

## Post-fledging survival of individual great tits: the effect of hatching date and fledging mass

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Pre-breeding survival is one of the major sources of individual variation in lifetime reproductive success. However, very little is known about the reasons for differences in survival among individuals during this important phase of the life cycle. Some studies, using local return rates as indices of survival, have shown a relationship between post-fledging survival and fledging date and mass in birds, most of them suggesting directional selection towards heavy masses and early fledging dates. Recent development of capture-recapture models allows the separate estimate of survival and recapture probabilities, as well as the inclusion of individual covariates into the modelling process. We used here these models to explore the relative effects of fledging date and fledging mass on local recruitment of individual great tit *Parus major* fledglings. Individual capture-recapture histories of 2051 fledglings (cohorts 1992–1999), 184 of which were recaptured as breeding birds during 1993–2000, were used in the analyses. Hatching date, offspring mass at day 15, their squared terms, and interactions between mass and date, were included as covariates into the modelling process. Models with age (fledglings and adults) and time (year) dependence were used. The probability of local recruitment increased with fledging mass in each of the years studied. Fledging date also affected recruitment but, against what is commonly thought, fledging early is not the best option every year. Either early, intermediate or late fledglings were favoured in different years. This between-year variation in the optimum fledging date offers an alternative explanation to the lack of evolution towards earlier breeding dates, in spite of the advantages of early breeding some years.

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Survival until first reproduction is one of the major sources of individual variation in lifetime reproductive success (Clutton-Brock 1988, Newton 1989). It is believed that a large proportion of the fledglings die before breeding, and short-lived hole-nesters are among the species with higher pre-breeding mortality (Newton 1989). However, due to the practical problems of estimating juvenile survival, very few studies provide good data on this trait (Dhondt 2001). Therefore, studies reporting accurate data on juvenile survival, as well as on the reasons for differences in survival among indi-

viduals during the pre-breeding period, are most needed.

The fate of individual fledglings is highly determined by two decisions adopted by their parents: the date of breeding, which determines the date of fledging, and the energy invested in feeding the chicks, which affects fledging mass. The date of fledging has been demonstrated to affect post-fledging survival in many studies, the usual pattern being that early fledglings experienced higher survival (Siikamäki 1998, Verboven and Visser 1998). However, offspring survival seems to be reduced

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in early breeders under some circumstances (Perrins and McCleery 1989, Nilsson 1994), so the seasonal pattern might vary between populations or between years (Van Noordwijk et al. 1981). On the other hand, heavier fledglings usually survive better than lighter ones (Both et al. 1999, Green and Cockburn 2001), while the possible lower survival of very heavy fledglings has been suggested but not convincingly demonstrated (Adriansen et al. 1998, Perrins and McCleery 2001).

Most studies analysing offspring survival have used local return rates (proportion of fledglings recaptured as breeding birds in the local population during the next year) as an index of local fledgling survival (or “local recruitment”). However, this entails some problems, since this procedure fails to control for the probability of recapture (Lebreton et al. 1992, Martin et al. 1995). Recent developments of models using capture-recapture data for open populations greatly improve the reliability of survival estimates, since they allow both recapture and survival rates to be estimated separately, and allow examination of how individual characteristics (such as fledgling mass or date of fledging) affect survival estimates (Lebreton et al. 1992, Skalski et al. 1993, White and Burnham 1999). Although some studies, mostly in non-passerines, have estimated local recruitment rates using these models (Ringsby et al. 1999, Frederiksen and Bregnballe 2000, Lepage et al. 2000), none, to our knowledge, has examined the effect of individual covariates on local recruitment.

Our objective was to estimate local recruitment rates of individual great tit *Parus major* fledglings, and explore the relative effects of hatching date and fledgling mass on their survival using capture-recapture models.

## Methods

### Study area and general field methods

Data used here were collected during a long-term study of a great tit population in Sagunto, eastern Spain (39°42'N, 0°15'W, 30 m a.s.l.). The study area was located within an extensive orange plantation, and wooden nestboxes were placed each year for the birds to breed (Barba et al. 1995). Data from 1992 to 2000 were used for the present study.

Survival from fledging to the first breeding season was the dependent variable actually studied. The relevant independent variables for this study were the date of fledging and the mass of the chicks at this time. The date of fledging was exactly known for a few nests, so we used the hatching date as a surrogate of fledging date. Exact hatching dates (of the first egg) were obtained for all the nests through daily visits around the expected date of hatching. Nestlings were ringed and weighed when they were 15 days old, and this mass was used as an index of fledgling mass, since it is virtually equal to fledgling mass

in this species (Barba et al. 1993). Almost all (ca 95%) successful parents were captured and ringed (or the ring read) while feeding 10–15 days old nestlings.

The analyses were based on individual capture-recapture histories of 2051 fledglings, 184 of which were recaptured as breeding birds in the studied population. Only fledglings from first broods were included, since further breeding attempts were scarce and generally unsuccessful.

### Survival analyses

Survival analyses were performed using Cormack-Jolly-Seber (CJS) models according to the statistical framework reviewed in Lebreton et al. (1992). We used program MARK (White and Burnham 1999) to model local survival rates, incorporating individual covariates and their interactions into the modelling process (White and Burnham 1999). We used a logit link function in the models, the relationship between survival ( $\phi$ ) and a covariate being:

$$\text{Logit}(\phi) = B_0 + B_1(\text{covariate})$$

$$\phi = \frac{e^{B_0 + B_1(\text{covariate})}}{1 + e^{B_0 + B_1(\text{covariate})}}$$

where  $B_0$  and  $B_1$  are constants. To ensure that the numerical optimisation algorithm finds the correct parameter estimates, the values of individual covariates were standardised using the option “Standardised Individual Covariates” from MARK. This method computes the mean ( $\bar{x}$ ) and standard deviation (s.d.) of the individual covariate. Then, each value is standardised by the transformation:  $(x - \bar{x})/\text{s.d.}$

Previous studies in the great tit (Verboven and Visser 1998), and in other bird species (Brinkhof et al. 1997), have found that the probabilities of survival of fledglings from the same nest were independent from each other. If this is so in our population, the frequencies of nests from which 0, 1, 2, etc. fledglings survived will follow a Poisson distribution. We have tested the goodness-of-fit of our data to a Poisson distribution with a  $\chi^2$  test (Zar 1996). The results ( $\chi^2_{300} = 347.44$ ,  $0.975 < p > 0.025$ ), suggest that local recapture probability of a fledgling is independent from those of its nestmates.

### Model selection

Model selection was done according to Lebreton et al. (1992). The validity of the CJS model to the data was assessed by the goodness-of-fit tests of program RELEASE (Burnham et al. 1987). TEST 2 of RELEASE tests if recapture probability at time  $i$  is the same for all

marked individuals present in the population at time  $i$ , while TEST 3 tests if every marked individual in the population after time  $i$  has the same probability of surviving to time  $i + 1$ .

The goodness-of-fit of tests considering age effects was checked using a parametric bootstrap approach. The parameter estimates (survival and recapture rates) of the model were used to simulate data. These simulated data exactly met the assumptions of the model, i.e. animals were totally independent and no over-dispersion or violations of model assumptions were included. Then we checked whether the deviance of the simulated data was larger than that observed. The number of simulations with deviance larger than the one we observed for our general model divided by the total number of simulations finally gave the probability of obtaining by chance a deviance value as large or larger than the one we observed. We used the significance level  $p < 0.05$  for rejecting the null hypothesis. Model notations follow those suggested in Lebreton et al. (1992).

## Results

### Goodness-of-fit of the model

We first considered one of the simplest structures of the CJS models, that including time-dependent survival and capture probabilities. This model is denoted  $\phi_{(t)}, P_{(t)}$ , where  $\phi$  is the probability of survival and  $P$  the probability of recapture, and  $t$  denotes time-dependence in each parameter. This simple model fitted the data poorly (TEST 2 + TEST 3,  $\chi^2 = 248.87$ ,  $DF = 24$ ,  $p < 0.001$ ). Results from TEST 3 ( $\chi^2 = 238.86$ ,  $DF = 13$ ,  $p < 0.001$ ) suggested a possible effect of age on survival probabilities. As survival and recapture probabilities of fledglings in their first year are likely to differ from those of adults, we included two age classes (fledglings,  $a_1$ , and adults,  $a_2$ ) in the model, both with time-dependence (Model  $\phi_{(a_1, a_2+) \times t}, P_{(a_1, a_2+) \times t}$ ). It was as-

sumed that adult survival between two consecutive years was constant (noted  $a_{2+}$  in the model). The goodness-of-fit parametric bootstrap approach supported that this model fitted the data satisfactorily ( $p = 0.55$ , 1000 simulations). Therefore, we started model selection from the model  $\phi_{(a_1, a_2+) \times t}, P_{(a_1, a_2+) \times t}$  (Table 1).

### Capture and survival probabilities

There was no significant effect of age (Table 1, Model 2 vs Model 1) or time (Table 1, Model 3 vs Model 1) on recapture probability. A model with constant recapture probability was the one with lower AICc (Table 1, Model 4). Thus, in the rest of the models fitted to the data we will hold recapture probability constant. Estimated recapture probability was 0.43 (s.e. = 0.03).

There was no time-dependent variation in survival probabilities (Table 1, Model 5 vs Model 4), but survival probabilities were age dependent (Table 1, Model 6 vs Model 4, and Model 7 vs Model 5). The final model selected (Table 1, Model 5) is the one with lower AICc. This indicated that local recruitment probability was 0.14 (s.e. = 0.01).

### Fledgling mass and the probability of local recruitment

To analyse the effect of fledgling mass on local recruitment we started from a model with age effects in survival probability and constant recapture rates (Table 2, Model 1; which correspond, using a simplified notation, to Model 5 in Table 1). The effects of mass and mass squared were included as covariates for the parameter  $a_1$ , i.e. local recruitment probability. Comparison between Models 1 and 2 (Table 2) suggested that there was a significant effect of fledgling mass on recruitment. Comparison between Models 3 and 2, to test for the relative importance of mass squared,

Table 1. Model selection for age effects on recapture and survival probabilities of great tits breeding in eastern Spain. For each model, the values for deviance (DEV), number of estimable parameters (np) and the Akaike's Information Criterion (AICc) are shown. Model notation is as follows:  $\phi$ , survival probability;  $P$ , recapture probability;  $t$ , time dependence (year);  $a_1$ , survival probability of fledglings;  $a_{2+}$ , survival probability of adults;  $\times$ , interaction between factors. Bold face denotes the selected model.

Models	DEV	np	AICc	Comparison between models
<b>Modelling recapture probability</b>				
(1) $\phi_{(a_1, a_2+) \times t}, P_{(a_1, a_2+) \times t}$	2023.9	28	2080.6	
(2) $\phi_{(a_1, a_2+) \times t}, P_{(t)}$	2028.9	22	2073.4	Age effect on recapture, (2) vs (1): $\chi^2_6 = 5.1$ , $p = 0.54$
(3) $\phi_{(a_1, a_2+) \times t}, P_{(a_1, a_2+)}$	2038.7	17	2072.9	Time effect on recapture, (3) vs (1): $\chi^2_{11} = 14.8$ , $p = 0.19$
<b>Modelling survival probability</b>				
(4) $\phi_{(a_1, a_2+) \times t}, P_{(constant)}$	2038.8	16	2071.1	
<b>(5) <math>\phi_{(a_1, a_2+)}, P_{(constant)}</math></b>	<b>2052.4</b>	<b>3</b>	<b>2058.4</b>	<b>Time effect on survival, (5) vs (4): <math>\chi^2_{13} = 13.6</math>, <math>p = 0.40</math></b>
(6) $\phi_{(t)}, P_{(constant)}$	2241.4	9	2259.5	Age effect on survival, (6) vs (4): $\chi^2_2 = 202.6$ , $p < 0.001$
(7) $\phi_{(constant)}, P_{(constant)}$	2245.4	2	2249.4	Age effect on survival, (7) vs (5): $\chi^2_1 = 192.9$ , $p < 0.001$

Table 2. Model selection for the relationship between recruitment probability and fledgling mass and hatching date of great tits in eastern Spain. Recapture probability was considered constant in all models, and it is not shown. All the notation refers to survival. Model 1 in this table corresponds to model  $\phi_{(a_1, a_{2+})}$ ,  $P_{(\text{constant})}$  in Table 1. Model notation is as follows: t, time dependence (year);  $a_1$ , survival probability of fledglings;  $a_{2+}$ , survival probability of adults;  $\times$ , interaction between factors;  $+$ , additive factors; m, mass;  $m^2$ , mass squared; hd, hatching date;  $hd^2$ , hatching date squared. Bold face denotes the selected model.

Models	DEV	np	AICc	Comparison between models
<b>Modelling mass</b>				
(1) $a_1, a_{2+}$	2052.4	3	2058.4	
(2) $a_1 (m), a_{2+}$	2044.0	4	2052.0	Effect of fledgling mass, (2) vs (1): $\chi^2_1 = 8.41$ , $p = 0.004$
(3) $a_1 (m + m^2), a_{2+}$	2041.1	5	2051.1	Effect of fledgling mass squared, (3) vs (2): $\chi^2_1 = 2.92$ , $p = 0.087$
(4) $a_1 (t \times m), a_{2+}$	2039.87	11	2061.9	Effect of $t \times m$ , (4) vs (2): $\chi^2_7 = 4.15$ , $p = 0.76$
<b>Modelling hatching date</b>				
(5) $a_1 (hd), a_{2+}$	2042.9	4	2050.9	Effect of hatching date, (5) vs (1): $\chi^2_1 = 9.61$ , $p = 0.002$
(6) $a_1 (hd + hd^2), a_{2+}$	2038.7	5	2048.7	Effect of $hd^2$ , (6) vs (5): $\chi^2_1 = 4.16$ , $p = 0.041$
(7) $a_1 (t \times (hd + hd^2)), a_{2+}$	2005.7	19	2044.0	Effect of $t \times (hd + hd^2)$ , (7) vs (6): $\chi^2_{14} = 33.01$ , $p = 0.029$
(8) $a_1 (t \times hd), a_{2+}$	2027.3	11	2049.4	Effect of $t \times hd^2$ , (8) vs (7): $\chi^2_8 = 21.6$ , $p = 0.006$
<b>Modelling interaction between hatching date and fledgling mass</b>				
(9) $a_1 [(t \times (hd + hd^2)) + m + hd \times m], a_{2+}$	2001.8	21	2044.2	
<b>(10) <math>a_1 [(t \times (hd + hd^2)) + m], a_{2+}</math></b>	<b>2001.8</b>	<b>20</b>	<b>2042.2</b>	<b>Effect of <math>hd \times m</math>, (10) vs (9): <math>\chi^2_1 = 0</math>, ns</b>

showed no significant effect of mass squared on local recruitment probability. Thus, local recruitment probability increased significantly with mass at fledging (Fig. 1).

Although we have already shown that the local recruitment rate did not differ between years (Table 1), the effect of fledgling mass on the probability of local recruitment could differ from year to year. To test this hypothesis we fitted a model with time variation in the effect of fledgling mass (noted as  $t \times m$ ). As recruitment was not different between years, we built a model with a common intercept for all years, i.e. similar recruitment rates between years but different effect of the covariate within each year (Table 2, Model 4). This model did not fit the data better than a model considering a constant effect of fledgling mass (Table 2, Model 4 vs Model 2), so we conclude that the effect of mass on recruitment probabilities did not differ between years.

### Hatching date and the probability of local recruitment

To analyse the effect of hatching date on the probability of local recruitment we started again from Model 1 (Table 2). The effect of hatching date and hatching date squared were both included as covariates for the parameter recruitment probability (Table 2, Model 6). Both hatching date (Table 2, Model 5 vs Model 1) and hatching date squared (Table 2, Model 6 vs Model 5) were significant. Therefore, there was a non-linear relationship between local recruitment probability and hatching date.

As above, we tested the hypothesis of time variation in the effect of hatching date on the probability of local recruitment, fitting a model with time variation in the effects of hatching date and hatching date squared

(Table 2, Model 7). This model fitted the data better than a model considering a constant effect of hatching date and hatching date squared (Table 2, Model 7 vs Model 6). The term hatching date squared was also significant after introducing time variation (Table 2, Model 8 vs Model 7). Therefore, there was a significant effect of hatching date and hatching date squared on the probability of local recruitment, but the effect of these two covariates differed significantly between years (Table 2, Model 7). The analysis of the logit function parameters showed that in 3 out of 8 years (1995, 1996 and 1999) the functions suggest better survival probabilities for early fledglings, the probabilities decreasing seasonally (Fig. 2). In other three years (1993, 1994 and 1998), the pattern was similar but the very early fledglings showed decreased survival probabilities. Just an inverse pattern, with very early and very late

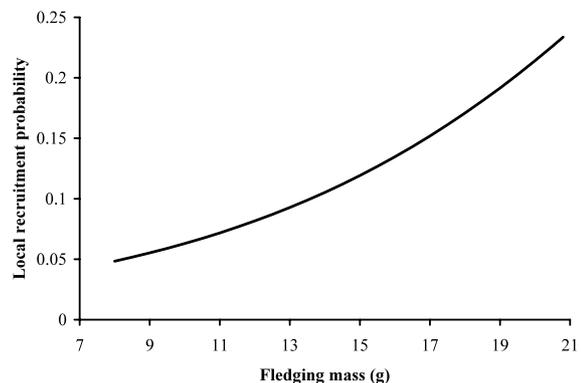


Fig. 1. Local recruitment probability ( $\phi$ ) of great tits in relation to fledgling mass (m) (Model  $\phi_{(a_1 m, a_{2+})}$ ,  $P_{(\text{constant})}$ ). Fitted regression was:  $\text{logit } \phi = -4.01 (\pm 0.81) + 0.14 (\pm 0.05) m$ . Line is shown over the range of nestling masses on day 15. Mean standardised fledgling mass ( $\pm$  s.d.) was  $16.47 \pm 1.89$  g.

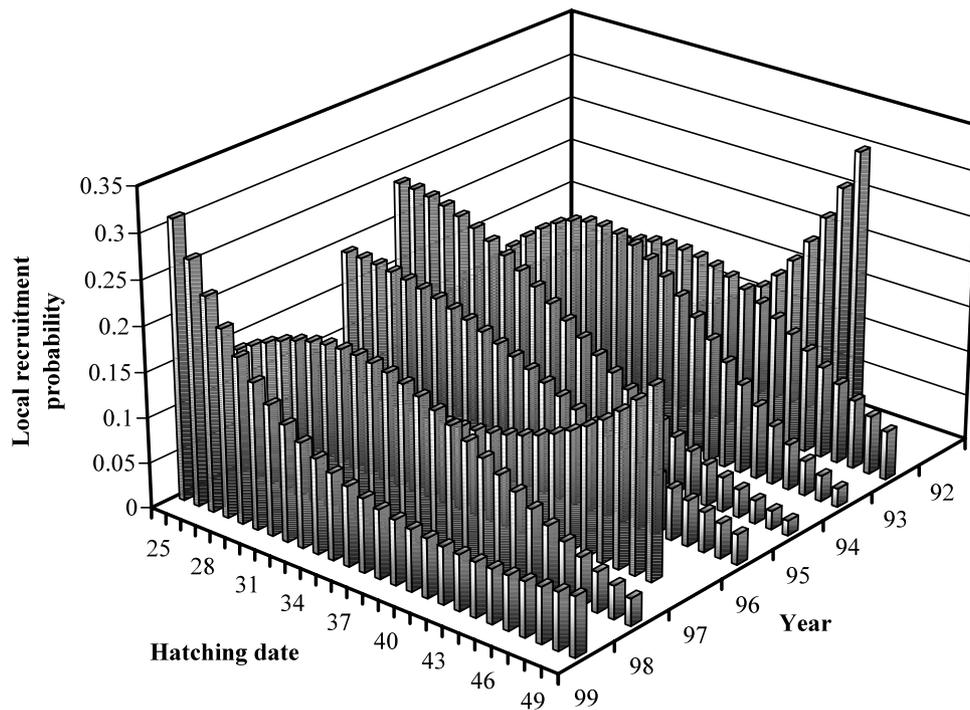


Fig. 2. Local recruitment probability ( $\phi$ ) of great tits in relation to hatching date (hd) and year. Fitted regressions were: 1992:  $\text{logit } \phi = -2.0 - 2.63 \text{ hd} + 1.24 \text{ hd}^2$ ; 1993:  $\text{logit } \phi = -2.0 + 4.07 \text{ hd} - 2.03 \text{ hd}^2$ ; 1994:  $\text{logit } \phi = -2.0 + 4.38 \text{ hd} - 2.51 \text{ hd}^2$ ; 1995:  $\text{logit } \phi = -2.0 - 4.90 \text{ hd} + 3.08 \text{ hd}^2$ ; 1996:  $\text{logit } \phi = -2.0 + 6.34 \text{ hd} + 3.27 \text{ hd}^2$ ; 1997:  $\text{logit } \phi = -2.0 - 7.44 \text{ hd} - 4.14 \text{ hd}^2$ ; 1998:  $\text{logit } \phi = -2 + 1.86 \text{ hd} - 3.48 \text{ hd}^2$ ; 1999:  $\text{logit } \phi = -2 - 3.07 \text{ hd} + 3.12 \text{ hd}^2$ . Mean standardised hatching date and hatching date squared ( $\pm$  s.d.) were respectively  $35.66 \pm 8.18$  and  $1339.08 \pm 665.98$ . Dates are presented as "april dates" (1 = 1 April, 31 = 1 May, etc.). Curves are shown over the observed range of hatching dates for each year.

fledglings surviving better was found in 1997, while in 1992 there was a seasonal increase in survival probabilities.

### Interaction between hatching date and fledgling mass

To elucidate the relative importance of being early and/or heavy, we fitted a model with both covariates (mass and hatching date) and their interaction. We then compared this (full) model with reduced nested models, where one of the covariates was not included. These comparisons will test for the relative importance of the covariate not included in the reduced model. We started from a model with local recruitment probability as a function of the covariates mass, hatching date and hatching date squared, and the interaction between hatching date and mass. We considered a model with different effect of hatching date each year, i.e. time effects in hatching date and in hatching date squared (Table 2, Model 10). The interaction term between hatching date and fledgling mass was not significant (Table 2, Model 10 vs Model 9).

To analyse the relative effect of mass at fledging on the probability of local recruitment once the effect of hatching date had been considered, we compared Model 10 with Model 7 (Table 2). Model 10 differed from Model 7 in that local recruitment probability was not a function of the covariate mass. The change in deviance was significant (LRT = 3.85, DF = 1,  $p = 0.049$ ), suggesting that a model without mass did not fit the data as well as a model including the effects of hatching date, hatching date squared and mass.

We proceeded in a similar way to test for the relative significance of the covariates hatching date and hatching date squared. Model 2 (Table 2), which did not consider the effect of hatching date, did not fit the data as well as Model 10 (Table 2), which included it (LRT = 42.22, DF = 16,  $p < 0.001$ ).

The final model selected (Table 2, Model 10) suggested that (1) local recruitment was constant throughout the study, (2) there was a significant effect of hatching date on the probability of local recruitment, but this effect was different each year, (3) the probability of local recruitment increased with mass at fledging, and (4) the effects of hatching date and fledgling mass on local recruitment were independent.

## Discussion

This is, to our knowledge the first study estimating the effects of hatching date and fledgling mass on recruitment probability using capture-recapture models. These models are an improvement over the so far used logistic regressions to detect the effect of independent variables on local return rates.

Results presented here showed that there was a significant effect of both hatching date and fledgling mass on the probability of local recruitment. A main finding was that, contrary to what is commonly thought, early fledgling is not necessarily the best option, since late-fledged offspring had better survival prospects some years (Fig. 2). Apart from this effect of hatching date, the probability of local recruitment increased with fledgling mass each of the years studied. These relationships are discussed below.

### Possible influence of natal dispersal on the interpretation of the results

A common problem in virtually all studies estimating recruitment is that some fledglings could emigrate and establish outside the study plot. Recent estimations suggest that most surviving fledglings settle far from their natal site, and often outside the study area for most studies (Lambrechts et al. 1999, 2000). Moreover, this is more frequent in relatively small plots placed within a continuous habitat (Matthysen et al. 2001), as is the case in our study area. Therefore, the “local recruitment” estimate presented here (which excluded offspring dispersal outside the nestbox area) is certainly an underestimate of the real recruitment rate. However, the relevant point to the present study is whether or not there was differential dispersal of early vs late, or heavy vs light offspring. Some studies on natal dispersal of great tits did not find differences in dispersal between early and late, or between heavy and light fledglings of first broods (Gustafsson 1987, Smith et al. 1989, Lindén et al. 1992, Verhulst et al. 1997, Verboven and Visser 1998). Our recruitment estimate included only first-clutch fledglings, so differential dispersal seems unlikely to bias our results on the relative effect of the factors examined over post-fledgling survival.

### Effect of fledgling mass on local recruitment

That heavier fledglings survive better than lighter ones has been known for many years, and the reasons for this widely discussed (see Perrins and McCleery 2001 for a recent review). However, the exact relationship between survival and fledgling mass varies both between species and between populations (reviewed in Magrath (1991), see also Perrins and McCleery (2001)

for references to great tit studies). Adriaensen et al. (1998) revised the relationship between fledgling mass and survival for the blue tit *P. caeruleus* and concluded that in about half of the studies the relationship was non-linear. Our final model suggested that local recruitment probabilities increased with fledgling mass. This effect remained after considering the effect of hatching date, since both fledgling mass and hatching date had a significant effect to explain post-fledgling local survival, and there was no interaction between them. We are aware that, although in the analysis presented the quadratic effect of mass was not significant, a model considering a non-linear effect of mass on recruitment got a similar AICc value than the model selected (Table 2), suggesting that both models fitted our data. Thus, we cannot completely exclude the possibility of a quadratic relationship between fledgling mass and local recruitment, and more data on very heavy offspring could change the shape of the relationship.

Blakey and Perrins (1999) examined the relationships between local return rates and fledgling mass in several great tit studies. They suggested that years can be grouped into “poor years”, where being heavy is important and survival is positively related to fledgling mass, and “good years”, where fledgling mass is relatively unimportant. Our analyses included 8 years, and being heavy seemed to be important in each of them. This suggests poor conditions for offspring survival after leaving the nest in this habitat, so that heaviest fledglings are always favoured. The long-term effect of this directional selection would merit further investigation.

### Effect of hatching date on local recruitment

The decline of breeding performance of many bird species as the season progresses is one of the best-established patterns in avian reproduction (Daan et al. 1989). Late-fledged chicks usually have reduced recruitment probabilities (Verboven and Visser 1998, and references therein), and even lower chances of producing fledglings in their first breeding season (Visser and Verboven 1999).

Results presented here show two important points. First, the relationship between hatching date and the probability of recruitment was non-linear, and second, the shape of this relationship differed between years. Lepage et al. (2000) found between-year differences in the slope of the seasonal decline of post-fledgling survival in snow geese *Anser caerulescens atlanticus*, but the trend was always negative. Similar results (i.e. negative slopes) have been obtained in great tit populations using local return rates (Perrins and McCleery 1989, Verboven and Visser 1998). However, Van Noordwijk et al. (1981), also using return rates, suggested that there was no consistent advantage in breeding earlier.

Most of these analyses suffered the possible bias of not considering recapture probabilities. Therefore, to our knowledge, this is the first study showing between-year variability in the trend of the relationship between local recruitment probability and hatching date.

Since most studies emphasised the advantages of early breeding, and laying dates show moderate to high heritability (Van Noordwijk et al. 1981), some hypotheses have been put forward to explain why this directional selection does not cause the birds to evolve earlier breeding. These included the costs of egg formation (Perrins 1996), the absence of correlation between breeding date and fitness (Price et al. 1988), and the effect of (usually late-breeding) immigrants (Norris 1993). All these hypotheses assume that breeding earlier would increase fitness. Our results strongly support those of Van Noordwijk et al. (1981; see also Perrins 1965), namely that in different years, either normalising, disruptive, or directional selection occurred. Therefore, a relatively long series of years would be necessary to calculate net selection pressures towards early or late breeding, and short studies may fail to catch most of the variability. At present, it is difficult to say whether the patterns found in our population actually differ from that of others, or the differences are due to the different methodology of analysis. It also remains to be studied whether early breeding pairs always recruit more offspring, in spite of the lower survival probabilities of early fledged ones some years. This could be achieved if early breeders produce more fledglings during the season (e.g. through higher fledgling production per clutch, or laying more clutches per year), so that they compensate the lower survival some years.

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