

Bullfinch *Pyrrhula pyrrhula* breeding ecology in lowland farmland and woodland: comparisons across time and habitat

FIONA M. PROFFITT,¹ IAN NEWTON,² JEREMY D. WILSON^{3*} & GAVIN M. SIRIWARDENA⁴

¹Edward Grey Institute of Field Ornithology, Department of Zoology, University of Oxford, Oxford OX1 3PS, UK

²Centre for Ecology and Hydrology, Monks Wood, Abbots Ripton, Huntingdon PE28 2LS, UK

³The Royal Society for the Protection of Birds, Dunedin House, 25 Ravelston Terrace, Edinburgh EH4 3TP, UK

⁴British Trust for Ornithology, The Nunnery, Thetford IP24 2PU, UK

Bullfinch *Pyrrhula pyrrhula* populations decreased by 33% in Britain over the years 1977–82, the period of steepest decline. The timing of this decline and its greater severity on farmland (–65%) than in woodland (–28%) point to agricultural intensification as a likely environmental cause, but previous analyses of survival rate and breeding success data have not been able to identify a clear demographic mechanism. As part of an investigation into the causes of the decline of Bullfinch populations, we conducted an intensive study of breeding phenology and success in farmland and woodland habitats of Oxfordshire and neighbouring counties in 1999–2001, using a combination of nest monitoring and autumn mist-netting. Breeding success data were supplemented with nest record and mist-net capture data collected in the same geographical area during the 1960s and 1990s to compare pre- and post-decline productivity. We found a change in the distribution of first-egg dates, with median first-egg dates 17–18 days later in the 1990s. This reflected a change in the centre of gravity of the breeding season rather than the timing of its start and end, with proportionally fewer birds laying in May and early June, and proportionally more between then and the end of July. We found no significant difference in any aspect of productivity per breeding attempt between the two periods, although there was a trend towards higher egg period failure rates in the 1990s. October age ratios indicated higher annual productivity in the 1990s. We found no significant differences between farmland and woodland in Bullfinch breeding success or timing of breeding. The cause of the decline of Bullfinch populations in both woodland and farmland, and the greater severity of the decline in farmland, seems more likely to be found in: (a) the impacts of habitat deterioration on breeding densities, (b) constraints on survival probability outside the breeding season and/or (c) the impacts of increasing populations of Sparrowhawks *Accipiter nisus* on the ability of Bullfinches to exploit resources in some habitats. Further investigation of the breeding ecology and phenology of Bullfinches would best be focused on understanding the causes and possible demographic consequences of the shift in first-egg date distribution in favour of later-summer nesting attempts.

Information on demographic rates can provide insight into the mechanisms of population change and help diagnose underlying environmental causes of population decline (Green 1995, Newton 1998, Peach *et al.* 1999). The European Bullfinch (*Pyrrhula pyrrhula*) was added to the UK Red List of Birds of

Conservation Concern in 1996 because of a severe population decline in the preceding 20 years (Gibbons *et al.* 1996). Analyses of Common Birds Census (CBC) data indicated that the decline was greatest between 1977 and 1982, coinciding with a period of rapid agricultural intensification, and was more severe on farmland (–65%) than in woodland (–28%), although significant in both habitats. Analyses of national Nest Record Scheme (NRS) and ring recovery

*Corresponding author.

E-mail: Jeremy.Wilson@rspb.org.uk

data sets found that variation in adult survival, first year survival, egg period failure rates (EFR) and nestling period failure rates (NFR) fitted the population trend sufficiently closely that any or all could have contributed to the decline, and ruled out only changes in clutch and brood size as potential demographic causes of recent trends (Siriwardena *et al.* 2001). Of these, EFR gave the best fit to the Bullfinch population trend, primarily because it fell after the period of steepest population decline in 1977–82. However, the number of breeding attempts and post-fledging survival and, therefore, annual productivity were unknown and changes in these factors could not be ruled out as demographic mechanisms of decline.

Analyses of nest record cards for multi-brooded species are generally biased toward earlier nests (Crick & Baillie 1996). This bias could be a particular problem for Bullfinches because they have a relatively long breeding season, and their well-hidden nests become more difficult to find as foliage density increases through the season (Newton 2004). We therefore used a combination of intensive field study and historical nest record data from observers who had searched intensively throughout the Bullfinch breeding season to test:

- (1) whether the breeding season has shortened, reducing the opportunity for Bullfinches to make repeat nesting attempts;
- (2) whether productivity of individual nesting attempts had changed between the 1960s and 1990s;
- (3) whether breeding success differed between farmland and woodland, and whether these differences might explain the divergence in population decline between the two habitats;
- (4) whether annual productivity at the population level, as estimated from October age ratios, was correlated with the Bullfinch population trend since the 1960s.

METHODS

Timing of breeding

We assessed patterns of breeding phenology from: (1) first-egg dates (i.e. the date the first egg of each clutch was laid) of nests monitored, both as part of our intensive study and by NRS recorders in Oxfordshire and neighbouring counties; and (2) moult scores of juveniles caught during the post-breeding moult, which are a close correlate of fledging date (following Newton 1966, 1999, Newton & Rothery

2000). We used mist-nets to catch Bullfinches in September–October 1999 and August–November 2000 on farmland at Otmoor (SP5615) and in nearby mixed woodland at Whitecross Green Wood (SP6015) on the Oxfordshire/Buckinghamshire border. Additional moult data were collected by ringers operating at Gordano Valley (ST4373) and Pope's Hill (SO6814), both in Gloucestershire, and in Treswell Woods (SK7680), Nottinghamshire, in 2001. The 1960s moult data were collected by Ian Newton at Wytham Woods (SP4608), Oxfordshire, in 1962–66.

Juvenile body moult was scored according to Newton's method (Newton 1966), ranging from 0 (moult not yet started) to 6 (moult completed), with five stages of moult based on which feather tracts were moulting. We back-calculated the approximate date of moult onset using the formula: moult start date = capture date – [(moult score – 0.5) * 10], assuming that each moult stage lasted 10 days (Newton 1966, 1999, Newton & Rothery 2000) and that all birds were caught at the midpoint of a particular stage. Recaptured birds were excluded from analyses, as were birds that had either not commenced or had completed moult (Newton & Rothery 2000). We used general linear models (in MINITAB, Release 13.20, Minitab Inc. 2001) to test for differences between the 1960s and 1990s data and for effects of habitat, with catch date as a covariate to control for differences in mist-netting dates between the two periods.

Estimating productivity per breeding attempt

We collected data on clutch size, brood size, nest failure rates and causes of nest failure from five main sites in Oxfordshire and Warwickshire in 1999–2001 (Table 1), following the BTO's Nest Record Scheme protocol (Crick & Baillie 1996, Crick *et al.* 1999, 2003).

We also obtained records from the NRS for Oxfordshire for the period 1960–70 and 1991–98 and from two major contributors to the scheme: Henry Mayer-Gross and Colonel G.O. Stephens, from the neighbouring counties of Berkshire and Buckinghamshire. Most of the 1960s records came from these two recorders, who reported that they operated throughout the Bullfinch breeding season. Most of the 1990s records came from two expert nest-finders, Ron Louch and Dave Tompson, who also searched throughout the season and assisted with this study in 1999–2001. Data from first and subsequent breeding attempts were pooled because they could

Table 1. Study sites for nest monitoring 1999–2001 (total no. of nests = 290).

Site	Years monitored	County ^a	Central grid ref.	Habitat	Area (ha)	No. of nests found (location)
Otmoor – Charlton	1999–2000	Oxon	SP5715	farmland	131	64
Otmoor – other	1999–2001	Oxon	SP5713	farmland	c. 465	31
Whatcote	1999	Warks	SP3044	farmland	134	9
Whitecross Green Wood	1999–2001	Oxon	SP6015	woodland	62	86
Asham Meads	1999–2001	Oxon	SP6015	farmland	23	14
Sydlings Copse/College Pond	1999–2001	Oxon	SP5610	woodland, scrub	17	32
Other	1999–2001	Oxon, Berks, Bucks	n/a	woodland, farmland, garden	0	54

^aOxon: Oxfordshire; Warks: Warwickshire; Berks: Berkshire; Bucks: Buckinghamshire.

not be differentiated. Throughout this paper, we shall refer to nest data from 1960 to 1970 as '1960s' and from 1991 to 2001 as '1990s' data.

Calculating nest survival rates

Daily nest failure rates were corrected for the number of days the nest had been 'exposed' (i.e. monitored) using Johnson's (1979) extension of the Mayfield method (Mayfield 1961, 1975). This reduces the bias introduced by the fact that nests found later during a given stage (e.g. egg or nestling stage) are more likely to survive to the point of outcome (hatching or fledging) than nests found earlier in that stage. We calculated separate daily failure rates for the egg period, nestling period and whole nest period (WFR), from first-egg to nest fate, using the number of days over which a nest was known to have been exposed in each period and whether the nest failed or survived, assuming a constant survival rate within each period. We assumed an egg period of 16 days and nestling period of 15 days, being the mid-point of the range of usual values for southern England (Cramp & Perrins 1994). Nests for which the outcome was unknown were scored as having survived the known exposure period and nests for which failure date could not be assigned to the egg or nestling period with any certainty were excluded from calculations of failure rates in the egg and nestling periods, but included in whole nest period calculations. We excluded nests that had failed or whose chicks had fledged upon discovery and those with an interval of > 10 days between final and penultimate nest checks. These decisions followed standard BTO procedure.

We modelled daily nest failure rates using binomial logistic regression with a logit link function in

MINITAB, with nest fate (1 = failed, 0 = survived) as the binomial numerator and number of exposure days as the binomial denominator, in accordance with Aebischer (1999). Standard errors for daily failure rates were calculated using Johnson's (1979) formula. We also made univariate comparisons of failure rates between the 1960s and 1990s and between farmland and woodland, with *P*-values compared with a Dunn–Šidák corrected α -level of 0.025 (Sokal & Rohlf 1981).

Estimating annual productivity

Because Bullfinches are generally secretive during the breeding season and are capable of making movements of more than 20 km between breeding attempts (Newton 2000), it is extremely difficult to assess the number of breeding attempts made by individual females in the wild. We therefore used October captures of Bullfinches to estimate annual productivity from the ratio of juveniles to adults (following Newton 1999, 2000).

We operated mist-nets in 1999–2000 at the Otmoor and Whitecross Green Wood study sites. To attract Bullfinches to the nets, we used tape lures of Bullfinch contact calls played on a Sony TCM-323 cassette-recorder through Sony SRS-A11 speakers. All Bullfinches were ringed and aged according to plumage characteristics given in Svensson (1992).

To compare age ratios in different time periods in which Bullfinch populations were increasing, decreasing or stable nationally (Table 2), we obtained catch data from ringing groups and extracted additional data from the BTO's Species Data Forms (BRC19), which covered the period 1970–84 (although there were few records from the 1980s). We tested for

Table 2. National Bullfinch population trends derived from BTO census data.

Time period	Trend	Source
1962–74	Increasing	CBC (Siriwardena <i>et al.</i> 2000)
1975–82	Decreasing	CBC (Siriwardena <i>et al.</i> 2000)
1983–95	Stable	CBC (Siriwardena <i>et al.</i> 2000)
1996–2001	Decreasing	CBC (Baillie <i>et al.</i> 2001); BBS ^a (Raven & Noble 2001)

^aBTO/Joint Nature Conservation Council/RSPB Breeding Bird Survey.

effects of year, time period and broad habitat type (see below) on the proportion of juveniles among birds caught in October using binomial logistic regression models in GenStat (Release 4.21, Genstat 5 Committee 1993), with number of juveniles as the binomial numerator and total number of captures as the binomial denominator. Because of large differences in sample sizes among the different datasets, we weighted the regressions by \sqrt{n} . As the data were overdispersed, we used the GenStat facility to estimate the dispersion parameter empirically and correct standard errors accordingly. Habitat was classified into broad types derived from the BTO habitat codes (BTO 1997) as follows: 1, Homestead (rural habitations); 2, Farmland; 3, Scrub; 4, Woodland; 5, Other/unspecified. Individuals were included in the age-specific totals only once, irrespective of the number of times they were caught during the month in question.

RESULTS

Timing of breeding

The median first-egg date over the season as a whole was 17 days later in the 1990s than in the 1960s (Mann–Whitney *U*-test, $P = 0.018$ two-tailed, $n = 286$;

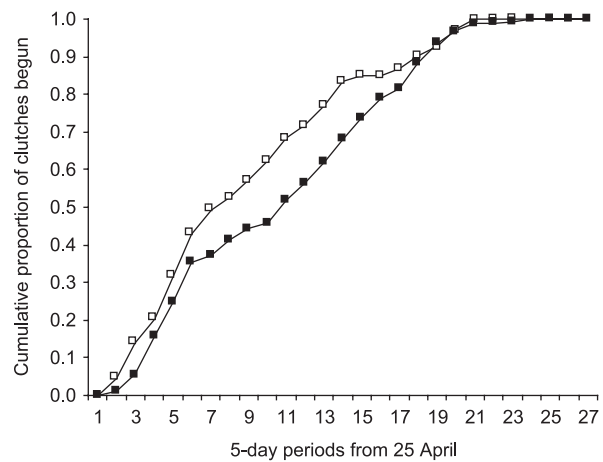


Figure 1. Cumulative proportion of Bullfinch clutches begun over the course of the breeding season in the 1960s (open squares) and 1990s (filled squares). All data from Oxfordshire and neighbouring counties.

Table 3). When the very earliest and latest nests were excluded, using the 5th and 95th percentiles as cut-offs, the median first-egg date was 18 days later in the 1990s than in the 1960s (Mann–Whitney *U*-test, $P = 0.006$, $n = 258$; Table 3). No comparisons between time periods within habitats or between farmland and woodland were significant at $P < 0.05$.

The distributions of first-egg dates (Fig. 1) show that although the recorded Bullfinch breeding season began and ended at almost exactly the same time in the 1990s as it did in the 1960s, the cumulative distribution of nesting attempts is right-shifted; a higher proportion of Bullfinch nesting attempts were later in the season in the 1990s than in the 1960s.

Juveniles that were caught later in the season had also begun moult later. This was presumably because earlier moulting juveniles would have completed moult and not be included in the sample from later dates and also because post-fledging mortality and dispersal would result in a greater proportion of the

Table 3. First-egg dates (FED) from nests monitored in the 1960s and 1990s.

	1960s	<i>n</i>	1990s	<i>n</i>	Difference
Median FED, all clutches	28 May	114	14 June	172	+17 days ($P = 0.018$)
Median FED, 5th–95th percentile	27 May	103	14 June	155	+18 days ($P = 0.006$)
FED, 5th percentile	30 April	114	3 May	172	
FED, 95th percentile	28 July	114	27 July	172	
Minimum FED, all clutches ^a	26 April	114	26 April	172	
Maximum FED, all clutches ^b	3 August	114	18 August	172	

^aEarliest first-egg date; ^blatest first-egg date.

Table 4. Effects of catch date and decade on moult start date of juveniles. General Linear Model with decade fitted as a fixed effect.

Source	Type III sums of squares	df	F	P	Direction
Catch date ^a	169 431	1	1151.61	< 0.001	+ ve
Decade	4 368	1	29.69	< 0.001	1960s: 30 August ± 2.51 days se (<i>n</i> = 608)* 1990s: 22 August ± 1.79 days se (<i>n</i> = 94)*
Error	102 840	699			
Total		701			

*Least squares means calculated at average catch dates (1 = 1 July).

^aIncluded in the model as a covariate to control for its effect on moult start date and because the mean catch date was earlier in the 1960s (14 September ± 0.98 se, *n* = 608; 1990s) than in the 1990s (6 October ± 2.29 se, *n* = 94; GLM *P* < 0.001, *df* = 701).

Table 5. Untransformed parameter estimates and results of likelihood ratio tests for the effect of first egg date on nest failure rates in Oxfordshire and neighbouring counties 1960–1970, 1991–2000 (binomial logistic regression).

Failure rate	Intercept ^a	se	Slope (FED)	se	df	P	<i>R</i> _L ²
EFR	-3.9530	1.0390	-0.021618	0.005653	2453	0.0001	0.088
NFR	-2.0387	0.3796	-0.018602	0.005244	1563	0.0003	0.030
WFR	-3.2303	0.6056	-0.018104	0.003587	4372	< 0.0001	0.048

*R*_L² = (Total Deviance – Residual Deviance)/Total Deviance (Guisan & Zimmerman 2000, Pampel 2000).

^aIntercept estimate calculated for Year = 1960.

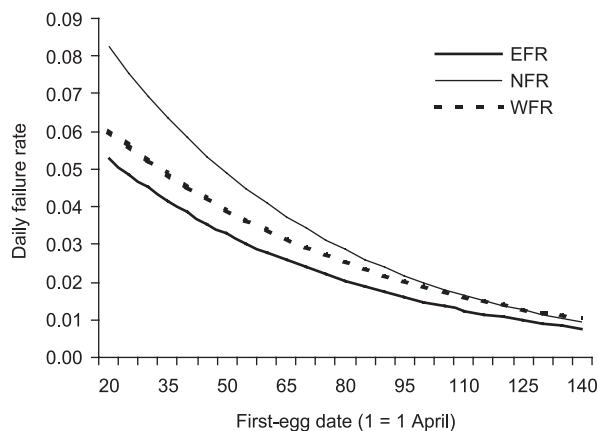
earlier moulting birds being unavailable for capture at later sampling dates. In addition, the latest juveniles would still be in nests when the earliest were in moult, so not available for capture until later in the season. After accounting for the effect of capture date, the moult onset date of captured juveniles was 8 days earlier, on average, in the 1990s than the 1960s and the difference was significant (Table 4).

We could not make habitat comparisons for the 1960s because all the data were collected in woodland. For the 1990s, there was no significant difference in the onset of moult of juveniles caught in farmland and woodland (pairwise *t*-test, *P* = 0.3687, *df* = 74).

Productivity per breeding attempt

Results of comparisons of productivity per breeding attempt between the 1960s and 1990s are summarized in Appendix 1. We found no significant differences in daily nest failure rates, clutch or brood sizes, or in hatching success for clutches that hatched at least one chick. However, there was a trend towards higher egg period failure rates in the 1990s (*G*-test, *P* = 0.037, *df* = 364) which was not significant at *P* = 0.05 when corrected for multiple univariate tests.

In multivariate models of nest failure rates, the only significant effects were of year and first-egg date on egg period and whole nest period failure rates and first-egg date on nestling period failure rates.

**Figure 2.** Relationship between first-egg date and daily nest failure rates during the egg (EFR), nestling (NFR) and whole nest period (WFR).

Parameter estimates for the first-egg date term are presented in Table 5. Year was treated as a factor in these analyses and intercept estimates are presented for the base year, 1960.

Nest failure rates declined over the season (Fig. 2) and, for the egg and whole nest periods, varied annually (Fig. 3).

We found no significant difference between farmland and woodland in any of the measures of productivity per breeding attempt. Predation was the greatest cause of nest failure, accounting for 68% of all known

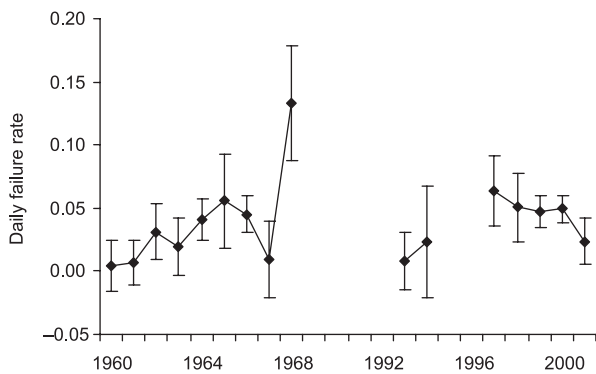


Figure 3. Annual variation in daily nest failure rate during the egg period, Oxfordshire and neighbouring counties 1960–1968 (open diamonds) 1993–2001 (filled diamonds), with standard error bars. Failure rates for some years not shown due to very small sample sizes ($n < 5$ nests).

total nest failures (65% and 60% of egg period and nestling period failures, respectively – proportions uncorrected for exposure days and including nests that were already predated when found).

Annual productivity estimated from October age ratios

After controlling for the effect of different data sources (in most cases, a source was a specific geographical location, although the BRC19 data are derived from multiple sites), the modelled proportion of juveniles in October mist-net catches of Bullfinches was highest in the period 1983–95 when the population was stable (Table 6).

The proportion of juveniles caught in October was significantly higher in the 1990s than in the 1960s (1962–70: 0.77, $se = 0.02$, $n = 619$; 1990–2001: 0.84, $se = 0.02$, $n = 365$; $P = 0.012$, $df = 67$) and was significantly higher on farmland (0.84, $se = 0.03$, $n = 135$) than in woodland (0.77, $se = 0.01$, $n = 1353$; $P = 0.032$, $df = 70$). However, the habitat effect dis-

appeared after controlling for data source ($P = 0.600$, $df = 61$), suggesting that it may have been a site-specific rather than habitat-specific effect. We therefore also tested for an effect of habitat using only the BRC19 data, sampled from a large number of sites. In this dataset, we found no effect of habitat on October age ratios ($P = 0.582$, $df = 66$).

DISCUSSION

Analyses of first-egg dates revealed that median first-egg date was 17–18 days later overall during the 1990s than during the 1960s, although this affected the centre of gravity of the breeding season rather than the timing of its start and end. Specifically, proportionally fewer birds laid in May and early June and proportionally more between then and the end of July (Fig. 1). There was no difference between farmland and woodland in either measure of timing of breeding.

The reasons for the shift towards later egg laying during the middle of the Bullfinch breeding season, after the first nesting attempts, are unknown. Hypotheses that could be tested in future work include: (1) that adult condition is now poorer, causing birds to require longer interclutch intervals; and (2) that environmental conditions (especially food availability and weather) are now relatively poor early in the season, but better later in the season than in the 1960s. This second hypothesis is perhaps especially promising because Bullfinches have been found to exploit ripening oilseed rape seed as a food source for nestlings (Proffitt 2002), a food resource which becomes available later in the breeding season, and is known to allow successful later nesting attempts in intensive agricultural landscapes where it is grown (Moorcroft & Wilson 2000). A third plausible hypothesis is that nest survival rates during first nesting attempts are now higher, thus delaying the number and date of repeat nesting attempts. However,

Table 6. Numbers and ratio of juvenile (juv) and adult Bullfinches caught in October during time periods with different national population trends, for all sites combined.

Period	Trend	No. of juv.	No. of adults	Proportion (se) juv. (raw) ^a	Juv:Adult (raw) ^a	Proportion juv. (model) ^b	Juv:Adult (model) ^b
1962–74	Increasing	769	264	0.74 (0.01)	2.91	0.70	2.33
1975–82	Decreasing	1123	363	0.76 (0.01)	3.09	0.73	2.70
1983–95	Stable	352	70	0.83 (0.02)	5.03	0.89	8.09
1996–2001	Decreasing	173	28	0.86 (0.02)	6.18	0.75	3.00
Overall		2417	725	0.77 (0.01)	3.33		

^aCalculated from raw data; ^bcalculated from back-transformed parameter estimates of model including data source and time period, with calculations made using the parameter estimate for the BRC19 data source.

in these data sets at least, there is no evidence of an interaction between decade and first-egg date affecting measures of nest success.

Analyses of onset of juvenile moult showed that, after controlling for effects of catch date, captured juveniles had begun to moult (and hence fledged) on average 8 days earlier in the 1990s than in the 1960s. This could be due to: (1) earlier cessation of breeding in the 1990s; (2) a change in seasonal patterns of nest success, such that earlier nests were relatively more successful than later nests in the 1990s; (3) a change in post-fledging mortality, so that more early young survived; (4) a change in moult rate and/or (5) a change in juvenile behaviour in a way that has affected capture probability as a function of age since fledging. Evidence against hypotheses (1) and (2) is presented in this paper because the breeding season is, overall, later now than in the 1960s and there no evidence of an interaction between decade and first-egg date affecting measures of nest success. Hypotheses (4) and (5) would both be testable with new data, but it is difficult to identify plausible scenarios for these changes. Hypothesis (3) is perhaps worthy of greatest attention because, contrary to the above hypothesis, the recovery of Sparrowhawk *Accipiter nisus* populations (Newton & Haas 1984) might be predicted to have increased mortality risk to Bullfinches. Put in perspective, however, a shift of just 8 days in the predicted fledging date of captured juveniles does not suggest a dramatic change in phenology of successful Bullfinch nesting attempts or the subsequent survival prospects of young birds since the 1960s.

The lack of trends in clutch and brood size is consistent with analyses of national nest record data (Siriwardena *et al.* 2000, Baillie *et al.* 2001). Daily nest failure rates during the 1960s were similar to national estimates for Bullfinches calculated from nest record cards (Siriwardena *et al.* 2000) and failure rates during the 1990s were similar to those found in other recent studies of finches and buntings in southern England (Kyrkos 1997, Bradbury *et al.* 2000, Moorcroft 2000, Whittingham *et al.* 2001). The fact that we found no variation between broad habitat types (woodland and farmland) in measures of per nest breeding success contrasts with findings from national analyses of NRS data, which showed that egg period failure rates were higher in woodland than farmland (Siriwardena *et al.* 2001). This may simply reflect limited statistical power in our data sets, along with the fact that the 1990s data are derived from a fine-grained matrix of well-wooded farmland in a confined geographical area.

We found that annual productivity, as measured by the corrected ratio of juveniles to adults caught in October, was highest in 1983–95 when the national Bullfinch population had stabilized following decline. These trends are consistent with data from the Constant Effort Sites scheme, which show a 13% increase between 1984 and 1998 in the proportion of juveniles caught between May and August inclusive (Baillie *et al.* 2001). Changes in age ratios may also reflect changes in the relative probabilities of catching juvenile and adult birds. For instance, a decline in late summer food availability (e.g. due to agricultural intensification) may make juveniles more likely to disperse and an increase in predation risk (due to increased numbers of Sparrowhawks) may make adults more sedentary. One might also expect to trap more of the dispersing age-class (i.e. juveniles) in farmland, as they travel between patches of woodland, the preferred habitat (Gregory & Baillie 1998).

In summary, this study suggests that the more severe decline of Bullfinch populations on farmland has not been driven by changes in per nest breeding success. This is consistent with Siriwardena *et al.* (2001), who found that nesting success in terms of daily egg survival was actually higher on farmland than in woodland. The shift towards later breeding of Bullfinches could indicate constraints on total annual productivity, but equally may indicate seasonal shifts in availability of key food resources, and this is an aspect of Bullfinch breeding phenology and ecology that merits specific investigation.

Overall, we found no major differences in breeding success or phenology between farmland and woodland and, nationally, population trends have been synchronous in the two habitats. This suggests that whatever environmental factors are influencing Bullfinch productivity in these two habitat types are operating synergistically, probably aided by flows of individuals between them. The cause of the decline of Bullfinch populations in both woodland and farmland, and the greater severity of the decline in farmland, seems more likely to be found in: (1) the impacts of habitat deterioration on densities of birds settling to breed (Proffitt 2002); (2) constraints on survival probability outside the breeding season (Proffitt 2002); and/or (3) the impacts of increasing populations of Sparrowhawks on the ability of Bullfinches to exploit resources in some habitats (Newton 1993). Further investigation of the breeding ecology and phenology of Bullfinches would best be focused on understanding the causes and possible demographic consequences of the shift in first-egg

date distribution in favour of mid-summer nesting attempts.

We thank Kim Fenton, Allan Perkins, Ron Louch, Dave Tompson, Guy Anderson and Phil Barnett for field assistance and landowners for access to field sites. We are grateful to the Gordano Valley, Newbury, Steyning, Tresswell Woods and Wicken Fen ringing groups and John Phillips for providing ringing data and to the many ringers who contributed to the BRC19 Bullfinch records. We also thank the many volunteers who contributed Bullfinch data to the Nest Record Scheme. This study was supported by a CASE PhD Studentship to FMP, financed jointly by the Natural Environment Research Council and the Royal Society for the Protection of Birds.

REFERENCES

- Aebischer, N.J.** 1999. Multi-way comparisons and generalized linear models of nest success: extensions of the Mayfield method. *Bird Study* **46** (Suppl.): S22–S31.
- Baillie, S.R., Crick, H.Q.P., Balmer, D.E., Bashford, R.I., Beaven, L.P., Freeman, S.N., Marchant, J.H., Noble, D.G., Raven, M.J., Siriwardena, G.M., Thewlis, R. & Wernham, C.V.** 2001. *Breeding Birds in the Wider Countryside: Their Conservation Status 2000*. BTO Research Report no. 252. Thetford: British Trust for Ornithology.
- Bradbury, R.B., Kyrkos, A., Morris, A.J., Clark, S.C., Perkins, A.J. & Wilson, J.D.** 2000. Habitat associations and breeding success of yellowhammers on lowland farmland. *J. Appl. Ecol.* **37**: 789–805.
- BTO.** 1997. *Ringling Schedule Instruction Manual*. Thetford: British Trust for Ornithology.
- Cramp, S. & Perrins, C.M., eds.** 1994. *The Birds of the Western Palearctic*, Vol. 8. Oxford: Oxford University Press.
- Crick, H.Q.P. & Baillie, S.R.** 1996. *A Review of the BTO's Nest Record Scheme. its Value to the United Kingdom, Channel Islands and Country Agencies, and its Methodology*. Report no. 159. Thetford: British Trust for Ornithology.
- Crick, H.Q.P., Dudley, C. & Glue, D.E.** 1999. *Nest Record Scheme Handbook*. Thetford: British Trust for Ornithology.
- Crick, H.Q.P., Baillie, S.R. & Leech, D.I.** 2003. The UK Nest Record Scheme: its value for science and conservation. *Bird Study* **50**: 254–270.
- Genstat 5 Committee.** 1993. *Genstat Release 3 Reference Manual*. Oxford: Clarendon Press.
- Gibbons, D., Avery, M., Baillie, S., Gregory, R., Kirby, J., Porter, R., Tucker, G. & Williams, G.** 1996. Bird Species of Conservation Concern in the United Kingdom, Channel Islands and Isle of Man: revising the Red Data List. *RSPB Conservation Rev.* **10**: 7–18.
- Green, R.E.** 1995. Diagnosing causes of bird population declines. *Ibis* **137** (Suppl.): S47–S55.
- Gregory, R.D. & Baillie, S.R.** 1998. Large-scale habitat use of some declining British birds. *J. Appl. Ecol.* **35**: 785–799.
- Guisan, A. & Zimmerman, N.E.** 2000. Predictive habitat distribution models in ecology. *Ecol. Modelling* **135**: 147–186.
- Johnson, D.H.** 1979. Estimating nest success: the Mayfield method and an alternative. *Auk* **96**: 651–661.
- Kyrkos, A.** 1997. *Behavioural and demographic responses of Yellowhammers to variation in agricultural practices*. DPhil thesis, University of Oxford.
- Mayfield, H.F.** 1961. Nesting success calculated from exposure. *Wilson Bull.* **73**: 255–261.
- Mayfield, H.F.** 1975. Suggestions for calculating nest success. *Wilson Bull.* **87**: 456–466.
- Minitab Inc.** 2001. *Minitab Release 13.20*. State College, PA: Minitab Inc.
- Moorcroft, D.** 2000. *The causes of the decline in the linnet Carduelis cannabina within the agricultural landscape*. DPhil Thesis, University of Oxford.
- Moorcroft, D. & Wilson, J.D.** 2000. The ecology of Linnets *Carduelis cannabina* on lowland farmland. In Aebischer, N.J., Evans, A.D., Grice P.V. & Vickery, J.A. (ed). *Ecology and Conservation of Lowland Farmland Birds*: 173–181. Thetford: British Trust for Ornithology.
- Newton, I.** 1966. The moult of the Bullfinch *Pyrrhula pyrrhula*. *Ibis* **108**: 41–67.
- Newton, I.** 1993. Studies of west palearctic birds 192. Bullfinch. *Br. Birds* **86**: 638–648.
- Newton, I.** 1998. *Population Limitation in Birds*. London: Academic Press.
- Newton, I.** 1999. An alternative approach to the measurement of seasonal trends in bird breeding success: a case study of the bullfinch *Pyrrhula pyrrhula*. *J. Anim. Ecol.* **68**: 698–707.
- Newton, I.** 2000. Movements of Bullfinches *Pyrrhula pyrrhula* within the breeding season. *Bird Study* **47**: 372–376.
- Newton, I.** 2004. The recent declines of farmland bird populations in Britain. An appraisal of causal factors and conservation actions. *Ibis* **146**: 579–600.
- Newton, I. & Haas, M.B.** 1984. The return of the Sparrowhawk. *Br. Birds* **77**: 47–70.
- Newton, I. & Rothery, P.** 2000. Timing and duration of moult in the Bullfinch *Pyrrhula pyrrhula*: an appraisal of different analytical procedures. *Ibis* **142**: 65–74.
- Pampel, F.C.** 2000. *Logistic Regression: a Primer*. Thousand Oaks: Sage Publications.
- Peach, W.J., Siriwardena, G.M. & Gregory, R.D.** 1999. Long-term changes in over-winter survival rates explain the decline of reed buntings *Emberiza schoeniclus* in Britain. *J. Appl. Ecol.* **36**: 798–811.
- Proffitt, F.M.** 2002. *Causes of population decline of the bullfinch Pyrrhula pyrrhula in agricultural environments*. DPhil thesis, University of Oxford.
- Raven, M. & Noble, D.** 2001. The Breeding Bird Survey: 1994–2000. *BTO News* **237**: 12–14.
- Siriwardena, G.M., Baillie, S.R., Crick, H.Q.P. & Wilson, J.D.** 2000. The importance of variation in the breeding performance of seed-eating birds in determining their population trends on farmland. *J. Appl. Ecol.* **37**: 128–148.
- Siriwardena, G.M., Freeman, S.N. & Crick, H.Q.P.** 2001. The decline of the Bullfinch *Pyrrhula pyrrhula* in Britain: is the mechanism known? *Acta Ornithol.* **36**: 143–152.
- Sokal, R.R. & Rohlf, F.J.** 1981. *Biometry: the Principles and Practice of Statistics in Biological Research*, 2nd edn. New York: Freeman.
- Svensson, L.** 1992. *Identification Guide to European Passerines*. Stockholm: Lars Svensson.
- Whittingham, M.J., Bradbury, R.B., Wilson, J.D., Morris, A.J., Perkins, A.J. & Siriwardena, G.M.** 2001. Chaffinch *Fringilla coelebs* foraging patterns, nestling survival and territory distribution on lowland farmland. *Bird Study* **48**: 257–270.

Appendix 1. Summary of productivity per breeding attempt in the 1960s and 1990s. Figures in parentheses are standard errors. Hatching and fledging success only includes nests where exact clutch and brood size were known.

Measure of productivity	1960s	1990s	<i>n</i>	<i>P</i> -value ^a	Direction
Mean clutch size	4.69 (0.06)	4.61 (0.05)	299	0.752	ns
Mean brood size	3.98 (0.09)	3.89 (0.09)	230	0.715	ns
Proportion eggs hatched (successful) ^b	0.89 (0.03)	0.87 (0.02)	159	0.553	ns
Proportion chicks fledged (all broods) ^c	unavailable	0.47 (0.05)	79	n/a	
Proportion chicks fledged (successful) ^d	unavailable	0.77 (0.04)	48	n/a	
Number chicks fledged per attempt	unavailable	0.94 (0.10)	240	n/a	
Daily nest failure rate: egg period	0.026 (0.007)	0.039 (0.006)	365	0.037	ns
EFR 95% CI	0.012–0.040	0.027–0.051			
Daily nest failure rate: nestling period	0.030 (0.010)	0.032 (0.006)	254	0.783	ns
NFR 95% CI	0.010–0.050	0.020–0.044			
Daily nest failure rate: whole nest period	0.033 (0.004)	0.043 (0.003)	492	0.055	ns
WFR 95% CI	0.025–0.041	0.037–0.049			

^aClutch and brood size: log-linear models; hatching success: Mann–Whitney *U*-test; nest failure rates: *G*-test, binomial logistic regression.

^bExcluding nests where no chicks hatched, i.e. all nests that successfully hatched at least one chick.

^cIncluding nests where no chicks fledged, 1999–2001 only.

^dExcluding nests where no chicks fledged, i.e. all nests that successfully fledged at least one chick, 1999–2001 only.