Do brood sex ratio, nestling development and sex affect fledging timing and order? An experimental study on great tits

Reinder Radersma*, Joost M. Tinbergen, Jan Komdeur
Animal Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen

The process of nest leaving (fledging) in hole-breeding passerines is largely unexplored, although it is potentially an important facet of reproduction. We used the great tit, Parus major, to investigate whether fledging timing and order were affected by nestling development and sex, as well as sex ratio in the brood the nestlings were raised in. Because of the difference in size and competitiveness between male and female nestlings, we expected to find an effect of sex and brood sex ratio (BSR) on the process of fledging. To explore its effect on fledging experimentally, we manipulated BSR by swapping 6-day-old nestlings in all 14-day-old nestlings to determine timing and order of fledging.

The brood age at fledging was best explained by average wing length of the brood (negative), average body mass of the brood (positive) and hatching date (negative). In contrast to our hypothesis, BSR did not affect fledging time. Also, the asynchrony of fledging within broods did not depend on BSR. Within broods, fledging order was not affected by sex or by the interaction between sex and BSR. Nestlings with long wings on day 14 fledged earlier than nestmates with shorter wings. Although females were lighter at day 14, they had similar length wings as their male nestmates. Nestlings should keep up with their nestmates during development, because developmental status relative to nestmates, rather than sex-specific competition, influenced the process of fledging.

Although nest leaving (fledging) is the most drastic transition between habitats in the life of a passerine altricial bird, the process of fledging has been studied much less extensively than other facets of reproduction. This discrepancy is partly caused by the difficulty of predicting the moment of fledging and therefore the ability to observe the process (Johnson et al. 2004). The few studies on the process of fledging generally report that fledging of a brood starts when one of the nestlings reaches a certain threshold wing development (marsh tits, Poecile palustris, and pied flycatchers, Ficedula hypoleuca: Nilsson & Svensson 1993; tree swallows, Tachycineta bicolor: Michaud & Leonard 2000; pied flycatchers: Kern et al. 2001). Parental manipulation, in which parents try to force their offspring to leave the nest by depriving them of food (Johnson et al. 2004) or by displaying food in front of the nest (Michaud & Leonard 2000), is thought to play a minor role in the process of fledging (Nilsson 1990; Johnson et al. 2004).

In the only other study on the fledging process in great tits, Parus major, the order of fledging depended on nesting body mass relative to that of the nestmates. Nestlings with an average body mass left the nest first, shortly thereafter followed by the heaviest nestlings and eventually followed by the lightest ones (Lemel 1989). The author hypothesized that (average-weight) subordinate nestlings try to evade competition with the (heaviest) dominant siblings by fledging first. Moreover, the lightest nestlings followed despite not being ready to fledge, to avoid starvation, because parental visits to the nest decreased drastically once most nestlings fledged (Lemel 1989). In contrast, studies in other passerines have found that fledging order correlates with wing development rather than body mass. Nestlings with the best developed wings fledged first (marsh tits: Nilsson 1990; tree swallows: Michaud & Leonard 2000; house wrens, Troglydaes aedon: Johnson et al. 2004).

So, generally, fast-developing broods and individuals stay in the nest for less time than slower-developing broods and individuals. We therefore hypothesize that faster-developing broods fledge earlier than slow-developing broods and faster-developing individuals leave the nest before slow-developing individuals. Two important aspects that are not covered by previous studies on timing and order of fledging are the influence of nestling sex and brood sex ratio (BSR). In great tits, male fledglings are 4% heavier than female fledglings (Nicolaus et al. 2009). There is no sexual size dimorphism at hatching, but sexual size dimorphism gradually
increases during the nestling phase. Because male nestlings are fed at the same rate as female nestlings (Michler et al. 2010), males either digest food more efficiently or allocate more resources to growth, than females do. We therefore expect males to reach the threshold state of development, and to fledge, earlier than females. We also expect male-biased broods to fledge earlier than female-biased broods. Fledging asynchrony is expected to be larger in mixed broods and, within broods, males should leave the nest before females.

When sex-specific size dimorphism leads to differences in the competitiveness of both sexes, expectations slightly change. Male nestlings might have a competitive advantage over female nestlings for access to food, because of the sexual size dimorphism (Oddie 2000). This competitive advantage is especially present under food-limited conditions, as experimentally shown by Oddie (2000). Sex-specific differences in competitive ability are hypothesised to result in more severe and competitive rearing conditions in broods with a male-biased BSR than in broods with a female-biased BSR (Uller 2006). Since fledging can be seen as a way to evade competition (Lemel 1989), we might expect fledging to be initiated earlier in the more competitive male-biased broods than in the less competitive female-biased broods. As a consequence of the relatively early initiation of fledging in male-biased broods, we predict more nestlings to be physically unprepared to fledge in male-biased broods. These nestlings should delay their own fledging, and therefore we expect greater fledging asynchrony in male-biased broods than in female-biased broods.

With this experimental study on the great tit, we sought to investigate whether nestling development, nesting sex and BSR determined timing and order of fledging. In addition, we investigated which other characteristics of broods (brood size, hatching date, sex of first fledgling and the averages of all individual traits) and individuals (wing length, tarsus length and body mass) were related to timing and order fledging.

METHODS

Data Collection

We focused on 25 first broods of the great tit from the Lauwersmeer (53°20’N, 06°12’E) population in the Netherlands in 2007. First broods are defined as broods in which the first egg was laid no later than 30 days after the laying of the first egg of the earliest clutch of the population in 2007 (6 April) and which were not replacement broods after a failed breeding attempt. Potential replacement broods were characterized by being slightly later than most broods, in combination with a very short nest-building phase, and were excluded from the analysis. Some of the potential replacement broods were definitely identified as replacement broods, because the colour-ringed female had been seen earlier with a failed brood.

The research area consists of 600 nestboxes spread over 12 areas with 50 nestboxes each: 47.8% of these were occupied by great tits with a failed brood.

In 2007, we visited the nest daily until day 6 to mark and to take a blood sample from the late-hatched nestlings. On day 5 all nestlings were counted and missing individuals were identified and noted. On day 6 all nestlings were weighed with a spring balance to the nearest 0.1 g, later referred to as body mass at day 6 (BM_6), and banded for individual identification. Subsequently, nestlings from nests of the same age were swapped (brought from one nest to another) to get an experimental range of BSRs, and eggs that did not hatch were removed. The nestlings were kept warm with heat pads and transported by car. The whole swapping process took less than 30 min for an individual nestling. At least one nestling per nest was swapped to control for swapping effects. After swapping, all broods had at least one individual of each sex. The BSRs were either female biased (approximately 25% males), male biased (approximately 75% males) or balanced (approximately 50% males). The female- and male-biased BSRs corresponded to approximately 1.3 times the standard deviation from a balanced BSR. This study took place in the context of a larger project, in which not only BSRs but also brood sizes were changed. Because we could not select enough broods with an unchanged brood size, we included broods that were increased or decreased at most by only one nestling. This study included 11 nests with a brood size reduction of one, 10 nests with a brood size increase of one and four nests with an unchanged brood size. The brood size change did not influence the results (see Results).

When the oldest nestling of a nest was 14 days old, all nestlings were weighed to the nearest 0.1 g (BM_14), the tarsus (TL_14) was measured to the nearest 0.1 mm, and the length of the third primary feather was measured to the nearest 0.5 mm by using a stop ruler (WL_14). A passive integrated transponder (Trovan ID100, www.trovan.com; 2.1 × 11.5 mm, 0.1 g, 0.5–1% of BM_14) was implanted subcutaneously above the shoulder blade according to the method described in Nicolaus et al. (2008). Also at day 14 we placed at the nestbox entrance an antenna attached to a reading device (Trovan 665), which registered the date and time of fledging of each individual in the nest and, therefore, the fledging order as well. From day 19 onwards, nestboxes were checked every second day to see whether the young had fledged. After the completion of fledging, the antenna and reading device were removed, and the nestbox was cleared to check for dead nestlings in the nest material. The data from the reading device were downloaded with Trovan LID650/665 software version 603.

Data Analyses

Below, individual characteristics, which were averaged within broods, are marked by the prefix ‘brood’. The standard deviations from the means of individual characteristics within broods are marked by the prefix ‘brood SD’. The age at fledging was calculated as the number of days between the day the first egg in a nest hatched and the day the focal nestling fledged. This leads to an overestimation of the age of late-hatched nestlings. However, within-brood differences in hatching age occur naturally. This will probably result in differences in size and development, which might have implications for the fledging order, but since we were interested in finding out how variation in different growth factors (as well as sex and BSR) affects variation in fledging age and order, we see the variation in the moment of hatching as a source of variation in growth. We therefore took into account the variation in hatching moment in the different growth factors. For sex-specific hatching order, the overestimation of the age of late-hatched nestlings might influence fledging order or age, but late-hatched nestlings (individuals born at least 2 days later than the first-hatched nestling in a brood) had the same probability of being either male or female as the other nestlings in this study population in 4 consecutive years (2005: χ² = 0.64, N = 2283, P = 0.42; 2006: 0.42; 2007: 0.28; 2008: 0.15).
formation. The divided by the SD) to compare the effect size of the variables in the 2008: \( \chi^2 = 1.02, N = 2373, P = 0.31; 2008: \chi^2 = 1.96, N = 1800, P = 0.33 \). Brood age at fledging was the mean fledging age of all young within a brood. The individual age at fledging is always given in whole days, but the brood age at fledging is not because this is expressed as mean age (in days).

We calculated a fledging asynchrony parameter, which is a measure for the spread in the timing of fledging observed in a brood. This parameter allowed us to compare the asynchrony between broods. To calculate fledging asynchrony, we took for all fledglings the time (h) between the fledging of the first fledged nestmate and the focal fledging and calculated the standard deviation of these differences per brood. We also looked at fledging asynchrony by comparing the logarithm of the time between fledging of two subsequent individuals with their difference in WL14. Since nestlings do not fledge at night, we subtracted the time between sunset and sunrise from the time difference when there was a night between fledging of the two nestlings. This measure was transformed by adding 1 and taking the natural logarithm to make it normally distributed. The fledging asynchrony is defined as the within-brood standard deviation of the above-described values.

To compare broods of different sizes, we linearly transformed the fledging ranks to values varying from 0 to 1, with 0 for the first arcm (the last fledged individual). These linearly transformed values are referred to as fledging order, while the ranks are referred to as fledging ranks. To compare nestlings within broods, we calculated relative WL14 (WL14 minus the mean brood WL14) and relative BM14 (BM14 minus the mean brood BM14).

We tested whether the first fledging leaving the nest might thereby avoid monopolization of the food by its nestmates sitting in the nest opening, as proposed by Lemel (1989). We calculated for each individual the proportion of time spent in the nestbox opening. A bird sitting continuously in the nest opening was read every 3 s by the reading device, and we used the number of these readings to estimate this proportion of time. We ranked these proportions within broods (highest proportion first) and referred to them as monopolization ranks.

Two families of general linear models were used for the analyses. In the first model family we tried to explain the between-brood variation in brood age of fledging by means of brood characteristics (see Results for the full list). In the second model family we tried to explain the fledging order within broods. In this case we used both individual and brood characteristics (see Results for the full list). In model family 2, we introduced a factor ‘swap’, which equalled 1 for swapped nestlings and 0 for other nestlings. Brood age at fledging showed a normal distribution, but the distribution of fledging order was uniform. Fledging order, however, was not skewed (198 = 0.00, \( P = 0.500 \)) and the best model explaining fledging order did not show heteroscedasticity (1932 = 144.6, \( P = 0.213 \)). Since general linear models are rather insensitive to distributions deviating from normality (Gelman & Hill 2007), we constructed general linear models to explain fledging order. For both model families, all continuous variables were inserted in the model as z scores (normalized, centred and divided by the SD) to compare the effect size of the variables in the model. To normalize hatch date, we performed an inverse transformation. The z scores of the relative WL14 and the relative BM14 were calculated by subtracting the average z score within a brood from the individual z score.

The statistical full models of the two model families were constructed in R (R Development Core Team 2009) with the package arm (Gelman et al. 2009). Using a classical backwards elimination method, the best-fitting statistical models were constructed. We rejected variables with the highest \( P \) value one by one, until all variables had a \( P \) value smaller than 0.05. We report nonsignificant parameters retested after elimination in the final model.

**Ethical Note**

To investigate whether the swapping procedure had any adverse effects on the nestlings, we investigated whether swapping affected BM14 or survival until day 14. Swapped nestlings were not lighter at day 14 (12192 = 0.131, \( P = 0.254 \)) and did not survive less well until day 14 (12207 = 0.001, \( P = 0.975 \)) than nestlings that were not swapped to another brood. In 2004 we conducted a survey to investigate whether taking blood samples from 2-day-old nestlings had any adverse effects. We took blood samples from about 60% of the nestlings in the study population. Nestlings from which blood samples were taken were not lighter at day 14 (13206 = 0.66, \( P = 0.51 \)) and did not survive less well until day 14 (14844 = −0.021, \( P = 0.98 \)). In a previous study in the same population no adverse effects of the implantation of passive integrated transponders were found on fledging success, winter condition, survival or recruitment (Nicolaus et al. 2008).

The study was carried out with the approval of the Institutional Animal Care and Use Committee of the University of Groningen.

**RESULTS**

**Brood Characteristics**

The average brood age at fledging ±SD was 19.6 ± 13.9 days (N = 25). The difference in time of fledging between the first and the last young within a nest ranged from 7 min 13 sec to 263 min (about 4 h 28 h when we subtracted the time between sunset and sunrise) and showed a log normal distribution with an average ± SD of e1.91 ± 1.79 min (about 136 min). A small number of nestlings died between days 6 and 14 (5.7%, 11 of 194) and between day 14 and fledging (4.4%, 8 of 183). Mortality within a brood was not affected by BSR (1.233 = 0.784) or by brood size (1.233 = 0.696).

**Individual Characteristics**

WL14 and BM14 were positively associated (1.233 = 81.8, \( P = 0.001 \)). Males were heavier than females (BM14), but the sexes did not differ in wing length (144; Table 1). We did not find any differences between swapped and nonswapped individuals in the following nestling traits: BM (1.233 = 0.412, \( P = 0.522 \)), BM14 (1.233 = 1.61, \( P = 0.207 \)), WL14 (1.233 = 1.15, \( P = 0.286 \)), TL14 (1.233 = 0.317, \( P = 0.574 \)), relative BM14 (1.233 = 1.64, \( P = 0.202 \)), relative WL14 (1.233 = 0.052, \( P = 0.821 \) ) and monopolization rank (1.233 = 0.003, \( P = 0.960 \)).

The nest entrance monopolization ranks were positively correlated with fledging ranks (Fig. 1). The more a nestling sat in the nestbox opening, compared to its nestmates, the higher the chance that it fledged first.

**Brood Age at Fledging**

The variance in brood age at fledging was not explained by the variance in BSR (1.233 = 0.583, \( P = 0.453 \)). The best model explaining

| Table 1 | Average ± SD day 14 body mass (BM14), day 14 wing length (WL14) and fledging order (between 0 and 1, see Methods) of male and female nestlings in the Lauwersmeer great tit population and the differences between the sexes in these traits |
|---|---|---|---|---|---|
| | Males | Females | Sex-specific differences |
| | (N=85) | (N=90) | Difference | t | df | P |
| BM14 (g) | 16.07 ± 1.91 | 15.39 ± 1.41 | 0.68 | 1.136 | 200 | 0.266 |
| WL14 (mm) | 29.72 ± 3.57 | 29.61 ± 3.68 | −0.11 | −0.192 | 172.873 | 0.848 |
| Fledging order | 0.53 ± 0.35 | 0.47 ± 0.33 | 0.06 | 1.070 | 170.681 | 0.285 |
the brood age at fledging included brood WL14, hatching date and brood BM14 as explanatory variables (Table 2, Fig. 2). An increase in brood WL14 by 1 SD (2.7 mm) resulted in a decrease in brood age at fledging by 1.04 SD (=1.3 days). An increase in the average hatching date by 1 SD (=3.4 days) resulted in an increase in brood age at fledging by 0.36 SD (=0.45 days). A decrease in the average hatching date by 1 SD (=3.8 days) resulted in a decrease in brood age at fledging by 0.36 SD (=0.45 days). An increase in brood BM14 by 1 SD (=1.3 g, and controlled for WL14 and hatching date) resulted in an increase in brood age at fledging of 0.45 SD (=0.58 days).

**Fledging Asynchrony**

Fledging asynchrony was not affected by BSR ($F_{1,173} = 0.182$, $P = 0.674$), by brood SD WL14 ($F_{1,173} = 0.218$, $P = 0.645$) or by brood SD BM14 ($F_{1,173} = 0.320$, $P = 0.577$). We did find a close to significant association between the difference in WL14 between two subsequent fledging nestmates and the natural logarithm of the difference in their fledging times ($F_{1,148} = 3.82$, $P = 0.052$).

**Fledging Order**

The fledging order (within broods) was not affected by sex alone ($F_{1,173} = 1.15$, $P = 0.284$) or by the sex*BSR interaction ($F_{1,171} = 0.521$, $P = 0.471$). Both relative WL14 ($F_{1,173} = 49.5$, $P < 0.001$) and relative BM14 ($F_{1,173} = 27.8$, $P < 0.001$) were associated with fledging order. Whether an individual was swapped or not was almost significantly associated with fledging order ($F_{1,173} = 3.36$, $P = 0.068$). The best model explaining fledging order included only relative WL14 (Table 3, Fig. 3). An increase in relative WL14 by 1 SD (=2.67 mm) resulted in a decrease in fledging order by 0.214 (1.7 places forward in the fledging order for a brood of eight young).

**DISCUSSION**

In this study we did not find any support for BSR or nestling sex affecting fledging order or timing. The experimentally changed BSR did not affect brood age at fledging. Fledging asynchrony did not...

---

Table 2

<table>
<thead>
<tr>
<th>Variable</th>
<th>Estimate</th>
<th>SE</th>
<th>t</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age at fledging</td>
<td>Intercept</td>
<td>0</td>
<td>0.125</td>
<td>~0</td>
</tr>
<tr>
<td></td>
<td>Brood WL14</td>
<td>-1.037</td>
<td>0.175</td>
<td>-5.94</td>
</tr>
<tr>
<td></td>
<td>Hatching date</td>
<td>-0.355</td>
<td>0.139</td>
<td>-2.56</td>
</tr>
<tr>
<td></td>
<td>Brood BM14</td>
<td>0.449</td>
<td>0.178</td>
<td>2.52</td>
</tr>
</tbody>
</table>

Rejected terms

- **Sex** (first fledging)
- **Change in brood size**
- **BSR**
- **Brood TL14**
- **Brood BM6**
- **Brood size**
- **Treatment**
- **Female biased**
- **Male biased**
- **Sex** (first fledging)*BSR

All variables were normalized, centralized (minus the average) and standardized (divided by the SD), except for the factorial variables **sex** (first fledging) and treatment. All rejected variables were tested separately in the final model. WL14: day 14 wing length; BM6: day 6 body mass; BM14: day 14 body mass; TL14: day 14 tarsus length; BSR: brood sex ratio.

1. To normalize hatching date we performed an inverse transformation; therefore the negative effect of the z score corresponds to a positive effect of the real hatching date.
2. Where 1 is male and 0 is female.
3. Effect of more female-biased broods and male-biased broods compared to broods with a balanced BSR.
variables were normalized, centralized (minus the average) and standardized (divided by the SD), except for the factorial variables swap and sex. All rejected variables were tested separately in the final model. WL14: day 14 wing length; BM14: day 14 body mass; BSR: brood sex ratio.

1 Where 1 is swapped and 0 is nonswapped individual.

All variables were normalized, centralized (minus the average) and standardized (divided by the SD), except for the factorial variables swap and sex. All rejected variables were tested separately in the final model. WL14: day 14 wing length; BM14: day 14 body mass; BSR: brood sex ratio.

1 Where 1 is swapped and 0 is nonswapped individual.

Where 1 is male and 0 is female.
body mass and size, because body mass gain levels off prior to fledging. As such, the prime position of the dominant nesting is challenged more and more. To ensure its prime position, the largest nestling is forced to leave the nest, because parents tend to feed fledglings over nestlings (Nilsson & Svensson 1993).

Apart from the negative association between brood age at fledging and brood WL14, age at fledging was positively associated with hatching date. Various studies have shown that nestling growth rate decreases over the breeding season, as a consequence of changes in food abundance (e.g. Naef-Daenzer & Keller 1999). In our study, this decrease in growth rate cannot be the sole reason for the date effect, because we controlled for the brood BM14 and the brood WL14. There must be an additional reason why nestlings fledge at an older brood age later in the season. It could be that the lower food abundance later in the season (Van Balen 1973; Van Noordwijk et al. 1995) makes it more difficult for the parents to find food. A higher mobility of the fledglings will therefore be more beneficial, since this will increase the food intake rate. When mobility depends on wing development, we can expect that individuals fledging later in the season need better developed wings once outside the nest. Alternatively, fledglings need better wing development outside the nest later in the season because of predation. Individuals that fledge later in the season have a higher risk of being predated (Geer 1982; Götmark 2002). This increase is believed to relate to the fact that predators (e.g. sparrowhawks, Accipiter nisus) synchronize their reproduction to the fledging peak of their prey (e.g. great tits), leading to an increase in predator food consumption over the breeding season (Götmark 2002). At the same time frequency-dependent selection on wing development caused by predation might play a role. If fledglings improve their predator avoidance skills with age, the fraction of fledglings with poor skills will decrease over the breeding season, because later in the season a larger fraction of fledglings is experienced. Late-fledged individuals will therefore be more vulnerable to predation, because they are less experienced than the earlier fledging individuals, which makes them the easy prey (Geer 1982). Therefore it might be adaptive for late-born fledglings to stay longer in the nest and to develop their wings better to increase their ability to fly and avoid predation, assuming that predation in the nest stays constant or increases at a slower rate over the season.

The positive relation between fledging age and hatching date might indicate a decrease in sibling competition in the nest over the season. This might be caused by a decrease in brood size over the season (Kluijver 1951; Perrins 1965), although we would then expect brood size to contribute to the best model instead of hatching date. The increase in variation in development within a nest might reduce sibling competition over the season, since the prime feeding position of the best developed nestling will be less challenged.

In addition to hatching date, brood BM14 had a positive effect on age at fledging, when controlled for brood WL14. Broods that were relatively heavy for their wing development stayed in the nest longer than broods that were relatively light. A high wing loading (body mass per wing area) negatively influences flight performance (Pennycuick 1975). Therefore, broods that are relatively heavier for their wing size may need to stay longer in the nest to grow larger wings. Larger wings reduce the wing loading and ensure sufficient flight performance when fledging. This would be advantageous for escaping predation, improving mobility and increasing foraging ability. We do not expect a reverse causality, in which broods that stay longer in the nest become relatively heavy for their wing development, because body mass stabilizes before day 14 (so more than 5 days prior to fledging), while wing length keeps increasing after day 14 (Orell 1983).

In the best model explaining brood age at fledging, both brood WL14 and brood BM14 were in the same model, although there was an association between these two variables. This is not problematic, however, because the effect of brood WL14 did not change drastically when brood BM14 was removed from the model and brood BM14 was positively associated with brood age at fledging, while brood WL14 was negatively associated.

**Fledging Asynchrony**

There were large differences in fledging asynchrony between broods. Against our expectations, we did not find fledging asynchrony was related to within-brood variation in wing development, implying that fledging was not triggered by the wing development of the fledglings. Yet, when analysed in more detail we did find that the time between the moments of fledging of two successive fledglings showed a positive trend with the difference in their wing development. This trend might imply that the larger the difference in development between fledglings, the more time there was between their fledging moments.

**Sex-specific Fledging Strategies**

For both the age of fledging and fledging order, wing length seemed to be important. If there were a fitness benefit for fledging earlier and/or fledging as the first of a nest, we would expect nestlings to invest in wing development rather than, for instance, body mass. Nilsson & Svensson (1996) experimentally showed that, under competition, the wings of smaller nestlings grow at a rate expected for their age, but at the cost of a reduced increase in body mass. In this way, the smaller nestlings keep up better with the wing length of larger nestlings, suggesting that wing development has priority over body mass gain. We found that the sexes differed in BM14 but not in WL14. Along similar lines, we hypothesize that it may be adaptive for females to allocate relatively more resources to wing development to ensure either earlier fledging or fledging as one of the first in the nest.

**Fledging Order**

Fledging order depended on relative WL14. This result agrees with most studies in passerines (Nilsson 1990; Michaud & Leonard 2000; Johnson et al. 2004). We also found that the first fledged young spent more time in the nestbox opening immediately before fledging than its nestmates. These results contradict Lemel’s (1989) idea that competition between nestmates caused fledging and subordinate young fledge first to break the monopolization of the nestbox opening by the dominant siblings. Perhaps local environmental factors led to much more severe competition between nestmates in Lemel’s (1989) study than in the other studies, resulting in a stronger effect of body mass on fledging order.

Both relative BM14 and swapping contributed almost significantly to the model when these parameters were added to the model separately (Table 3). The close to significant negative association between relative BM14 and fledging order indicates that body mass might play a role in fledging order, but the effect size of relative BM14 is much smaller than of relative WL14. The almost significant positive association between swapping and the fledging order is particularly interesting. If not by chance, this effect of swapping must be caused by a difference between the swapped and nonswapped nestlings. The difference may be either a response to the swapping procedure or a consequence of nonrandom selection by the experimenter. We cannot distinguish between these explanations. For all measured traits, with the exception of fledging order, swapped and nonswapped individuals did not differ. Of course, responses or nonrandom selection can be related to nestling traits that we did not measure. Because both relative BM14...
and swapping did not improve the model, were not significant and had an effect size that was at least two times smaller than the effect size of wing length, we did not incorporate them in the final model.

Conclusions

Sex and BSR did not influence timing and age of fledging of the brood. Age of fledging depended highly on wing development, which suggests that nestlings wait to reach a certain state of development before fledging. To fleege in synchrony, nestlings should keep up with their nestmates during development. Therefore, we hypothesize that it may be adaptive for females to allocate relatively more resources to wing development to ensure fledging at the same time as their male siblings. Our findings that BSR and nesting sex did not affect the timing and order of fledging is consistent with this view. To investigate the adaptiveness of timing and order of fledging, studies are needed to look at the consequences of these for survival.

Acknowledgments

We are grateful to the following persons for their contribution to this study: Christiaan Both (suggesting the problem, discussion), Niels Dingemanse (discussion), Sandra Häydn (fieldwork), Martin Keiser (fieldwork), Bart Kempenaers (discussion), Kevin D. Matson (comments on the manuscript), Stephanie P. M. Michler (fieldwork, discussion), Marion Nicolaus (fieldwork, discussion, comments on the manuscript), Jeroen Reimerink (fieldwork), Richard Ubels (fieldwork, database maintenance, discussion), Marco van der Velde (molecular sexing) and the students of the ‘Animal Ecology and Research’ course (fieldwork). We thank two anonymous referees for their constructive comments on the manuscript. We also thank the Dutch State Forest Service and the Ministry of Defence of the Netherlands for permission to work on their land and for making use of their facilities. Funding was provided by The Netherlands Organisation for Scientific Research (NWO-VICI grant: 86503003 to J.K.) and the University of Groningen.

References


