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Breeding success of Spotted Flycatchers *Muscicapa striata* in southern England – is woodland a good habitat for this species?

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The UK population of the Spotted Flycatcher *Muscicapa striata* has declined markedly in the last 30 years but there have been few recent studies of the species. This study examined the relationship between nest success and the predominant habitat type around Spotted Flycatcher nests in two contrasting areas of England. A breeding population in eastern England, a region where numbers of Spotted Flycatchers are known to have decreased dramatically in recent decades, was compared with another in southwest England, where numbers have remained stable or even increased. Whilst there was no difference in breeding success between the two study areas, there were significant differences between habitats, with garden nests more successful than those in farmland or woodland, at both egg and chick stages. Estimates of productivity per nesting attempt were also lower in farmland and woodland, with nests in gardens fledging twice as many chicks as those in either woodland or farmland. The proximate cause of lower success in farmland and woodland was higher nest predation rates during both egg and chick stages. In terms of nesting success, farmland and woodland appear to be similar in quality for this species, but both appear to be suboptimal habitats when compared with gardens, providing evidence of a problem on the breeding grounds for this species, in at least these two habitats.

The Spotted Flycatcher *Muscicapa striata* is one of the UK's most rapidly declining birds: in the 25-year period 1978–2003, the breeding population fell by an estimated 82% (Baillie *et al.* 2006). The species was placed on the 'Red' list of birds of conservation concern in the UK (Gibbons *et al.* 1996) and was included on the list of 26 priority bird species in the UK Biodiversity Action Plan, with a species action plan being published in 1998 (Anon. 1998b). This action plan identified a specific requirement for a study of the summer ecology and habitat use of the species.

Throughout their range, Spotted Flycatchers are dependent on a landscape that provides both accessible space for catching flying insects and raised perches from which to make foraging flights or 'sallies' (Cramp & Perrins 1993). They occur in a range of habitats which comprise a mix of trees and open space, including parkland, gardens, orchards, woodland edge, open woodland and lines or copses of mature trees on farmland. In the UK, the species has shown similar population declines in both woodland and farmland (Freeman & Crick 2003). Potential causes of decline during the breeding season include reduced abundance and availability of invertebrate food, loss of foraging habitat and reduced nest survival, which in some open-nesting passerines is known to be affected by surrounding habitat (Martin & Roper 1988, Kelly 1993, Tarvin & Smith 1995).

However, a dearth of recent published research into the breeding ecology of Spotted Flycatchers hinders our ability to evaluate the potential causes, and problems may also exist in staging and/or over-wintering areas. Population declines have been linked to reduced survival of first-year birds (Freeman & Crick 2003) and there has also been an indication of a reduction in breeding productivity as a result of

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reductions in brood size and chick-stage nest survival rate (Baillie *et al.* 2006). Analyses of the BTO/JNCC/RSPB Breeding Bird Survey and other census data have highlighted potential regional differences in population trends, suggesting that there may be factors operating at a regional scale that are contributing to the national population decline. Small-scale, recent autecological studies of birds breeding in the UK have suggested that nests in trees may be more likely to fail than those placed either on or in buildings (Kirby *et al.* 2005), which concurs with the findings of Stoate and Szczur (2006), who reported lower survival of nests in woodland when compared with those within gardens. However, the relatively small scale of these studies did not make it possible for the authors to compare breeding success in different regions or across the range of habitats in which Spotted Flycatchers breed. If the population decline of Spotted Flycatchers is associated with factors operating at a regional level, an understanding of the causal factors affecting breeding success at a regional scale may therefore be an important prerequisite for the development of a recovery plan for this species.

This paper presents results from a study of Spotted Flycatchers breeding in three broad habitat types, garden, farmland and woodland, in two regions of England with contrasting landscapes and population trends for the species. We test the hypothesis that nest survival is associated with region and habitat and examine whether this may be contributing to the observed population declines.

METHODS

Study sites

Data were collected from two study areas: in Devon (southwest England) in 2004, 2005 and 2006, and Bedfordshire and Cambridgeshire (Beds./Cambs., eastern England) in 2005 and 2006. There is evidence for recent population decline in eastern England, compared with stability or increase in southwest England (Noble *et al.* 2001, Noble & Raven 2002, Amar *et al.* 2006).

The study area in Devon (centred on the parish of Aveton Gifford in the South Hams area) covered approximately 3200 ha, of which *c.* 2670 ha was farmland, 160 ha woodland and 111 ha villages and rural gardens. Woodland blocks in the study area were generally small, with only one over 20 ha, or linear in nature (following field edges and water courses) and were primarily deciduous. Grassland (largely used for cattle and sheep grazing, but also some for the production of hay and silage) accounted for over two-thirds of all farmland, with tilled land accounting for less than a third.

The Beds./Cambs. study site covered approximately 3200 ha of which *c.* 2280 ha was farmland, 440 ha woodland and 123 ha 'human sites' (which included villages and rural gardens). Woodland blocks in the study area ranged in size from less than 1 ha to approximately 92 ha, with five blocks being greater than 20 ha in area. Approximately 60% of the woodland in the study area was deciduous and 10% coniferous, the remaining 25% being mixed (i.e. made up of at least 10% each of deciduous and coniferous trees). In contrast to the Devon study area, grassland only accounted for about one-quarter of the farmed area with the remaining three-quarters being tilled land.

Data collection

All potentially suitable Flycatcher habitats were regularly searched by observers from early May through to late August in each year of data collection. Territories were located by observing territorial bird behaviour (singing, territorial disputes, strong alarm calling in response to observer, carrying food or nesting material). Nests were located either by searching likely locations within a territory, or by observations of bird behaviour (following adults to or from nests, or occasionally hearing calls of begging chicks). Once nests had been located, they were visited at regular intervals (usually every 3 days) to ascertain the outcome, following methods described in Crick *et al.* (1994, 2003). Contents of accessible nests (nest height approx. 6 m or less) were checked using a mirror on a telescopic pole. Activity at higher nests was observed using binoculars or telescope, thus allowing data to be gathered from most nests. Nests were deemed to have been successful if chicks had reached fledging age and the nest showed signs of success (well-trodden lining, droppings and/or feather scale present), if fledged young were seen nearby, or if adult activity indicated fledged chicks in the vicinity (alarm calling or feeding). The cause of nest failure (abandonment or predation) was determined either directly using evidence recorded by remote digital nest cameras following methods described by Bolton *et al.* (2007), or by interpretation of signs at or around the nest, based on experience gained from the camera evidence. The presence of a camera at Spotted Flycatcher nests had no significant effect on nest survival (egg stage

$\chi^2 = 0.03$, $P = 0.86$; chick stage $\chi^2 = 0.55$, $P = 0.46$, D.K.S. unpubl. data). This was based on a comparison of nests with cameras ($n = 49$ egg stage, $n = 53$ chick stage), and nests without ($n = 129$ egg stage, $n = 140$ chick stage), using the modelling method as described below for nest survival (total exposure days during egg stage $n = 1731$, chick stage $n = 2035$; total number of failures of nests without cameras $n = 63$, nests with cameras $n = 25$). Nests were recorded as predated if found empty (of either eggs or chicks that were too young to fledge) or if there were signs of nest damage with remains of eggs or chicks in the vicinity. Nests were considered to have been abandoned if (in the absence of parental activity) intact eggs remained in the nest beyond the expected hatching period, or dead nestlings (without any signs of aggressive injury) were found in the nest. Although it is acknowledged that in some cases such determination of the cause of nest failure may be equivocal, given the frequency of nest visits we believe that in the majority of cases it was possible to ascribe nest failures correctly.

Habitat classification

In each study area all discrete habitat patches were identified using 1 : 10 000 Ordnance Survey maps, and, following field survey, were ascribed to a habitat category according to the habitat coding system developed by Crick (1992). Habitats were surveyed once during the period of the study. Although cropping patterns in individual fields may have changed to some degree on an annual basis, no major land-use changes were observed in either site during the study, and it was assumed that the main habitat classification for each patch (e.g. woodland, farmland, gardens) remained constant. Field survey maps were digitized using MapInfo Professional 7.8 (MapInfo Corp. 1984–2004), so that the extent of each habitat type around individual nests could be calculated. Each nest was categorized as being in one of three broadly defined habitats, 'garden', 'woodland' or 'farmland', based on the most prevalent habitat within a 50-m radius of the nest. This distance was chosen as it has been previously shown that most foraging by provisioning adults is undertaken within 50 m of the nest (Davies 1977). In each of these broad habitat categories Flycatchers were found nesting in a range of locations. As it has previously been suggested that higher nests have increased survival probability (Kirby *et al.* 2005), height was also recorded using a calibrated measuring stick for lower nests and a Bushnell Yardage Pro™ laser rangefinder for higher nests.

Analyses

Nests were defined as active once the first egg had been laid. First egg date (the day the first egg was laid) was determined either by direct observation or by back calculation from either hatching date, assuming an average incubation period of 13 days starting from the date the last egg was laid (Cramp & Perrins 1993), or an estimate of chick age. Hatching date was the day the first egg hatched, and was considered as day 1 of the nestling period. The average nestling period was assumed to be 14 days (Cramp & Perrins 1993). Successful nests were defined as those fledging at least one offspring. Nest survival rates were estimated using methods described by Mayfield (1975), with exposure days being calculated from the first egg date (for nests found before egg-laying started) or the date of finding for an active nest. For failed nests, the date of failure was estimated as the mid-point between the date the nest was last known to be active and the date it was found to have failed. Analyses were carried out using the GENMOD procedure of SAS (SAS Institute Inc. 2002–03) and, following Aebischer (1999), used a generalized linear model with binomial error term and logit link function with success/failure as the response variable and exposure days as the binomial denominator. Significance was assessed by comparing the likelihood ratio statistic to the χ^2 distribution with the appropriate degrees of freedom. Separate models were constructed for the egg and chick stages to determine whether factors affecting nest survival differed between these two phases of the nesting period. Categorical variables entered into each model were habitat type (three-level factor: farmland, garden or woodland), region (two-level factor: Devon or Beds./Cambs.), and year (three-level factor: 2004, 2005, 2006). The interaction between habitat and region was also included in the initial model to test for regional differences in nest success between habitats. Since it has previously been suggested that higher nests have increased survival (Kirby *et al.* 2005), linear and quadratic height terms were included in the model, and linear and quadratic terms for first egg date (measured as days from 1 May) were included to control for seasonal effects. Within the three different habitats considered here, Flycatchers build their nests in a variety of locations. In garden and farmland habitats, nests will frequently be located in or on buildings as well as in trees. Using a subset of the data from these two habitats only, models were also constructed with an additional categorical variable, nest location (two-level factor: building or tree) to test whether actual location is an important predictor of nest survival. The interaction effect habitat*location was also included in the initial model to test for any habitat-related differences in survival between the two nest locations.

Initially, full models were fitted, including all the predictor variables, and these results are presented to support our minimal models as recommended by Whittingham *et al.* (2006). Subsequently, minimum adequate models were selected using a backwards deletion process (Crawley 1993), with each variable being removed and replaced sequentially. Following each iteration, the variable explaining the least amount of variance was removed until only significant variables were retained. Mayfield logistic regression assumes that nests are independent samples. As Spotted Flycatchers occasionally re-use previously used nests (either within or between seasons), data from such nests were only included for the first time the nest was used – any subsequent re-use of the nest-site was excluded from the analyses. All other nesting attempts were considered independent as they were located at a different site and at a different time (Hatchwell *et al.* 1996, Cresswell 1997). This resulted in a reduced data set being used for the purposes of the statistical modelling. Models were checked for over-dispersion using the ratio of the residual deviance to the remaining degrees of freedom (Crawley 1993, Aebischer 1999). Daily nest survival estimates, s, expressed as a proportion, were derived from back-transformation of the least squares means estimates generated by the minimum adequate models. Mayfield survival estimates for each nest stage were calculated as $100(s^x)$, where x is the approximate length of the appropriate nest stage in days (16 and 14, egg and chick stage, respectively). Estimates of overall nest survival were then generated simply by multiplying the survival probabilities for egg and chick stages.

A crude estimate of nest productivity (p) was calculated in relation to habitat based on methods described in Donald *et al.* (2002), using the formula:

$$p = ch(1 - l)(se^{16})(sc^{14})$$

where p is defined as the number of chicks leaving the nest, c is mean clutch size, h is the proportion of eggs hatching, l is the proportion of chicks dying before fledging (excluding whole nest failures), and se and sc are the egg-stage and chick-stage daily survival estimates, respectively (with 16 and 14 being the length of these two stages in days).

RESULTS

In total, 248 nests were monitored during the course of the study (Table 1). In Devon, 171 nests provided sufficient data for analysis, with 74 categorized as in farmland, 60 in gardens and 37 in woodland habitat. In Beds./Cambs. 77 nests were located and provided sufficient data for analysis. Of these, seven were categorized as farmland, 54 as garden and 16 as woodland habitat.

Within the three habitat categories, birds nested in a variety of locations. In gardens, however, nests were predominantly located either on or in built structures (76%), whereas in woodland the majority of nests (89%) were located in trees. In farmland, nests were found in reasonably equal numbers in trees (39%) and built structures (61%). Clutch initiation (date of first egg) followed a bimodal pattern (Fig. 1) and clutch size decreased as the season progressed (Fig. 2; Spearman rank-order correlation $r_s = -0.646$, $P \leq 0.001$). In Devon, the earliest first egg date was

Table 1. A summary of the nest data collected during the study.

	Devon			Beds./Cambs.	
	2004	2005	2006	2005	2006
No. of nests found	67	54	50	40	37
(farm/garden/wood)	29/26/12	(21/18/15)	(24/16/10)	(5/29/6)	(2/25/10)
Median 1st egg date	9 June	5 June	11 June	12 June	11 June
Median hatch date	26 June	22 June	27 June	29 June	27 June
No. of successful nests (%)	40 (59.7)	29 (53.7)	35 (70.0)	30 (75.0)	26 (70.3)
No. of abandoned nests (%)	8 (11.9)	7 (13.0)	2 (4.0)	3 (7.5)	1 (2.7)
No. of depredated nests (%)	19 (28.4)	18 (33.3)	13 (26.0)	7 (17.5)	10 (27.0)

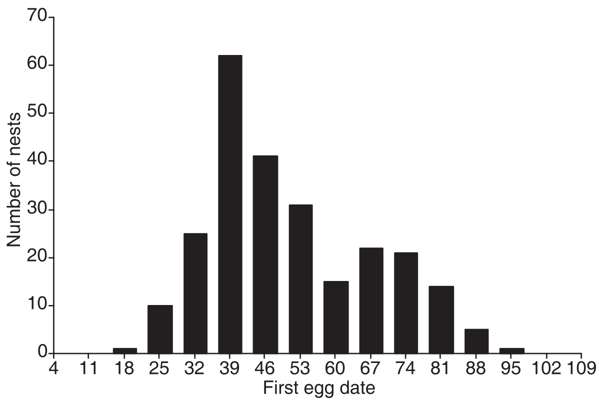

Figure 1. The distribution of clutch initiation dates (first egg dates day 1 = May 1). Data from both study areas and all years combined with nests grouped by 7-day period.

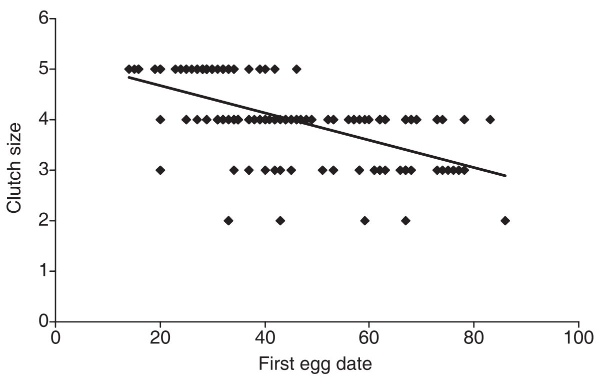

Figure 2. Clutch size in relation to first egg date (day 1 = 1 May). Data from all years and habitats combined. The continuous line indicates the linear regression of clutch size vs. first egg date.

15 May and the latest 25 July and nest height ranged from 0.9 to 20.0 m (mean 3.34 ± 0.16 m). In Beds./Cambs., the earliest first egg date was 14 May and the latest 17 July and nest height ranged from 1.1 to 15.0 m (mean 3.59 ± 0.25 m). Using data from complete clutches only, mean clutch size was 4.06 ± 0.09 in farmland ($n = 50$), 4.05 ± 0.08 in gardens ($n = 93$) and 3.89 ± 0.16 in woodland ($n = 28$). For nests that survived the egg stage, the proportion of eggs that hatched was 0.951 in farmland, 0.934 in gardens and 0.908 in woodlands. Using data from nests that were successful, of those eggs that hatched, the proportion of chicks that died before fledging was 0.050 in farmland nests ($n = 37$), 0.103 in gardens ($n = 85$) and 0.182 in woodland nests ($n = 20$).

Predation of eggs or chicks was the most frequently observed cause of nest failure, with only a small number of nests being abandoned (Table 2). Predation accounted for 71.4% of nest losses in gardens, 75.0% in farmland and 83.3% in woodland. However, whilst over a third (35%) of woodland and farmland nests were predated, only 17% of garden nests were (Table 2).

Table 2. The overall causes of nest failure in relation to the habitat of the breeding site.

	Farm	Garden	Woodland
No. of nests found	81	114	53
No. of abandoned nests (%)	9 (11.1)	8 (7.0)	4 (7.5)
No. of depredated nests (%)	27 (33.3)	20 (17.5)	20 (37.7)

Table 3. Full models of daily nest survival rates during the egg and chick stages incorporating categorical and continuous variables. The significant result is shown in bold type.

Independent variable	*df*	Egg stage χ^2	Egg stage *P*	Chick stage χ^2	Chick stage *P*
Categorical					
Habitat	2	**6.64**	0.0362	5.41	0.0669
Region	1	0.12	0.7338	0.04	0.8457
Year	2	2.66	0.2650	1.23	0.5403
Continuous					
Height	1	1.66	0.1974	0.00	0.9611
(Height)^2	1	3.14	0.0766	0.05	0.8182
First egg date	1	1.57	0.2107	0.08	0.7776
(First egg date)^2	1	3.10	0.0783	0.71	0.4006
Habitat*Region	2	1.16	0.5601	0.34	0.8452

To ensure statistical independence, a reduced data set was used for the modelling procedure comprising data from 218 nests (Devon: $n = 146$, 64 farmland, 50 garden and 32 woodland; Beds./Cambs.: $n = 72$, seven farmland, 50 garden and 15 woodland). When full models were fitted, habitat type was the only variable influencing daily nest survival rates significantly at the egg stage (Table 3), and was almost significant at the chick stage. For nests at the egg stage, the minimum adequate model retained habitat type, the linear effect for first egg date and height (linear and quadratic terms) as significant predictors of daily nest survival (Table 4). Daily nest survival rates during egg-stage nests in woodlands and farmland did not differ significantly (Fig. 3a; $\chi^2 = 0.02$, $P = 0.90$), but nests in both of these habitat types had a significantly lower daily survival than those in gardens (Fig. 3a; for woodland nests $\chi^2_1 = 7.97$, $P = 0.0047$;

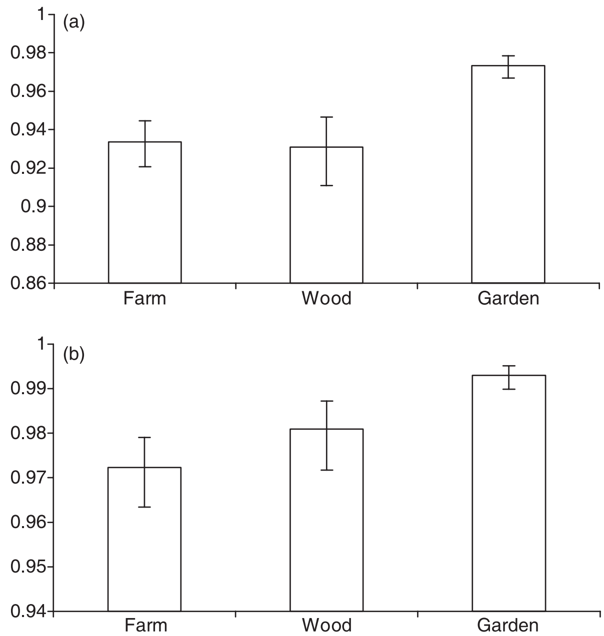

Figure 3. Daily nest survival estimates for habitat type (based on the back-transformed least squares mean estimates from the minimum adequate models) for (a) egg-stage and (b) chick-stage nests. Sample sizes for egg and chick stages, respectively: farmland, $n = 51$ and $n = 51$; woodland, $n = 28$ and $n = 34$; garden, $n = 75$ and $n = 85$.

Table 4. Variables retained in the minimum adequate models of daily nest survival rate.

Independent variable	*df*	Parameter estimate	χ^2	*P*
Egg stage				
Intercept	1	1.0549	2.88	0.0896
Habitat	2	–	13.99	0.0009
First egg date	1	0.0260	7.66	0.0056
Height	1	0.2769	2.21	0.1370
$(\text{Height})^2$	1	–0.0296	3.92	0.0477
Chick stage				
Intercept	1	2.1579	12.49	0.0004
Habitat	2	–	10.64	0.0049
First egg date	1	0.0410	10.03	0.0015

farmland nests $\chi^2_1 = 10.97$, $P = 0.0009$). The retention of the quadratic term for height indicates a curvilinear relationship with nest survival (Table 4). The minimum adequate model for chick-stage nests retained both habitat and the linear effect for first egg date (Table 4). As in egg-stage nests, daily nest survival at chick stage did not differ significantly between nests in woodland and farmland (Fig. 3b; $\chi^2_1 = 0.62$, $P = 0.43$), but nests in both these habitats had significantly lower survival than those in gardens (Fig. 3b; for woodland nests $\chi^2_1 = 3.92$, $P = 0.048$; farmland nests $\chi^2_1 = 9.68$, $P = 0.0019$). The linear effect for first egg date was retained in both models, indicating that nest survival increases as the season progresses (Table 4). Based on the daily nest survival estimates for the egg and chick stages from the minimum adequate models the Mayfield estimates for nest survival over the entire nesting period were 22.4% for farmland nests, 58.8% for garden nests and 24.2% for woodland nests. The models produced over-dispersion estimates of 1.23 and 0.78 (for egg and chick stages, respectively), indicating a good fit to the data (Crawley 1993).

Table 5. Variables retained in the minimum adequate models of daily nest survival rate for farmland and garden data only. A nest location variable was included in the full model, but was not retained in the MAM.

Independent variable	*df*	Parameter estimate	χ^2	*P*
Egg stage				
Intercept	1	2.3994	30.97	< 0.0001
Habitat	1	–0.9434	10.80	0.0010
First egg date	1	0.0304	7.72	0.0055
Chick stage				
Intercept	1	3.0090	22.51	< 0.0001
Habitat	2	–1.4198	9.99	0.0016
First egg date	1	0.0457	8.05	0.0046

Construction of models to test for an effect of nest location, using a subset of the data from farmland and garden nests (farmland: $n = 71$, 41 building, 30 tree; garden: $n = 100$, 73 building, 27 tree), resulted in minimum adequate models that retained only habitat and the linear effect for first egg date for both egg- and chick-stage nests (Table 5).

Estimates of productivity per nesting attempt were lower in both woodland (0.70 fledglings per nesting attempt) and farmland (0.82 fledglings per nesting attempt) than in garden nests (1.99 fledglings per nesting attempt).

DISCUSSION

The main finding of this study is that nest success of Spotted Flycatchers is closely associated with the habitat in which they breed, with birds breeding in woodland and farmland habitats having significantly lower nest success than those nesting in gardens. Moreover, productivity estimates also reflect this trend, suggesting that the number of young fledged per nesting attempt is also particularly low for birds nesting in woodland and farmland.

Although Kirby *et al.* (2005) suggested that higher nests were more successful than those lower down, results from this study indicate that the relationship is curvilinear in nature and may therefore not be as simple as previously suggested. Further analyses at the nest-site scale, including incorporation of more detailed nest location variables, such as level of nest concealment, would be required to establish more fully the effect of nest height on survival. In common with many other open-nesting passerines (Lack 1954, Ricklefs 1969, Söderström *et al.* 1998, Donald *et al.* 2002), predation was the greatest source of nest failure in each of the study areas, and differences in nest success between the habitats in this study most likely reflect differences in predation rates. As the presence of a predator or predation of an adult bird may also be a cause of desertion, total nest loss to predation is likely to be underestimated. There are several potential mechanisms whereby predation rates may differ between habitats. Habitat characteristics may influence nest concealment and/or predator access to nests, as well as influencing predator type, abundance or distribution (Evans 2004). These two mechanisms may also act in combination to alter the search efficiency of potential nest predators (Bowman & Harris 1980, Tarvin & Smith 1995), allowing predators that rely on visual cues to locate nests more easily. Additionally, predation risk may also be altered by differences in parental behaviour at the nest. Such differences in behaviour may be brought about by other habitat-related factors, including differences in the abundance or availability of food for both the adults and the chicks. If this was the case, adults may modify their provisioning behaviour, therefore altering the level of activity at or near the nest, thereby varying the overall predation risk. Additionally, hungry chicks often call continuously (Davies 1977), possibly making them more susceptible to predation (Evans *et al.* 1997), although this would not have been a factor during the egg stage.

Although there was an indication from Kirby *et al.* (2005) that birds breeding in trees may have reduced nest survival, the results presented here suggest that nest survival is influenced by the habitat surrounding the nest, rather than the fact that the nest is in a building or a tree. In contrast to most woodland, farmland and mature gardens typically include both trees and buildings, and birds are able to utilize both of these as nest-sites. However, within these two habitats, the choice of nest location does not appear to influence survival. Results from this study support those of Stoate and Szczur (2006), who reported a reduced nest survival of birds breeding in woodland compared with those in gardens. Additionally, this study shows that the association of nest success with habitat appears to be comparable between regions with differing population trends. Low productivity in farmland and woodland habitats suggested by this study supports similar recent evidence from the British Trust for Ornithology (BTO) Nest Record Scheme of reduced productivity driven by lower brood sizes and increased chick-stage nest failure rates (Baillie *et al.* 2006). Low nest survival rates and, hence, productivity in woodland and farmland provide evidence of a problem on the breeding grounds for this species, in at least these two habitats. Differences in annual productivity play a large role in determining changes in population size in short-lived species (Saether & Bakke 2000). The bimodal pattern of clutch initiation date in this study most likely reflects peaks in nesting activity associated with first and second nesting attempts. In the case of failed first attempts, replacement clutches are normally laid (Cramp & Perrins 1993). Following successful first attempts, Summers-Smith (1952) estimated that only 20% of Spotted Flycatchers are double-brooded, with Kirby *et al.* (2005) estimating this same figure to be 14%. A negative correlation between clutch size and first egg date such as found in this study is often indicative of a single-brooded rather than a multibrooded species (Klomp 1970, Crick *et al.* 1993), although Crick *et al.* (1993) additionally showed that multibrooded long-distance migrants also have seasonal declines in clutch size. In migratory species, such as the Spotted Flycatcher, the length of the breeding season is often constrained by the date that adults return from the wintering quarters, and birds that breed early are more likely to attempt second broods (Ogden & Stutchbury 1996). Development of models that include re-nesting may be required in order to understand more fully how the variation in productivity per nesting attempt reported in this study relates to individual fecundity and the observed population declines.

The lack of a significant difference between nest success in farmland and woodland habitats is consistent with earlier analyses (Freeman & Crick 2003), which suggested that population declines have been similar in these two habitat types, hence leading them to conclude that some broad-scale factor was probably driving population declines. However, as gardens are not adequately represented by Common

Bird Census data, Freeman and Crick (2003) were unable to construct separate models for this habitat type. Interestingly, however, the results reported here suggest that habitat-specific differences may exist in breeding success. In order to support the generality of these findings, analyses of national data sets, such as that collected as part of the BTO Nest Record Scheme, may be required in order to explore whether similar habitat-related differences in breeding success exist at a national scale.

Regardless of low fecundity, Spotted Flycatchers still nest in good numbers in woodland and farmland habitats in Devon. Although nests were still found in these habitats in Beds./Cambs., the majority of birds nesting in this region are found in gardens, this probably being a true reflection of the breeding distribution in this region as both study areas were thoroughly searched for breeding birds and it is unlikely that nesting attempts would have been missed. Given the differential usage of the three habitats, the overall productivity is higher in Beds./Cambs. than in Devon (weighted mean 1.62 fledglings per nest in Beds./Cambs. compared with 1.20 in Devon). This is surely a paradox, given the population trends in the two regions. Aside from the possibility, albeit unlikely, that there may be differential over-winter survival, possibly as a result of a regional migratory divide, there are a number of reasons why the Devon population is stable whilst that in Beds./Cambs. is declining. Current estimates of per nest productivity suggest that recent population trends in these two regions are not dependent on this particular aspect of demography. One possibility is that there may be subtle differences in re-nesting probability resulting from differences in habitat quality as yet unexplored, such that individual nest estimates do not reflect whole season fecundity. Alternatively, there may be density-dependent processes operating, with the higher breeding density in Devon resulting in some birds utilizing suboptimal habitats for nesting.

No regional differences in nest success were detected during this study, despite the increasing evidence for differing regional population trends (Noble *et al.* 2001, Noble & Raven 2002, Amar *et al.* 2006), but habitat-specific differences were clear. It is possible that the population in Devon is now undergoing the same processes that have already led to the decline in eastern England, but why this should be the case remains unclear. In contrast to data for Devon, woodland and farmland appear to be relatively unimportant breeding habitats for the species in Beds./Cambs. This cannot have been the case historically, and indeed, anecdotal evidence suggests that Spotted Flycatchers were once found commonly in both woodland and farmland in Bedfordshire and Cambridgeshire, and that they have now disappeared from many 'traditional' sites. Data from the BTO's Common Bird Census for the period 1962–88 show consistent declines in both farmland and woodland populations, with the most notable declines being in farmland populations in western, eastern and southern England (Marchant *et al.* 1990). It is possible therefore that the severe population decline suggested for the East of England region is at least partly attributable to the loss of birds from these two key habitats. This may be the case if the habitat preference of Spotted Flycatchers has changed, or if the relative availability, absolute abundance or quality of one or more of the habitats has changed unequally between the two regions.

Population modelling, carried out by Freeman and Crick (2003), suggested that declines in first-year and possibly post-fledging survival were the most likely demographic causes of population decline for this species, further stating that changes in annual fecundity were unlikely to be important drivers. Although found in several habitats, the Spotted Flycatcher is often regarded as a woodland species and it is included in the suite of birds contributing to the composite index of woodland bird populations which forms part of the UK Government's wild bird indicator (Anon. 1998a, 1999, Gregory *et al.* 2003). Results presented here suggest that the species may not be doing well in this habitat, and that this pattern may be general across regions with differing population trends. Whatever the reasons behind the decline of Spotted Flycatchers in the UK, demographic factors that cause population decline may not always be the same as those that must be manipulated to achieve population recovery. In woodlands, for example, the potential exists, given suitable conditions, for breeding productivity to be increased from its current low level which may facilitate a population recovery. However, further research is required to investigate the mechanisms responsible for the habitat-related differences in breeding success reported here before recommendations on effective conservation measures can be made.

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REFERENCES

Aebischer, N.J. 1999. Multi-way comparisons and generalized linear models of nest success: extensions of the Mayfield method. *Bird Study* **46**: 22–31.

Amar, A., Hewson, C.M., Thewlis, R.M., Smith, K.W., Fuller, R.J., Lindsell, J., Conway, G., Butler, S. & MacDonald, M.A. 2006. *What's Happening to Our Woodland Birds? Long-Term Changes in the Populations of Woodland Birds*. RSPB research report number 19, BTO research report number 169. Sandy and Thetford: RSPB/BTO.

Anon. 1998a. *Sustainability Counts: Consultation Paper on a Set of 'Headline Indicators of Sustainable Development*. London: Department of the Environment, Transport and Regions.

Anon. 1998b. *UK Biodiversity Group Tranche 2 Action Plans, Vol. 1. – Vertebrates and Vascular Plants*. Peterborough: English Nature.

Anon. 1999. *Monitoring Progress (Indicators for the Strategy for Sustainable Development in the United Kingdom)*. London: Department of the Environment, Transport and Regions.

Baillie, S., Marchant, J.H., Crick, H.Q.P., Noble, D.G., Balmer, D.E., Coombes, R.H., Downie, I.S., Freeman, S.N., Joys, A.C., Leech, D.I., Raven, M.J., Robinson, R.A. & Thewlis, R.M. 2006. *Breeding Birds in the Wider Countryside: Their Conservation Status 2005*. BTO Research Report no. 435. Thetford: BTO (www.bto.org/birdtrends).

Bolton, M., Butcher, N., Sharpe, F., Stevens, D.K. & Fisher, G. 2007. Remote monitoring of nests using digital camera technology. *J. Field Ornithol.* **78**: 213–220.

Bowman, G.B. & Harris, L.D. 1980. Effect of spatial heterogeneity on ground-nest depredation. *J. Wildl. Manage.* **44**: 806–813.

Cramp, S. & Perrins, C.M. (eds) 1993. *The Birds of the Western Palearctic, Vol. 7*. Oxford: Oxford University Press.

Crawley, M.J. 1993. *GLIM for Ecologists*. Oxford: Blackwell Scientific Publications.

Cresswell, W. 1997. Nest predation rates and nest detectability in different stages of breeding in Blackbirds *Turdus merula*. *J. Avian Biol.* **28**: 296–302.

Crick, H.Q.P. 1992. A bird-habitat coding system for use in Britain and Ireland incorporating aspects of land-management and human activity. *Bird Study* **39**: 1–12.

Crick, H.Q.P., Gibbons, D.W. & Magrath, R.D. 1993. Seasonal-changes in clutch size in British birds. *J. Anim. Ecol.* **62**: 263–273.

Crick, H.Q.P., Dudley, C. & Glue, D.E. 1994. *The Nest Record Scheme Handbook*. Thetford: BTO.

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.

Davies, N.B. 1977. Prey selection and the search strategy of the Spotted Flycatcher (*Muscicapa striata*), a field study on optimal foraging. *Anim. Behav.* **25**: 1016–1033.

Donald, P.F., Evans, A.D., Muirhead, L.B., Buckingham, D.L., Kirby, W.B. & Schmitt, S.I.A. 2002. Survival rates, causes of failure and productivity of Skylark *Alauda arvensis* nests on lowland farmland. *Ibis* **144**: 652–664.

Evans, K.L. 2004. The potential for interactions between predation and habitat change to cause population declines of farmland birds. *Ibis* **146**: 1–13.

Evans, A.D., Smith, K.W., Buckingham, D.L. & Evans, J. 1997. Seasonal variation in breeding performance and nestling diet of Cirl Buntings *Emberiza cirlus* in England. *Bird Study* **44**: 66–79.

Freeman, S.N. & Crick, H.Q.P. 2003. The decline of the Spotted Flycatcher *Muscicapa striata* in the UK: an integrated population model. *Ibis* **145**: 400–412.

Gibbons, D.W., Avery, M., Baillie, S.R., Gregory, R.D., Kirby, J.R., Porter, R., Tucker, G.M. & Williams, G. 1996. *Bird Species of Conservation Concern in the United Kingdom, Channel Islands and Isle of Man: Revising the Red Data List*. Report no. 10. Sandy: RSPB.

Gregory, R.D., Noble, D.G., Field, R., Marchant, J.H., Raven, M.J. & Gibbons, D.W. 2003. Using birds as indicators of biodiversity. *Ornis Hungarica* **12–13**: 11–24.

Hatchwell, B.J., Chamberlain, D.E. & Perrins, C.M. 1996. The reproductive success of Blackbirds *Turdus merula* in relation to habitat structure and choice of nest site. *Ibis* **138**: 256–262.

Kelly, J.P. 1993. The effect of nest predation on habitat selection by Dusky Flycatchers in limber pine–juniper woodland. *Condor* **95**: 83–93.

Kirby, W., Black, K., Pratt, S. & Bradbury, R. 2005. Territory and nest-site habitat associations of Spotted Flycatchers *Muscicapa striata* breeding in central England. *Ibis* **147**: 420–424.

Klomp, H. 1970. The determination of clutch size in birds: a review. *Ardea* **58**: 1–124.

Lack, D. 1954. *The Natural Regulation of Animal Numbers*. Oxford: Oxford University Press.

MapInfo Corp. 1984–2004. *MapInfo Professional*, Version 7.8. Tory, NY: MapInfo Corporation.

Marchant, J.H., Hudson, R., Carter, S.P. & Whittington, P. 1990. *Population Trends in British Breeding Birds*. Tring: BTO.

Martin, T.E. & Roper, J.J. 1988. Nest predation and nest-site selection of a western population of the Hermit Thrush. *Condor* **90**: 51–57.

Mayfield, H.F. 1975. Suggestions for calculating nest success. *Wilson Bull.* **87**: 456–466.

Noble, D.G. & Raven, M.J. 2002. Regional trends in farmland birds in the UK. *Aspects Appl. Biol.* **67**: 141–146.

Noble, D.G., Raven, M.J. & Baillie, S.R. 2001. *The Breeding Bird Survey 2000*. BTO Research Report no. 265. Thetford: BTO.

Ogden, L.J.E. & Stutchbury, B.J.M. 1996. Constraints on double brooding in a Neotropical migrant, the Hooded Warbler. *Condor* **98**: 736–744.

Ricklefs, R.E. 1969. An analysis of nesting mortality in birds. *Smithson. Contrib. Zool.* **9**: 1–48.

Saether, B.E. & Bakke, O. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* **81**: 642–653.

SAS Institute Inc. 2002–03. *SAS/STAT Software*, Release 9.1. Cary, NC: SAS Institute Inc.

Söderström, B., Pärt, T. & Ryden, J. 1998. Different nest predator faunas and nest predation risk on ground and shrub nests at forest ecotones: an experiment and a review. *Oecologia* **117**: 108–118.

Stoate, C. & Szczur, J. 2006. Potential influence of habitat and predation on local breeding success and population in Spotted Flycatchers *Muscicapa striata*. *Bird Study* **53**: 328–330.

Summers-Smith, D. 1952. Breeding biology of the Spotted Flycatcher. *Br. Birds* **45**: 153–167.

Tarvin, K.A. & Smith, K.G. 1995. Microhabitat factors influencing predation and success of suburban Blue Jay *Cyanocitta cristata* nests. *J. Avian Biol.* **26**: 296–304.

Whittingham, M.J., Stephens, P.A., Bradbury, R.B. & Freckleton, R.P. 2006. Why do we still use stepwise modelling in ecology and behaviour? *J. Anim. Ecol.* **75**: 1182–1189.

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