Early morning fledging improves recruitment in great tits Parus major
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A potential key event linking the nestling phase to first-year survival is fledging (nest leaving) because this process is characterized by a major change of environments and therefore a sudden shift in selective forces. Here we assessed whether different facets of fledging predicted subsequent survival (measured as local recruitment) in Great Tits Parus major. Nestlings had a higher recruitment probability when they fledged early in the morning and when they were heavy. The existence of selection for fledging early in the day has been suggested before, but here we provide the first empirical evidence in support of that prediction.

**Keywords:** avian life history, body mass, nest leaving, survival, time of day.

In small passerines, variation in first-year survival explains a substantial part of variation in lifetime reproductive success (Clutton-Brock 1988). Numerous studies have shown that first-year survival is affected by conditions in the nestling phase, for instance body mass in the nest (e.g. Tinbergen & Boerlijst 1990, Naef-Daenzer et al. 2001). The mechanisms behind these effects are, however, poorly understood (Harrison et al. 2011).

The process of fledging (nest leaving) could be a key event linking nestling traits and first-year survival. Studies on fledging have shown that, within broods, fledging order correlates negatively with wing length (Nilsson 1990, Michaud & Leonard 2000, Johnson et al. 2004, Radersma et al. 2011). Between broods, fledging age correlates negatively with mean wing length of the brood (Nilsson & Svensson 1993, Michaud & Leonard 2000, Kern et al. 2001, Radersma et al. 2011). Those studies that reported correlations between fledging order and body mass found these correlations to be significant, but weaker than the correlations with wing length (Nilsson 1990, Michaud & Leonard 2000, R. Radersma, unpublished data). Few studies have linked the moment of fledging to survival. Freed (1988) found that House Wren *Troglodytes aedon* fledglings that were experimentally forced to fledge approximately 3 days prematurely did not have reduced survival in the first 3 weeks after fledging, but that short-winged individuals had lower survival than fledglings with longer wings. Bowers et al. (2013) demonstrated in a cross-fostering experiment with House Wrens that the age of the youngest siblings determined fledging of the entire brood. These studies suggest that well-developed offspring might postpone fledging to allow their siblings to catch up in development, which would be adaptive for the well-developed nestlings if this increased their inclusive fitness.

Here we focus on the moment of fledging. As young birds move from inside the nest to the outside world, they experience a dramatic change of environments and selective forces. We investigated, in Great Tits *Parus major*, the relative importance of fledging-related traits in explaining variation in first-year survival. We used an information-theoretical approach to select models (Burnham & Anderson 2002) with both individual and brood traits. We used model averaging to determine the relative contributions of those traits. Our traits of interest were:

- **Nestling body mass just prior to fledging and its square.** We predicted a positive correlation between body mass and first-year survival that levels off or drops at the highest body masses (e.g. Tinbergen & Boerlijst 1990, Naef-Daenzer et al. 2001).
- **Date of breeding.** We predicted a negative correlation between date and first-year survival (e.g. Verboven & Visser 1998, Naef-Daenzer et al. 2001).
- **Residual of wing length over fledging age as an estimate of the developmental state at fledging.** When survival probability outside the nest depends positively on developmental state while the survival probability in the nest is fairly independent of developmental state (as assumed by Roff et al. 2005), we predicted a positive correlation between first-year survival and residual wing length.
- **Time difference between the first and the last-fledged young.** Fledging asynchrony is often smaller than hatching asynchrony (Freed 1988, Schlicht et al. 2012, Bowers et al. 2013). This suggests that nestlings fledge with their siblings rather than at a
specific age or developmental state. This might be part of an adaptive strategy to improve survival. We therefore predicted a negative correlation between time difference and first-year survival of the whole brood.

- **Time of day of fledging.** Many studies have found that most young fledge in the morning (Lemel 1989, Nilsson 1990, Johnson et al. 2004, Schlicht et al. 2012). We predicted that there is selection for leaving early and therefore a negative correlation between first-year survival and time of day of fledging.

- **Fledging order.** Because best developed nestlings tend to fledge first (Nilsson 1990, Michaud & Leonard 2000, Johnson et al. 2004, Radersma et al. 2011), we predicted a negative correlation with first-year survival.

**METHODS**

**Data collection**

We used data from 179 Great Tits fledged from 26 broods in the Lauwersmeer population in the Netherlands (53°20′N, 06°12′E; 600 nestboxes) in 2007. We collected data on hatching date (as a measure of breeding date), body mass and wing length as described in Radersma et al. (2011). Simultaneously with this study we conducted an experiment on the effects of brood sex ratio on the process of fledging. For this purpose we manipulated the brood sex ratios at day 6 by cross-fostering (Radersma et al. 2011). To control for any effects of this experiment we added brood sex ratio as a covariate to the models and assessed whether cross-fostering affected individual traits.

When the oldest nestling of the brood was 14 days old, we fitted each nestling with three colour rings, which together with the uniquely numbered metal ring formed unique colour combinations. We also implanted passive integrated transponders (Trovan ID100) subcutaneously over the shoulder blades. In a previous study of Great Tits, no adverse effects of the implantation of transponders was found on year survival (Nicolaus 2008). We also attached a transponder reading device (Trovan 665) with antenna to the nestbox entrance, to register the date and time of fledging of each individual, and thus the fledging order. From day 19 onwards, we checked nestboxes every other day to monitor whether the young had fledged. Of the 26 nests, nine fledged before and 17 after the first check. We have no evidence that our visits promoted fledging: of the 17 nests that fledged after the first check, only four began fledging on the same day (one within 10 min and three more than 6 h later). We recorded an individual’s last registration by the reading device as its moment of fledging.

In the next year, 2008, we caught all breeding birds in the Lauwersmeer population at the nest with a spring trap when their nestlings were between 7 and 10 days of age, and identified local recruits by their metal rings. If we were unsuccessful in catching parents after two attempts, we took females from the nest at night and identified males by reading their colour rings with binoculars during the day.

**Data analysis**

To compare among broods of different sizes, we linearly transformed the fledging order to values varying from zero (first fledged) to one (last fledged). To calculate the time difference between first and last fledged young across days, we subtracted the time between sunset and sunrise if included in the interval. Brood sex ratio was calculated as the number of males divided by the total number of nestlings. We inserted all variables except fledging order and brood sex ratio in the models as z-scores (transformed when necessary, centred and divided by the standard deviation). We used a logistic regression model to model local recruitment as a function of all traits of interest. Brood identity was fitted as a random effect on the intercept to account for parental quality and territory differences. We generated all possible models with subsets of the traits and used model averaging to calculate the relative contributions of the various traits (all models are presented in Supporting Information Table S1). We calculated model-averaged estimates by weighting the effect sizes of the traits by the relative importance of the models the traits occur in, the so-called shrunken estimates (Burnham & Anderson 2002). We constructed the statistical models in R (R Core Team 2013) with the package MuMln (Barton 2013). We calculated Wilson confidence intervals for Figs 1 and 2 with the package Hmisc (Harrell 2013).

If well-developed individuals postpone fledging to increase their inclusive fitness (Freed 1988), we would expect survival to be affected by wing length variation within rather than between broods. To test this we repeated the analyses, but replaced residual wing length by the brood averages as well as the individual deviation from the brood mean (van de Pol & Wright 2009). We also replaced the time of day of fledging by the brood averages as well as the individual deviation from the brood mean to test whether a potential effect of time of day of fledging was a brood rather than an individual effect. As previously shown, individuals of a brood tend to fledge relatively close in time (Radersma et al. 2011).

**RESULTS**

Of the 179 fledglings, 15 (8.4%) recruited locally in the following year as breeding birds, a recruitment rate not significantly different from the remainder of the 2007
Figure 1. Local recruitment (dots with error bars and left axis) decreased with time of day of fledging in the Lauwersmeer Great Tit population. Raw data were binned per 20 data points (the last group contained 19 data points). Error bars represent the 95% Wilson confidence intervals. Function was back-transformed from z-scores and based on the model-averaged estimates. The bar plot represents the frequency diagram of time of day of fledging (grey bars, right axes). Data on 179 fledglings of 26 broods.

Figure 2. Local recruitment (dots with error bars and left axis) increased with fledging mass in the Lauwersmeer Great Tit population. Raw data were binned per 20 data points (the last group contained 19 data points). Error bars represent the 95% Wilson confidence intervals. Function was back-transformed from z-scores and based on the model-averaged estimates. The bar plot represents the frequency diagram of nestling mass (grey bars, right axes). Data on 179 fledglings of 26 broods.

cohort \( n = 1455, \, 9.0\%; \, \chi^2 = 0.017, \, P = 0.897 \). No birds were found breeding in 2009 or 2010 that were not breeding in 2008. We found no significant effects of cross-fostering on the individual traits (body mass, residual wing length, time of day of fledging; \( t \leq 1.096, \, P \geq 0.276 \)), and no effects of brood sex ratio on most traits of interest (\( -0.17 \leq \rho_S \leq 0.11, \, P \geq 0.346 \)). Only time of day of fledging was correlated with brood sex ratio \( (\rho_S = 0.41, \, P < 0.001) \), but we do not have any indication that brood sex ratio had a substantial effect on the results because its model-averaged estimate was non-significant and relatively small (\( > 4 \) times smaller effect than time of day of fledging; Table 1).

Of the traits considered, only time of day of fledging had a significant effect in the full model, with a higher probability of local recruitment for birds fledging earlier in the day \( (P = 0.033, \, \text{Table 1, Fig. 1}) \). Most young fledged during the morning \( (71\%, \, n = 179; \, \text{Fig. 1}) \). Nestling body mass was close to significant \( (P = 0.083, \, \text{Table 1, Fig. 2}) \), but its effect size was much smaller than the effect size for time of day of fledging \( (0.665 \text{ vs. } 1.028, \, \text{Table 1}) \). The square term for nestling body mass was not significant \( (P = 0.294, \, \text{Table 1, Fig. 2}) \). All other traits were non-significant in the full model and had a minor effect in model-averaging \( (> 9.5 \) times smaller effect than time of day of fledging; Table 1). Time of day of fledging and body mass were not correlated \( (r = 0.0064, \, P = 0.931) \), suggesting that they have additive effects on local recruitment.

To investigate further any effect of the collinearity between time of day of fledging and brood sex ratio, we repeated the analysis but replaced time of day of fledging and brood sex ratio by the residuals of the linear model between both variables (with time of day of fledging as dependant variable). The effect of time of day of fledging remained significant \( (z = 2.168, \, P = 0.030) \), which suggests that this effect is not the result of the collinearity with brood sex ratio.

When replacing time of day of fledging by a mean for the brood and an individual deviation from this brood mean, we found that the individual deviation significantly explained variation in recruitment probability \( (z = 2.106, \, P = 0.035, \, \text{shrunken estimate } = -1.033) \), whereas the brood effect was non-significant \( (z = 0.125, \, P = 0.901, \, \text{shrunken estimate } = -0.214) \). Thus the effect of time of day of fledging was an individual rather than a brood effect. Replacing residual wing length with the brood averages \( (z = 0.338, \, P = 0.735, \, \text{shrunken estimate } = -0.0307) \) and individual deviations from the brood average \( (z = 0.253, \, P = 0.800, \, \text{shrunken estimate } = -0.0232) \) did not improve the effect of residual
Table 1. Model-averaged estimates of terms explaining local recruitment of fledglings in the Lauwersmeer Great Tit population.

<table>
<thead>
<tr>
<th>Variables</th>
<th>Hypothesized effect</th>
<th>Estimated coefficients</th>
<th>se</th>
<th>z</th>
<th>P</th>
<th>Relative importance</th>
<th>Shrunken coefficients</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td></td>
<td>-3.093</td>
<td>0.803</td>
<td>3.849</td>
<td>&lt;0.001</td>
<td>1</td>
<td>-3.093</td>
</tr>
<tr>
<td>Time of day</td>
<td>Negative</td>
<td>-1.136</td>
<td>0.532</td>
<td>2.138</td>
<td>0.033</td>
<td>0.90</td>
<td>-1.028</td>
</tr>
<tr>
<td>Body mass</td>
<td>Positive</td>
<td>0.856</td>
<td>0.494</td>
<td>1.731</td>
<td>0.083</td>
<td>0.78</td>
<td>0.665</td>
</tr>
<tr>
<td>Body mass²</td>
<td>Negative</td>
<td>-0.443</td>
<td>0.425</td>
<td>1.043</td>
<td>0.297</td>
<td>0.33</td>
<td>-0.145</td>
</tr>
<tr>
<td>Residual wing length</td>
<td>Positive</td>
<td>-0.318</td>
<td>0.499</td>
<td>0.637</td>
<td>0.524</td>
<td>0.32</td>
<td>-0.103</td>
</tr>
<tr>
<td>Fledging order</td>
<td>Negative</td>
<td>0.163</td>
<td>0.341</td>
<td>0.478</td>
<td>0.633</td>
<td>0.28</td>
<td>0.046</td>
</tr>
<tr>
<td>Date of birth</td>
<td>Negative</td>
<td>0.050</td>
<td>0.532</td>
<td>0.095</td>
<td>0.925</td>
<td>0.26</td>
<td>0.013</td>
</tr>
<tr>
<td>Δ Fledging time</td>
<td>Negative</td>
<td>-0.0038</td>
<td>0.498</td>
<td>0.008</td>
<td>0.994</td>
<td>0.26</td>
<td>0.00096</td>
</tr>
<tr>
<td>Brood sex ratio</td>
<td>Neutral</td>
<td>-0.868</td>
<td>2.265</td>
<td>0.383</td>
<td>0.702</td>
<td>0.28</td>
<td>-0.240</td>
</tr>
</tbody>
</table>

Time of day and fledging time difference were log-transformed to normalize values. Fledging order was scaled between 0 and 1 to correct for brood size differences. All variables except fledging order were centralized (minus the average) and standardized (divided by the standard deviation). For date of birth the average and standard deviation of the whole 2007 breeding population were used. $z$-values and $P$-values are presented for the non-shrunken coefficients.

Wing length on local recruitment. Therefore, we did not find any direct fitness benefits for fledging in response to the development of siblings rather than individual development.

**DISCUSSION**

Local recruitment was explained mainly by time of day of fledging, with earlier fledging associated with higher local recruitment probability. This pattern was mainly explained by individual variation rather than variation between broods. Most young fledged during the morning, which could itself be a result of selection for early fledging and is consistent with previous studies of hole-breeding passerines (Lemel 1989, Nilsson 1990, Johnson et al. 2004).

A potentially important problem in using local recruitment as a proxy for survival is that dispersal may also be associated with the traits of interest (Verbouwen & Visser 1998, Tinbergen 2005). For example, variation in local recruitment in our study could result from a higher probability that late-fledging individuals leave the study area, perhaps as a result of competition. For Great Tits, other studies have found no correlation between natal dispersal distance and nestling body mass (Dingemanse et al. 2003), and we are aware of no studies that have investigated relationships between natal dispersal distance and time of day of fledging. Differentiating between survival and dispersal remains of great importance to understand the true fitness consequences of time of day of fledging, but we are not able to discriminate them in this study.

One explanation for survival being affected by time of day of fledging could be that the time between fledging and sunset is of crucial importance to survival. This could be due to a better chance for the early fledglings to find a good and safe roost for the night or, as suggested by Perrins (1979), to familiarize themselves with their surroundings before dark. A lower recruitment probability of late-fledged young would then be the result of higher mortality during the first night outside the nestbox. Higher mortality in the first few days after fledging has been demonstrated in Great Tits (Naef-Daenzer et al. 2001) and other passerines (e.g. Sullivan 1989, Naef-Daenzer et al. 2001).

Neither fledging order nor residual wing length contributed substantially to local recruitment, so there was either no or only weak selection for wing length at fledging. As shown by Freed (1988), inclusive fitness optimization might prevent the best developed individuals from initiating fledging before their siblings are sufficiently developed. This would reduce any within-brood selection for wing length and fledging order, but between-brood selection for wing length should remain. The fact that the estimates did not improve when replacing individual residual wing length by the brood averages and individual deviations from the brood averages suggests that all broods fledged with (close to) optimal wing lengths.

Within the studied broods, time of day of fledging had a greater effect on survival than did body mass. Not only did we find a correlation between survival and time of day of fledging, with a much smaller sample size than necessary to demonstrate a significant correlation between survival and body mass, but the effect size of time of day of fledging was larger, too. For the total range of measured values of time of day of fledging, the model predicted local recruitment probabilities between 0.00 and 0.22, whereas for the body mass models of Tinbergen and Boerlijst (1990) and Monró et al. (2002) the predicted recruitment probability ranges were 0.03–0.15, 0.06–0.17, 0.03–0.10 (Tinbergen & Boerlijst 1990) and 0.05–0.23 (Monró et al. 2002).
In conclusion, the order of fledging did not explain variation in local recruitment, although the best developed individuals of a brood fledge first. The pattern we revealed is that young that fledged early in the morning were more likely to recruit than young that fledged later during the day. If this is the case, seemingly small individual variation in behaviour may have large consequences for survival, and is thus of great importance to understanding fitness variation.

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REFERENCES


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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. All models explaining local recruitment in the Lauwersmeer Great Tit population.