Chick:egg ratio (hatching success combined with mortality of very young chicks) in year t
EFR_t	Daily failure rate of nests during the egg laying and incubation stage in year t
NFR_t	Daily failure rate of nests during the nestling stage in year t
EP	The length of the egg laying and incubation period, 15 days (Harrison 1975)
NP	The length of the nestling period, 12 days (Harrison 1975)
q	The component of productivity not accounted for by the number of fledglings per breeding attempt, i.e. the product of the average number of nesting attempts and immediate post-fledgling survival in year t . See Siriwardena et al. (2000b)

Here, q and N_1 (abundance in the first year of the series) are unknown parameters. N_t (for values of $t > 1$) follows via the recursive relationship described in equation 1. The remaining parameters were fixed at the annual estimates (1965–1997), derived from models of the same form as used in Siriwardena et al. (1999) or Siriwardena et al. (2000b), as appropriate, and fitted using the GENMOD procedure of SAS (SAS Institute, Inc. 1996). The sample sizes and average values for three key periods are presented in Tables 3 and 4.

Table 3. Numbers of ring-recoveries and nest record cards used to generate annual parameter estimates for use in population models.

Demographic parameter	Sample
Adult survival	745
First-year survival	850
Clutch size	1534
Chick:egg ratio and brood size	1363
Egg period daily nest failure rate	2472
Nestling period daily nest failure rate	1481

The parameters q and N_1 were estimated by the method of least squares, q being assumed to be constant throughout the time series considered. The simplex method (Nelder & Mead 1965; Press et al. 1989) was used to minimize functions in model fitting. After fitting this full model, we fitted various modifications to it in which different component parameters were allowed to vary or were held constant. In this way, we aimed to reveal the smallest set of temporally variable demographic parameters necessary to reproduce the Bullfinch’s CBC trend. These parameters would be those most likely to have varied to drive the trend. If no model produced a reasonable fit to the population trend, we would have evidence that important variation in the unknown component of productivity, q , is likely to have occurred.

Population models of the form described above contain an explicit assumption that immigration and emigration have been negligible. The evidence from ring-recoveries in Britain suggests that Bullfinches are extremely sedentary, with no indication that significant exchanges have occurred with the European mainland (Wernham et al., in press), so large-scale, long-distance movements are unlikely to produce bias in our results. Short-distance movements between woodland and farmland habitats could still occur and complicate the models fitted, but the similarity between the CBC trends in these habitats (Fig. 1) suggests that differential movements of this sort have not been significant.

Table 4. Estimates of demographic parameters during the major decline of the Bullfinch (1977–1982) and for the periods preceding (pre-) and following it (post-). Survival data could not be assigned to habitats and the estimates shown are taken from Siriwardena et al. (1998b). In bold — differences across the three periods that were significant at $p \leq 0.05$.

Demographic parameter	All habitats			Farmland only			Woodland only		
	Pre-	Decline	Post-	Pre-	Decline	Post-	Pre-	Decline	Post-
Annual adult survival (SE)	0.437 (0.018)	0.414 (0.021)	0.387 (0.025)	-	-	-	-	-	-
Annual first-year survival (SE)	0.327 (0.024)	0.356 (0.031)	0.321 (0.032)	-	-	-	-	-	-
Clutch size (SE)	4.58 (0.04)	4.68 (0.07)	4.69 (0.05)	4.58 (0.05)	4.76 (0.10)	4.64 (0.08)	4.59 (0.05)	4.61 (0.09)	4.72 (0.06)
Chick: egg ratio (95% CI)	0.915 (0.896-0.931)	0.947 (0.914-0.968)	0.906 (0.882-0.926)	0.911 (0.883-0.933)	0.934 (0.874-0.967)	0.947 (0.910-0.969)	0.920 (0.891-0.941)	0.957 (0.912-0.979)	0.884 (0.850-0.910)
Brood size (95% CI)	4.14 (0.05)	4.18 (0.09)	4.17 (0.06)	4.07 (0.06)	4.19 (0.14)	4.25 (0.08)	4.20 (0.06)	4.18 (0.11)	4.10 (0.07)
Daily nest failure rate: egg period (95% CI)	0.032 (0.028-0.037)	0.034 (0.027-0.043)	0.025 (0.021-0.030)	0.034 (0.027-0.041)	0.018 (0.010- 0.032)	0.019 (0.013-0.028)	0.033 (0.027-0.040)	0.044 (0.032-0.061)	0.029 (0.022-0.037)
Daily nest failure rate: nestling period (95% CI)	0.026 (0.022-0.031)	0.030 (0.021-0.041)	0.020 (0.015-0.026)	0.024 (0.018-0.033)	0.042 (0.025- 0.070)	0.018 (0.011-0.029)	0.029 (0.022-0.038)	0.024 (0.014-0.041)	0.020 (0.014-0.030)

Examining the annual variation in survival and nest failure rates revealed several extreme values near the beginning of the time series that were unrealistic, especially in combination, and prevented any integrated model from attaining a close match to the observed CBC trend. There are several possible explanations for these extreme values, including geographical biases caused by the contribution of local, intensive studies such as Ian Newton’s work in Oxfordshire (Newton 1972), the effects of localized culling and general effects of small sample sizes. Whatever the cause, the problems with the earlier years could explain why poor agreements between variations in demographic rates and population trends were found in previous studies. We concentrated subsequently on the period 1972–1997 to exclude the problem years while retaining the population decline and a brief period of stability preceding it (Fig. 1).

A full integrated model fitted to the CBC trend from 1972 to 1997 produced a good fit up to 1987, but the fit over the final 10 years of the time series was poor. The latter period featured more extreme survival estimates, especially for first-year birds, as well as small recovery sample sizes (Siriwardena et al. 1999), and holding survival constant but allowing variation with age (as previously found to be statistically significant: Siriwardena et al. 1998b, 1999), produced a much closer model fit (Fig. 2). This suggests that no variation in survival, in numbers of breeding attempts or in post-fledging survival rates is needed to explain the decline and that the variation in the parameters making up fledgling production per breeding attempt is sufficient. We held each of these parameters constant in turn to reveal which were necessary to reproduce the observed decline in the CBC index. The results indicated that

Table 5. Overall deviations from CBC Index (Deviation) from 1972 to 1997 of population models, in which one demographic rate at a time was allowed to take its annual estimates, while the others were held constant at their mean values.

Parameter varying in model	Deviation
None	0.580
Adult Survival Rate	0.893
First-year Survival Rate	2.75
Egg Period Failure Rate	0.976
Nestling Period Failure Rate	0.539
Brood Size	0.828
Clutch Size	0.585

approximately the correct magnitude of decline could be produced whichever variable was held constant, but that the tracking of the fluctuations in the trend was impaired most when variation in the egg period daily nest failure rate was omitted (Fig. 2). However, even the latter model produced a broadly acceptable fit to the CBC trend.

As a check on these results, we fitted a second set of models, starting with one where all parameters were constrained to be constant at their mean values and adding variation in one parameter at a time. The fit of each model to the CBC trend was assessed quantitatively by calculating the sum-of-squares of the deviations between the two time series: smaller sums-of squares (“overall deviations”) would indicate closer fits. The fit of the model with all parameters held constant was relatively good and the only model to generate an appreciably poorer fit was that adding variation in first-year survival rates (Table 5), reflecting the extreme values of some estimates of this parameter, as discussed above. The other models each produced a decline of approximately the right magnitude, adding a degree of inter-annual fluctuation to the smooth trend of the all-constant model (Fig. 3). Clutch size and brood size were the parameters that varied least between years and their variations each produced negligible deviations from the all-constant model trend. Only the model in which the nestling period failure rate was allowed to vary gave rise to an improved fit to the whole of the CBC trend and only the model with varying egg period failure rates produced a close fit over the period of most rapid population decline, 1977–1982 (Table 5, Fig. 3).

The results indicate that only clutch size and brood size can be ruled out as having varied to drive the decline of the Bullfinch across all habitats. The egg period daily nest failure rate may have been the most important single parameter

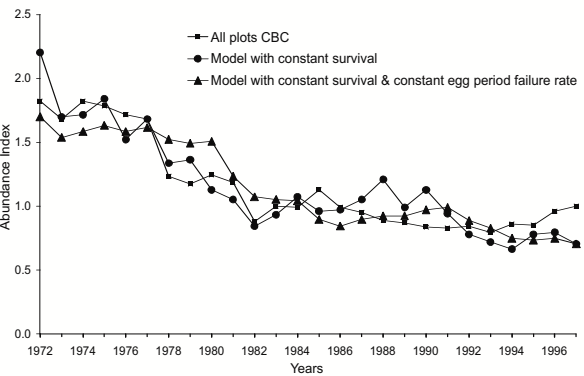


Fig. 2. CBC and integrated population model time series for 1972–1997

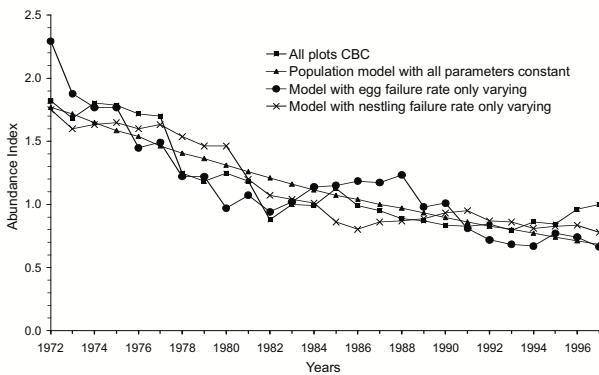


Fig. 3. CBC indices and integrated population models fitted by holding all parameters constant (b) and by allowing one parameter at a time to take the values of its independent annual estimates: variable egg period daily nest failure rate and nestling period daily nest failure rates.

over the period when the decline was most pronounced. Siriwardena et al. (2000b) found similar variation in this parameter over the key period of 1975–1987 for Bullfinch nests on farmland only. However, variation in the nestling period failure rate provided a marginally better prediction of all of the variation in abundance from 1972 to 1997. Variation in adult survival provided a similarly good prediction and variation in first-year survival appeared not to have been measured sufficiently accurately to allow its importance to be assessed with confidence. Variation in any or all of these four demographic rates could therefore underlie the decline observed in the CBC. We cannot rule out an additional role for changes in post-fledgling survival or in number of breeding attempts made, although the models suggest that such variation does not need to be invoked to explain the CBC trend.

DEMOGRAPHY AND HABITAT

The demographic models described above used data pooled across habitats, thus ignoring habitat-specific variation. Although the population trends (Fig. 1) suggest that broadly similar demographic mechanisms underlie the trends across habitats, the declines in farmland and woodland have differed in scale, indicating that some demographic differences exist. It is difficult to attach meaningful spatial references to ring-recovery data so as to allow analyses of survival rates with respect to environmental or habitat information, and such analyses have not been

done. Variation in breeding performance with respect to habitat can be investigated, however, and we conducted new analyses of the differences between farmland and woodland habitats. Nest record cards were assigned to farmland or woodland, or omitted if from neither habitat, based on the habitat codes recorded on the cards (Crick 1992, see also Siriwardena et al. 2000c). Testing for differences between farmland and woodland using standard statistical techniques (Siriwardena et al. 2000b, c) revealed a significant difference only for the egg period daily nest failure rate (likelihood-ratio test: $\chi^2_1 = 3.73$, $p = 0.05$), which was higher in woodland (0.033, versus 0.026 for farmland), contrary to what might be expected in a preferred habitat. Testing, by habitat, for differences between the pre-decline, decline and post-decline phases of the population trend (taking the decline to have run from 1977 to 1982) revealed some significant differences. Most notably, there was a tendency for the egg period failure rate to have declined over time in farmland only (Table 4). This is the converse of the pattern that would be expected if differential egg period failure rates had caused the different rates of decline in farmland and woodland. Overall, there was no clear evidence for the existence of different demographic mechanisms in each habitat that were obscured by the pooling of data in our main integrated population models.

The dependence of Bullfinch fledgling production on variation in the habitat within farmland has previously been investigated, considering the agricultural regime (arable, pastoral or mixed) at the territory and landscape scales (Siriwardena et al. 2000c) and the detail of agricultural land-use as revealed by the UK Ministry of Agriculture, Fisheries and Food June Agricultural Census (Siriwardena et al. 2001). Bullfinch fledgling production did not differ between arable and pastoral landscapes, but was significantly higher with mixed farming at the territory scale than with arable farming, pastoral farming was intermediate (Siriwardena et al. 2000c). Fledgling production also increased from 1962–1975 to 1976–1995 under all three territory-scale farming regimes, but significantly so only under arable farming (Siriwardena et al. 2000c). Meanwhile, there were several effects of individual agricultural land-use variables on the components of fledgling production that, taken together, suggest a general benefit of more extensive farming (Siriwardena et al. 2001). However, none of these analyses revealed any effect of the agricul-

tural habitat on the egg period daily nest failure rate and only one effect, of marginal statistical significance ($p = 0.073$, Siriwardena et al. 2001), on the nestling period failure rate, suggesting that hitherto untested environmental factors have influenced the potentially important parameters.

The latter results could point to factors specific to woodland habitats as being most important in driving the decline of the Bullfinch, with farmland populations either being affected indirectly through source-sink dynamics (Pulliam 1988) or directly through the occurrence of the "woodland-specific" factors in copses or hedgerows within farmland. However, the studies referred to above did not conduct complete investigations of the influences of farming practice on Bullfinch breeding success because potentially key variables, such as amounts of pesticide applied and characteristics of field boundaries, could not be tested (no data were available: Siriwardena et al. 2001). The proximate factors that determine egg period failure rates are likely to be nest predation and influences on parental nest desertion such as disturbance or predation on adult birds. Similar factors, as well as food availability and weather, will control nestling period failures. The importance of such factors for Bullfinches has yet to be investigated, but it is important to note that proximate causes do not necessarily reveal ultimate causes: for example, increased nest predation might ultimately reflect reductions in the available nest cover resulting from the removal or deterioration of hedgerows. Further, Thomson et al. (1998) found that Bullfinch population changes were not correlated with those of the Magpie *Pica pica*, a principal nest predator. There was also no correlation with changes in Sparrowhawk *Accipiter nisus* abundance.

CONCLUSIONS

The results summarized here suggest that changes to any or all of adult survival, first-year survival, the egg and nestling period daily nest failure rates could have contributed to the decline of the Bullfinch. If changes have occurred in more than one demographic rate, these changes could have been sequential or simultaneous and could perhaps each have affected birds in different geographical areas. Intensive field studies of Bullfinches throughout the year suggest that late winter mortality limits abundance (Newton 1972, pers. comm.) indicating that over-winter survival

might be the important demographic rate in terms of population change, as it appears to be for many farmland passerines (Siriwardena et al. 1998b, 2000b). Our analyses suggest that changes in post-fledging survival or numbers of breeding attempts have not been important, but the lack of a clearly accurate demographic model for the long-term population trend means that we cannot be certain about this. Newton (1999) found that up to two-fold variations in local Bullfinch productivity between each of five years in the 1960s were due primarily to changes in the amounts of late breeding, suggesting a strong influence on abundance of the proportion of the breeding population that are able to make several breeding attempts. In a pattern consistent with Newton's results, egg period failure rates decline as the breeding season progresses (although clutch and brood sizes fall) within the nest record sample for Bullfinch (G. M. Siriwardena, unpublished data). Despite this, we may have underestimated changes in productivity that were driven by effects specific to later breeding attempts because the Nest Record Scheme is biased in its coverage towards earlier nests, due to diminishing recorder activity as the summer progresses (Crick & Baillie 1996).

Several unknowns clearly remain in Bullfinch demography and the causes of the species' decline. Our ability to identify a demographic mechanism has probably been compromised by the limited sample sizes available in the relevant data sets, because sampling errors associated with each demographic parameter will have been carried through into the integrated models. Smaller samples are also more likely to have been influenced by biases due to the contributions of short-term, localized studies or due to fluctuations in culling effort. In addition, territory mapping for the CBC is likely to provide a less accurate picture of population change for Bullfinch than it is for more conspicuous and territorial species like Chaffinch *Fringilla coelebs* and Wren *Troglodytes troglodytes*, reducing the potential accuracy of analyses relating demographic variables to changes in abundance. Some small sample size effects may be ameliorated by applying recently developed techniques that combine demographic and census data in a single modelling framework (Besbeas P, Freeman S. N., Morgan B. J. T. & Catchpole E. A., unpublished manuscript), but any problems with the representativeness of the data will be harder to solve. Further analyses of historical data to investigate the effects of habitat

on demography are also unlikely to be very useful, unless new sources can be found for key woodland or farmland data (such as hedgerow characteristics) which were not collected as part of the bird monitoring schemes.

Without a strong demographic model for the decline of the Bullfinch, good hypotheses as to the ultimate cause of the CBC trend cannot be derived from the apparent temporal changes in demography. The effects of predation, of culling and of orchard management seem unlikely to have been significant (Newton 1972, Thomson et al. 1998, D.L. Thomson & I. Newton, pers. comm.), however, and there appear to have been no strong effects of a range of aspects of agricultural land-use, at least on breeding performance. The influence of climate change on Bullfinch populations has not been investigated and could have been important, but although a pattern for progressively earlier egg laying has been common among British birds (Crick et al. 1997, Crick & Sparks 1999), there has been no trend with respect to time for Bullfinch (Baillie et al. 2001). This suggests that climate change may have been relatively unimportant for this species. Other potential causes of the decline are reductions in the quality or quantity of hedgerows and in the quality and density of woodland understorey vegetation, the latter as a result of increases in deer grazing pressure (Vanhinsbergh et al. 2001). Intensive field studies asking tightly focused questions, ideally run concurrently at a range of geographically diverse sites, are recommended for future investigations of Bullfinch ecology and work in progress at the University of Oxford should provide a valuable contribution.

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[Jaki jest mechanizm spadku liczebności populacji gila w Wielkiej Brytanii?]

Gil wykazuje w Wielkiej Brytanii, podobnie jak w szeregu innych krajów europejskich, wyraźny spadek liczebności populacji, którego główne przyczyny nie są znane. Aby poznać zmiany demograficzne brytyjskiej populacji gila, autorzy dokonali przeglądu dotychczasowych publikacji omawiających jej stan, przedstawiają też modelową analizę populacji gila dla wszystkich środowisk jego występowania oraz osobno dla środowisk rolniczych i leśnych.

Dane wieloletniego brytyjskiego monitoringu ptaków (Common Bird Census — CBC) wykazują spadek populacji gila (Fig. 1) zarówno w środowiskach leśnych (28%) jak i w rolniczych (65%). Podobny kształt krzywej dla obu środowisk (Fig. 1) wskazuje, że spadek jest powodowany przez podobne mechanizmy demograficzne, działające jednak silniej w środowiskach rolniczych. Analizy modelowe (Fig. 2 i 3) wykazują, że zmiany wielkości zniesień i lęgów nie miały istotnego znaczenia dla tego spadku, podobnie jak liczba ptaków przystępujących do lęgów oraz przeżywalność młodych opuszczających gniazda. Najwyraźniejszy był związek tych zmian, w okresie najsilniejszego spadku, z wielkością dziennych strat gniazd w okresie składania i wysiadzania jaj (Fig. 3). Zaznaczyły się też zależności od strat gniazd w okresie wychowu piskląt, przeżywalności dorosłych ptaków oraz przeżywalności w pierwszym roku. Straty gniazd w początkowej fazie lęgowej były wyższe w środowiskach leśnych (preferowanych w stosunku do rolniczych). Ale w środowiskach rolniczych z czasem bardziej wzrastały (Tab. 4). Przeczy to ewentualnej zależności od liczebności występowania. Niezależnie od negatywnego wpływu intensyfikacji rolnictwa na występowanie gila (Tab. 1), nic nie wskazuje, żeby ten czynnik, ani też drapieżnictwo, miały znaczny bezpośredni wpływ na straty gniazd. Autorzy konkludują, że decydująca przyczyna spadku populacji jest nadal nieznana. Przypuszczają, że niedostatkim przeprowadzonej przez nich analizy jest niejednorodność danych podstawowych, na których się opierali, dotyczących odmiennych części brytyjskiej populacji gila.