

*Fledging Behaviour in the Blue Tit*  
(*Cyanistes caeruleus*):  
*Effects of Nestling and Brood Characteristics*

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Erstgutachter: Prof. Dr. Bart Kempenaers  
Zweitgutachterin: Prof. Dr. Susanne Foitzik

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## **ABSTRACT**

The trial of leaving the nest and flying for the first time is a unique feature in the development of young birds. Optimizing the time of fledging potentially has important consequences for immediate and long-term survival and leads to a trade-off between costs and benefits of staying in versus leaving the nest. We studied fledging behaviour in wild blue tits (*Cyanistes caeruleus*) using a transponder-based automated recording system and considered variation in the timing of fledging within as well as between broods. Broods were compared based on the level of inequality and competition among young present. Within broods we investigated effects of body size and mass, as well as sex and paternity (extra-pair or not) of individual nestlings. We also examined the connection between parental feeding behaviour and the timing of fledging. Our results indicate that the fledging time of individual young depends both on reaching a threshold size and on the energetic reserves they carry. These relationships were most pronounced for large broods and young late in the fledging order, possibly as a consequence of an increased risk of abandonment. Effects were also more influential in broods with extra-pair young, suggesting a role of intra-brood competition in the process of fledging. We did not find evidence that parental behaviour affects the timing of fledging. Thus, apart from developmental and nutritional state, the behaviour of siblings appears to be the most important determinant of fledging patterns.

## **INTRODUCTION**

Fledging is an important step in a young bird's life. It means leaving the safety of the nest and taking the first step towards independence from the parents. Fledging behaviour is also linked to fitness: not all nestlings will fledge, and not all fledglings will survive until independence. Indeed, mortality before and after fledging is high, and only drops after individuals have become fully independent (Magrath 1991; Naef-Daenzer et al. 2001).

Many studies have investigated various aspects of nesting success (e.g. Stephens et al. 2003; Tremblay et al. 2003; Goodenough et al. 2008) by examining characteristics of eggs and hatchlings that affect egg hatchability, nestling survival, and offspring recruitment to the breeding population (e.g. Both et al. 1999; Monrós et al. 2002; Onagbesan et al. 2007; Mattsson and Cooper 2009; Møller et al. 2009). In contrast – and despite its importance – relatively little is known about fledging behaviour, and about the parent's response to the fledging of their young. This is probably because it is difficult and time-consuming to observe fledging in the wild.

For an individual nestling, the timing of fledging must in some way depend on its developmental state since it needs at least the structural ability to fly out of the nest. Furthermore, fledging may require energy reserves. Flight is energetically demanding (Alexander 2005; Naef-Daenzer and Gruebler 2008), especially when performed by inexperienced young that have not yet reached full morphological maturity (Naef-Daenzer et al. 2001; Verspoor et al. 2007), and costs of thermoregulation are probably higher outside the nest due to increased heat loss (Forbes 2007). Therefore, we also expect nutritional state or condition to influence the timing of fledging. Indeed, there is evidence that within a brood nestlings in good condition or in advanced developmental state fledge earlier (Lemel 1989; Nilsson and Svensson 1993; Michaud and Leonard 2000; Johnson et al. 2004). On top of these individual nestling characteristics, fledging behaviour is also affected by interactions between all the individuals involved: all the young in a brood and their parents.

Although little is known about the fitness consequences of fledging early per se, it is known that in a population heavy nestlings (presumably early fledging individuals) are more likely to recruit to the study area in the next breeding season (Both et al. 1999; Naef-Daenzer et al. 2001; Monrós et al. 2002). Thus, the positive effect of mass and development can be mediated by fledging order. Furthermore, observational studies suggest that young begging for food outside of the nest are preferentially fed over those that are still in the nest (Lemel 1989; Nilsson 1990). This may lead to

early fledging young acquiring additional food, reinforcing developmental and nutritional advantages they have over their later fledging siblings, and thereby increasing their chance of recruitment.

There is substantial variation in fledging behaviour between broods (Zach 1982; Lemel 1989; Johnson et al. 2004). For instance, in the house wren (*Troglodytes aedon*) early fledging was associated with developmental state in some nests, but not in others (Johnson et al. 2004). However, the underlying causes of such variation have not yet been investigated in detail. One possible candidate is the level of intra-brood competition. Both direct interactions and scramble competition in the nest are costly to the young (Kilner and Drummond 2007; Kilner and Hinde 2008), and may therefore affect both their structural ability to fledge (through developmental state) and their energetic reserves (nutritional state). Also, if competitive interactions lead to a reallocation of resources within the nest towards superior nestlings, competition should increase the inequality among the young in their ability to obtain food. This will enlarge the spread in developmental and nutritional state within a brood. Thus, a high level of intra-brood competition could lead to an association between condition- or development-associated parameters and fledging order that is absent in broods with lower levels of competition.

We studied fledging behaviour in a nest box population of blue tits, *Cyanistes caeruleus*, using a transponder-based automated recording system (Johnsen et al. 2005). Blue tits are socially monogamous, cavity-nesting passerines, which fledge after spending 16-22 days in the nest, and stay in the family group for several days after fledging (Cramp and Perrins 1993). Nestlings as well as fledged young are fed by both parents. The day at which fledging starts is not completely predictable and fledging often takes more than one day (see below). By automatically recording the identity of all birds passing through the hole of a nest box, we obtained reliable data on the timing of fledging for 47 nests.

Our study has four main aims. First, we describe variation in fledging behaviour within and between broods. We report the timing of fledging for individual nestlings and the total duration of fledging of a brood (fledging asynchrony). Previous studies on other species found that most young fledged before noon. Also, it is often assumed that all young leave the nest in close succession (Nilsson 1990; Nilsson and Svensson 1993; Nilsson and Gårdmark 2001), although this may not always be the case (Johnson et al. 2004). Using the automatically recorded data we were able to

examine these aspects of fledging based on a large number of individuals.

Second, we test our hypothesis that inequality among young in a brood and the level of intra-brood competition can explain differences in fledging behaviour between broods. To do this, we consider four characteristics of a brood that reflect inequality and/or the level of competition. (a) Feeding rate. Parents vary in the amount and quality of food they bring to the nest. All other things being equal, competition should be higher in broods where parents feed less. (b) Brood size. In many studies brood size manipulations are employed to influence the level of intra-brood competition (e.g. Nilsson and Gårdmark 2001; Nicolaus et al. 2009a). (c) Multiple paternity. The presence of extra-pair young in a brood has been shown to enhance nestling competition, presumably reflecting a response to reduced indirect fitness costs with decreasing relatedness (Briskie et al. 1994; Boncoraglio and Saino 2008). (d) Variation among the young of a brood in traits relevant for fledging (such as body mass). This reflects inequality within a brood.

A third aim of our study is to investigate factors that can explain within-brood variation in fledging behaviour. Here, we address which attributes of a nestling influence its timing of fledging. We consider the role of nestling body size, mass, and condition (measured as body mass corrected for size, Merilä et al. 1999), as well as sex and paternity status. A recent study on blue tits has shown that extra-pair young are more often found among the first-laid eggs, and therefore also among the first to hatch (Magrath et al. 2009). Because hatching order often correlates with development (it directly reflects age) and may influence condition, extra-pair young may then fledge earlier than within-pair young. Alternatively, or additionally, extra-pair young may fledge earlier if they are superior competitors or in other respects of higher intrinsic quality (Foerster et al. 2003; Charmantier et al. 2004). We also consider differences between early and late fledglings within a brood. During the fledging process, parental care takes place at two different locations – inside the nest (feeding nestlings) and outside the nest (feeding fledglings) – and parents may shift their focus from nestlings to fledglings in relation to where the majority of young are. Different selection pressures may therefore act on a nestling's fledging decision depending on how many siblings have already fledged.

The final aim of this study was to investigate how parents change their feeding behaviour when fledging commences. We address whether feeding males and females respond differently to fledging, and whether males that have been cuckolded (and thus feed unrelated young) behave



differently than males that did not lose paternity. Parents may stimulate their young to fledge ('parental manipulation hypothesis': e.g. Bustamante and Hiraldo 1988; Michaud and Leonard 2000). After fledging has started, they may do this by reducing their feeding rate at the nest to encourage remaining nestlings to also leave the nest. We consider this possibility by comparing the feeding rate at the nest before and after fledging.

## **METHODS**

### ***General field procedures***

This project is part of a long-term study on the breeding biology of blue tits, conducted in a mixed deciduous and coniferous woodland ('Westerholz', 48°08' N 10°53' E) near Landsberg am Lech, Southern Germany. The study area is an unmanaged part of the forest ('Reiherschlag', ca. 40 hectares), which is dominated by mature oak trees and contains 277 small-holed (26 mm) nest boxes (since 2007) with 60 – 80 breeding attempts of blue tits each year.

In this population, egg-laying mostly takes place in April (mean±SE for date of first egg: 16.April±0.40; earliest first egg: 8<sup>th</sup> of April; latest first egg: 7<sup>th</sup> of May). In the years of the study, clutch size ranged from 5 – 17 (mean±SE: 10.75±0.10) eggs and young started to hatch (often asynchronously) 9 – 17 days (mean±SE: 11.81±0.11) after the last egg had been laid. The nestling period took 19 – 23 days (mean±SE: 20.04±0.08).

We captured all breeding birds inside the nest box, either in the winter preceding the breeding season (roosting), or during the breeding season (feeding 8-10 days old nestlings), marked them with a unique combination of colour bands, took a small blood sample (approx. 50 µl) for later parentage analysis, and measured (tarsus and wing length) and weighed them (Johnsen et al. 2005). We also equipped each adult with a small passive integrated transponder (EM4102 ISO animal tag 134.2kHz ISO, 8.5 mm x 2.12 mm, 0.067g), which was inserted under the skin on the back.

During the breeding season (March – June) nest boxes were visited on a weekly basis and daily close to the start of laying, hatching, and fledging. This enabled us to determine the duration of the hatching and nestling period in days. We banded young 14 days after the first young of the brood had hatched, measured their tarsus length (calliper, ±0.05 mm), and weighed them (electronic balance, ±0.1 g). We also took a small blood sample (approx. 50 µl) for later parentage analysis. Two or three days later (16 – 17 days post-hatch) young were equipped with a transponder of the same type as used for adults. Adults or nestlings carrying subcutaneous transponder tags do not show a reduction in fitness (Nicolaus et al. 2009b).

### **Recording system**

Nest boxes were equipped with a transponder reading device (small-size Radio Frequency Identification module; Elatec), which is triggered by birds with transponders passing through the nest hole. This makes it possible to determine the identity of these birds (Johnsen et al. 2005). Through a connected real-time clock (RTC; mikroElektronika) the time and date of events at the nest hole are also automatically recorded. Additionally, passive infra-red detectors (miniature movement alarm units; Hygrosens Instruments) and light barriers (OPIC Light Detectors IS471F and L8957 Low Cost Infra-red LED; Sharp and Hamamatsu Photonics) at the outside and at the inside of the nest box enabled us to recognize the direction of the bird's movement (leaving or entering the nest box, see Fig.A2 in Appendix). Data were stored on a SanDisk® Standard SD™ card (2GB) and processed by a Development Board (Olimex) for AT91SAM7S256 (Atmel) micro-controller. Electricity to run the system came from a 6 V battery (Valve Regulated Lead-Acid Battery with 6 V, 7.2 Ah; Panasonic).

In 2008 and 2009, 34 and 62 active nest boxes respectively, were equipped with the above system to record fledging behaviour. Feeding behaviour was recorded only in 2009. Because the time signal provided by the system was not entirely reliable, we calibrated it by passing a known transponder through the entrance hole of each box at a given time. This was done at least weekly during the breeding season, when the nest boxes were checked, and revealed a maximum drift of 22 minutes. Such time drift shifted all data from the corresponding nest box by this amount of time. Because time differences between nest boxes in this dimension are not influential for the type of question we are examining, any time drift was ignored in our analyses.

### **Paternity analysis**

Blood samples from adults and nestlings were used for parentage analysis using a set of 11 micro-satellite markers (PC3, PC4, PC7, PC8, PC9, Pocc1, Pocc6, MC4, Pat43, PK11, and PK12). For general procedures and details, see Delhey et al. 2003. For the 47 broods that are part of this study, we analysed paternity and established whether young were extra-pair for all but four young (three from a brood of three and one from a brood of nine; no extra-pair young found among remaining brood), where the quality of genetic material was insufficient. Molecular methods (using marker P2P8) were also used to determine the sex of all individuals, except for one young (from the brood

of nine from above) where the quality of genetic material was insufficient.

### **Fledging and feeding behaviour**

Experimental difficulties led to reduction of our initial sample of 96 broods. In 30 broods (19 in 2008, 11 in 2009) substantial data loss occurred due to technical problems (e.g. battery failure) and we excluded these broods. However, we did include broods where partial loss of data had occurred, whenever fledging was recorded for all nestlings except one (8 broods: 1 in 2008, 7 in 2009). In four broods (all in 2009), the fledging of young was apparently triggered by their handling (they fledged on the day of transponder implantation) and these broods were also excluded. In 15 nest boxes (7 in 2008, 8 in 2009) the breeding attempt failed before any young had fledged, further reducing our sample size. Hence, we had 47 broods (8 in 2008, 39 in 2009) for analyses of fledging behaviour. Since feeding behaviour was recorded just in 2009, only 39 broods are included for these analyses. For two of the female parents the implanted transponder was apparently without signal. Therefore only the male feeding visits were recorded and used for analyses. For analyses of between-brood variation in fledging behaviour we also used the 39 broods for which we had information on parental feeding behaviour, since we wanted to test for a relationship between parental care and fledging. In all analyses including information on paternity the two broods where paternity status could not be determined were excluded.

As a rough estimate of hatching asynchrony we determined the number of days on which hatchlings and eggs were found, based on the data recorded during the daily inspection of nest boxes. For broods where all young hatched between two consecutive inspections, hatching asynchrony was set to one day. We defined the duration of the nestling period as the number of days between hatching of the first young and fledging of the last nestling. This information can be obtained also for nest boxes without automatic data recording via the standard field protocol. Thus all available broods (66 in 2007, 67 in 2008, 53 in 2009) were used for this analysis. Fledging asynchrony is the duration of the fledging period, that is, the time between fledging of the first and the last young, based on the automatically recorded data. Fledging order is the sequence in which the young left the nest box. As outlined above, factors shaping the timing of fledging for individual young may depend on their position in the fledging order, because parents may shift their focus of care from the nest box to fledglings when the majority of young have left the nest. In a detailed analysis, we

therefore constructed a proxy for early and late fledging by splitting broods into half. We considered young leaving the nest among the first half as early fledging and young leaving the box among the second half as late fledging (see Nilsson 1990 for a similar classification). This categorization reflects whether the majority of young is still in the nest.

Parental feeding rates were estimated based on all recorded male and female visits to the box over the entire nestling period. Visiting rate is assumed to reflect feeding rate because blue tits bring only one prey item per visit (Cramp and Perrins 1993), and in the closely related great tit (*Parus major*) most of the visits to the nest are for feeding young (Eguchi 1980). Days were divided into 30 min periods and visits of each parent were counted for each interval between the first and last visit on a given day. For per capita feeding rates, the number of visits during a particular 30 min period was set in relation to the number of young present in the nest at the start of the interval. To compare feeding rates before and after the start of fledging, we calculated for both parents the average feeding rate per half hour, based on all visits recorded on the last four days of the nestling period. This interval is of the same length as the maximal fledging asynchrony and there is no systematic change in feeding rates at the nest during this period (see below). We then set this in relation to the average half-hourly feeding rate, based on all visits recorded after the first nestling had left the nest. The average hourly feeding rates reported are average half-hourly rates multiplied by two. Daily feeding rates were obtained for each day before fledging of the first young by summing up all visits of the corresponding day.

### **Statistical analysis**

We used general linear models (GLMs) or linear mixed-effect models (LMEs). GLMs were used when either no grouping structure existed, or when inclusion of the grouping structure did not improve the model, because it did not explain any variance. We graphically inspected whether the assumptions of normality of residuals and homogeneity of variance were fulfilled following Grafen and Hails (2002, pp.153-180). When necessary, data were transformed (log-, squareroot-, or z-transformed). The fledging events of young within one brood were not independent, but occurred in bouts. We therefore corrected for the autocorrelation structure of the data by including a continuous autoregressive process (corCAR1) into LMEs (Pinheiro and Bates 2000, pp.226-249 and 395-400; see Appendix for details). With this procedure, consecutive fledglings in a bout essentially receive

less weight in the model than fledglings that are further apart.  $r^2$ -values for LMEs were obtained using an estimate (pseudo- $r^2$ ) as described by Nagelkerke (1991). For analyses of between-brood variation in fledging behaviour, we were interested in differences between broods in the association between weight and fledging order. We therefore calculated the slope of the correlation between weight and fledging order for each brood. As the sample size for single broods is very small, this was done using robust linear models ('MM' structure), which are more robust against outliers (Venables and Ripley 2002, pp.156-163). All statistical tests are two-tailed. Statistical analyses were performed with the free software R 2.10.1 (R Development Core Team 2009). We used the add-on R packages nlme (Pinheiro et al. 2009) for LMEs, MASS for robust linear models (Venables and Ripley 2002), and lattice (Sarkar 2009) for graphics.

## **RESULTS**

### ***Brood and nestling characteristics***

We studied fledging behaviour in 47 broods, with a total of 477 nestlings, of which 430 fledged. All broods were cared for by both parents and all males except one were socially monogamous. For the one socially polygynous male, we here only consider the primary brood, that is, the breeding attempt that was initiated first (difference in first egg and hatching date: 20 and 18 days, respectively). On average fifty percent of the nestlings in a brood were female (mean $\pm$ SE: 50.1 $\pm$ 2.4%; range: 20% to 88%). At day 14, female nestlings were both smaller and lighter than their brothers (paired t-test; body mass: mean difference  $\pm$ SE = 0.47 $\pm$ 0.08 g,  $t_{46} = 5.72$ ,  $p < 0.0001$ ; tarsus length: mean difference  $\pm$ SE = 0.44 $\pm$ 0.05 mm,  $t_{46} = 8.81$ ,  $p < 0.0001$ ).

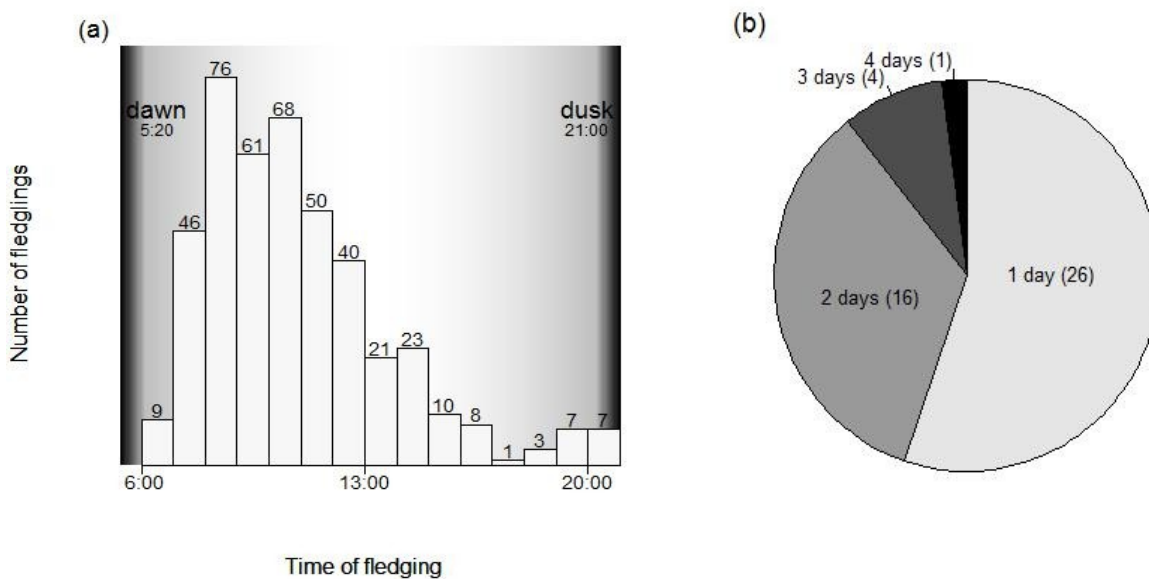
Among the 47 broods, 51% (23) contained at least one extra-pair offspring and overall 13.0% (56) of the nestlings were extra-pair (range among broods with at least one extra-pair young: 10-75%). Extra-pair young were on average heavier but not larger than their within-pair half-sibs (paired t-test; body mass: mean difference  $\pm$ SE: 0.39 $\pm$ 0.14 g,  $t_{22} = 2.78$ ,  $p = 0.01$ ; tarsus length: mean difference  $\pm$ SE = -0.001 $\pm$ 0.16 mm,  $t_{22} = 0.05$ ,  $p = 0.96$ ). Among all 56 extra-pair young, 52% were females. Nestling tarsus length and body mass on day 14 were highly correlated, among all young (correlation coefficient: 0.68, linear model:  $t_{428} = 19.03$ ,  $p < 0.0001$ ) and within broods (mean within-brood correlation coefficient: 0.63, linear mixed-effect model with 'brood ID' as random factor:  $t_{382} = 19.24$ ,  $p < 0.0001$ ).

### ***General fledging behaviour***

All young fledged during the day (after sunrise and before sunset) and 82% of the nestlings fledged during the first half of the day ( $\sim$  05:00-13:00; Fig. 1a). Nestlings typically fledged in groups of three (autocorrelation structure:  $\phi = 0.83$ ,  $r^2 = 0.55$ , see Appendix). Only 55% of the broods completed fledging within one day (mean length of fledging period  $\pm$ SE: 14.0 $\pm$ 2.4 hours; Fig. 1b). The extremes in fledging duration were 14 min and 4 days, respectively.

Hatching asynchrony also differed between broods (mean length of the hatching period  $\pm$ SE: 2.0 $\pm$ 0.1 days; range: 1 to 4 days). However, fledging asynchrony was not linked to hatching

asynchrony (linear regression: coefficient±SE = 0.07±0.28,  $t_{45} = 0.24$ ,  $p = 0.81$ ; fledging asynchrony log-transformed). Furthermore, fledging asynchrony (log-transformed) was also uncorrelated with the within-brood range in body mass (linear regression: coefficient±SE = 0.20±0.23,  $t_{45} = 0.90$ ,  $p = 0.37$ ) or tarsus length (linear regression: coefficient±SE = 0.32±0.43,  $t_{45} = 0.75$ ,  $p = 0.46$ ). Note that hatching asynchrony did predict the within-brood range in body mass and size at day 14 (linear regression: body mass: coefficient±SE = 0.26±0.12,  $t_{45} = 2.24$ ,  $p = 0.03$ ; tarsus length: coefficient±SE = 0.43±0.22,  $t_{45} = 1.91$ ,  $p = 0.06$ ).



**Fig. 1. General fledging behaviour.** (a) Time of day for the fledging events of the 430 individual young (72% fledged before 12:00 am). (b) Distribution of fledging asynchrony for the 47 broods (length of the fledging period).

On average, young had left the nest on the 20<sup>th</sup> day after hatching started (range: 15 to 23 days post-hatch, data from all years of the study combined). In 2009, but not in the earlier years of the study, the duration of the nestling period (time between hatching and fledging) tended to differ between broods with and without extra-pair young, whereby the last young in mixed paternity broods fledged on average±SE 0.4±0.4 days earlier (Welsh Two Sample t-test:  $t_{51} = 1.79$ ,  $p = 0.08$ ).

### ***Factors explaining between-brood variation in fledging behaviour***

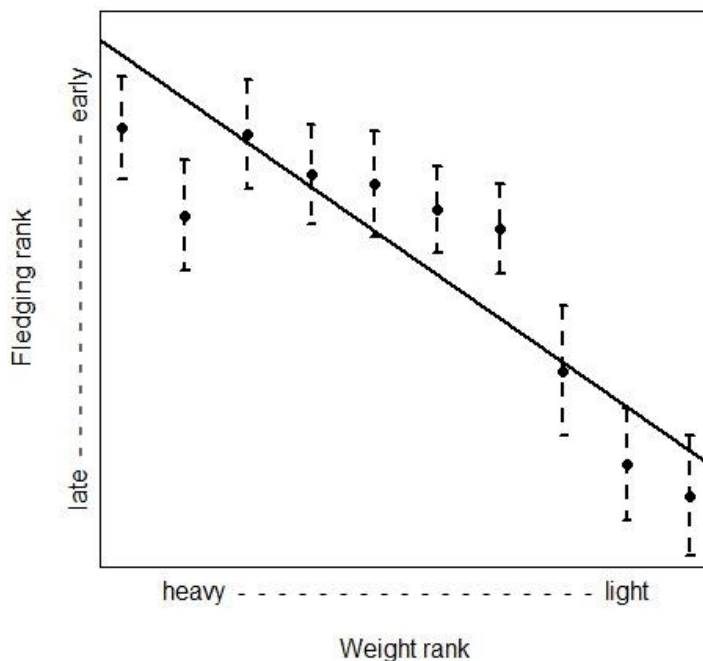
Nestling body mass was the strongest predictor of fledging order within a brood (see below) and we examined variation between broods in this relationship. The correlation between body mass and fledging time, quantified as the robust regression slope for each brood, was  $-1.34±0.49$  (mean±SE) and showed marked variation (range:  $-11.85$  to  $3.34$ ). This means that every extra gram of weight



advances fledging by 1.34 hours. Of the five variables reflecting inequality and competition (feeding rate, brood size, presence of extra-pair young in the brood, fledging asynchrony, and inequality in body mass), only brood size contributed significantly to variation in this slope. The relationship between body mass and fledging order was steeper when broods were larger (linear regression: 10% of variance explained, coefficient $\pm$ SE =  $-0.17\pm 0.07$ ,  $t_{37} = -2.23$ ,  $p = 0.03$ ; robust slope log-transformed). Also, there was a trend for steeper slopes with higher fledging asynchrony (linear regression: coefficient $\pm$ SE =  $-0.03\pm 0.01$ ,  $t_{37} = -1.84$ ,  $p = 0.07$ ; all other  $p$ -values  $> 0.10$ ; robust slope log-transformed). Effects of inequality in body mass were tested both using within-brood weight range and variance in weight as explanatory variables, leading to similar results (no effect).

***Factors explaining within-brood variation in fledging behaviour***

Body mass and tarsus length strongly influenced the timing of fledging for individual nestlings within broods: heavy and large young fledged earlier than light and small young (Fig. 2, Table 1). The effect of body mass was also present when accounting for the effect of body size (Table 2), indicating an important role of relative mass or condition for fledging order. Despite being lighter and smaller, females did not fledge later than males (Table 1) and the percentage of females in each fledging rank showed no systematic pattern (Fig. 3a). This means that given their body mass, females fledged earlier than males (Table 2). As expected from their greater body mass, extra-pair young fledged earlier than within-pair young (Table 1b; Fig.3b), although this was not the case when the autocorrelation structure was included into the model (Table 1a). In any case, there



**Fig. 2. Nestling body mass predicts fledging order** (both variables ranked, ranked body mass divided by nestling number to adjust for brood size). Shown are mean, SE, and the robust regression line ( $y = 3.40x + 3.35$ ).

was no additional effect of paternity on fledging order once the effect of body mass was taken into account (linear mixed-effect model: with autocorrelation:  $t_{377} = 0.65$ ,  $p = 0.52$ ; without autocorrelation:  $t_{377} = -1.70$ ,  $p = 0.09$ ).

**Table 1. Effect of nestling characteristics on fledging order (single effects) for all young.** Linear mixed-effect model using brood identity as random factor, (a) with and (b) without the autocorrelation structure ( $\phi = 0.83$ ,  $r^2 = 0.55$ ). The results were obtained by testing each variable in a separate model. Fledging order z-transformed.

(a)	coefficient±SE	statistic	p-value
tarsus length	-0.15±0.05	$t_{382} = -3.26$	$p = 0.001$
body mass	-0.18±0.04	$t_{382} = -4.94$	$p < 0.0001$
sex (female*)	-0.07±0.05	$t_{381} = -1.48$	$p = 0.14$
paternity (extra-pair**)	0.01±0.09	$t_{379} = 0.11$	$p = 0.92$

(b)	coefficient±SE	statistic	p-value
tarsus length	-0.23±0.07	$t_{382} = -3.40$	$p = 0.001$
body mass	-0.26±0.04	$t_{382} = -5.94$	$p < 0.0001$
sex (female*)	-0.01±0.1	$t_{381} = -0.10$	$p = 0.92$
paternity (extra-pair**)	-0.31±0.13	$t_{379} = -2.31$	$p = 0.02$

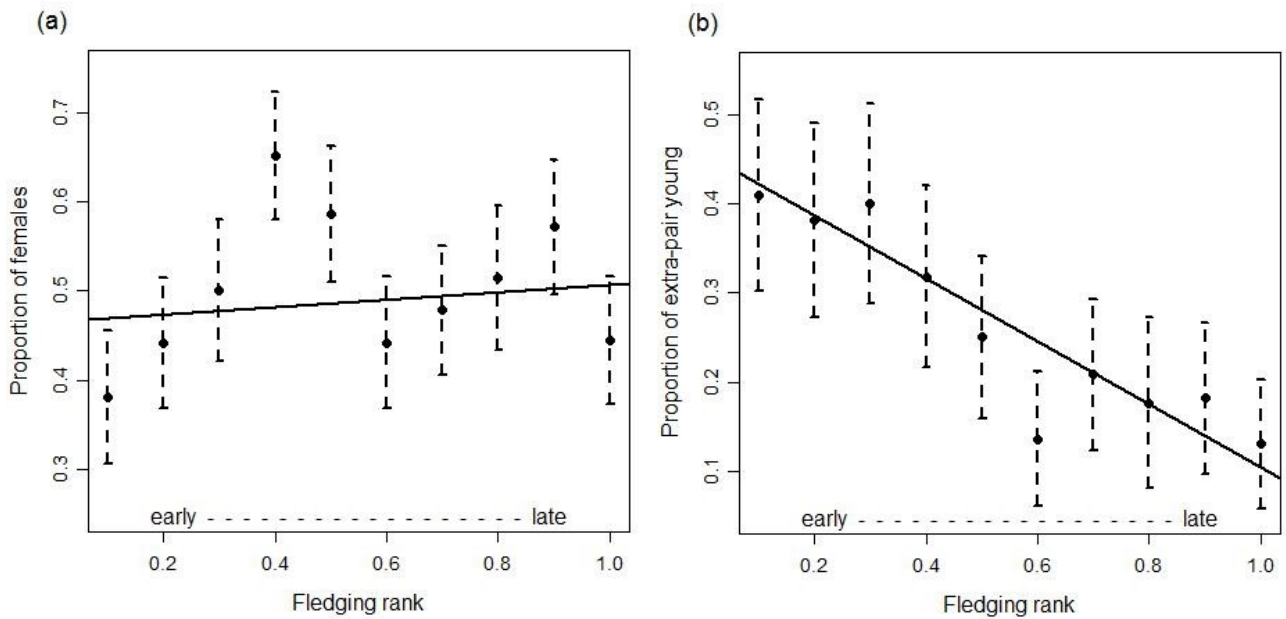
\* Effect for a female nestling in comparison to a male nestling.

\*\* Effect for an extra-pair nestling in comparison to a within-pair nestling.

**Table 2. Effects of nestling characteristics on fledging order (combined effects) for all young.** Linear mixed-effect model using brood identity as random factor including the autocorrelation structure ( $\phi = 0.83$ ,  $r^2 = 0.55$ ). The results were obtained by adding each variable sequentially to the model (from top to bottom). Thus, in contrast to Table 1, effects shown here take into account effects of variables added previously. Fledging order z-transformed.

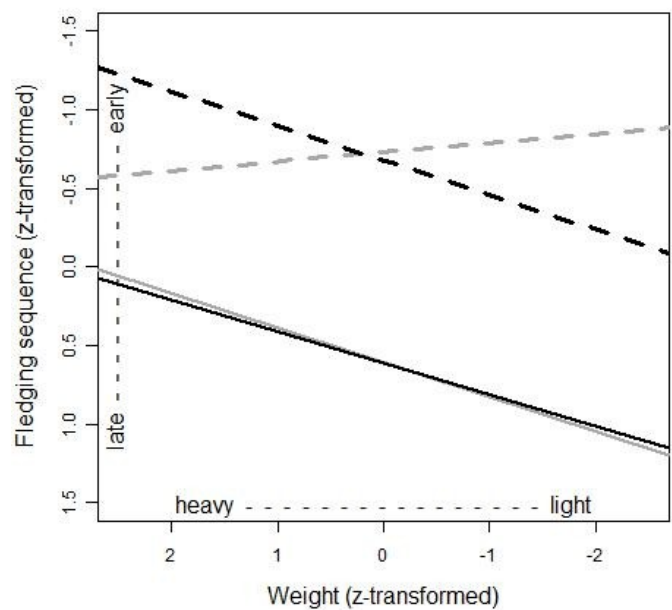
	coefficient±SE	statistic	p-value
<b>all young</b>			
tarsus	-0.15±0.05	$t_{382} = -3.26$	$p = 0.001$
weight	-0.17±0.05	$t_{381} = -3.66$	$p < 0.001$
sex (female*)	-0.20±0.05	$t_{379} = -3.81$	$p < 0.001$

\* Effect for a female nestling in comparison to a male nestling.



**Fig. 3. Fledging order in relation to nestling sex and paternity.** The proportion of (a) females and (b) extra-pair young in each fledging rank (fledging rank divided by nestling number to adjust for brood size). Shown are mean, SE, and the robust regression line ((a):  $y = 0.04x + 0.46$ ; (b):  $y = -0.35x + 0.46$ ).

We then conducted the analyses separately for early and late fledging young. The effect of body size (tarsus length) on fledging order was found among late, but not among early fledglings. An additional effect of relative body mass was absent among early fledging young from broods without extra-pair paternity (Table 3). Similarly, in broods without extra-pair young the correlation between body mass and fledging order was present only for the late fledglings (Fig. 4; linear regression; interaction term: coefficient $\pm$ SE =  $0.27\pm 0.10$ ,  $t_{197} = 2.69$ ,  $p = 0.008$ ; weight and fledging order z-transformed) while it was equally strong for



**Fig. 4. Early fledglings and multiple paternity.** The influence of body mass on fledging sequence (both z-transformed) among early (broken lines) and late fledglings (solid lines) in broods with (black) and without (grey) extra-pair young. Lines are the regression lines from the model of table 3.

early and late fledglings in mixed paternity broods (Fig. 4; linear regression; interaction term: coefficient $\pm$ SE =  $-0.02\pm 0.09$ ,  $t_{213} = -0.23$ ,  $p = 0.82$ ; weight and fledging order z-transformed). Indeed, in multiple paternity broods the first fledgling was significantly heavier than the second (paired t-test: mean difference  $\pm$ SE =  $0.43\pm 0.26$ ,  $t_{22} = 3.46$ ,  $p = 0.002$ ), while this was not the case in broods without extra-pair young (paired t-test: mean difference  $\pm$ SE =  $-0.15\pm 0.39$ ,  $t_{21} = -0.81$ ,  $p = 0.43$ ). Interestingly, in multiple paternity broods this effect was not caused by the paternity status of the young per se, because it was also present when restricting the test to multiple paternity broods where the first two fledglings were sired by the social male (paired t-test: mean difference  $\pm$ SE =  $0.39\pm 0.39$ ,  $t_8 = 2.33$ ,  $p = 0.05$ ).

**Table 3. Effects of nestling characteristics on fledging order (combined effects) for different groups of young.** Linear model – inclusion of grouping structure and autocorrelation did not improve the model and lead to similar results. The results were obtained by adding each variable sequentially to the model (first tarsus, then weight). Separate analysis for early (first half) ((a), (b)) and late (second half) fledging young ((c), (d)), and for young from nests with ((a), (c)) and without ((b), (d)) extra-pair young. Fledging order and weight z-transformed.

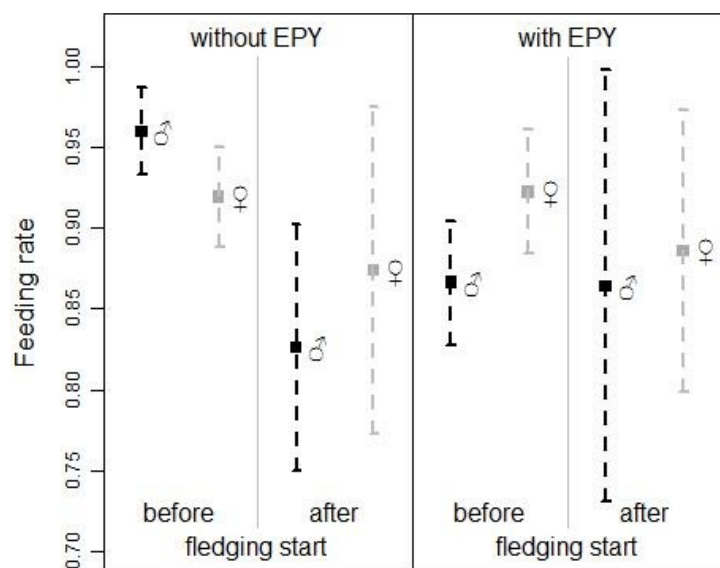
	coefficient $\pm$ SE	statistic	p-value
<b>(a) early young from mixed paternity broods</b>			
tarsus	$-0.10\pm 0.08$	$t_{100} = -1.23$	$p = 0.22$
weight	$-0.24\pm 0.10$	$t_{99} = -2.27$	$p = 0.03$
<b>(b) early young from uniform paternity broods</b>			
tarsus	$0.03\pm 0.08$	$t_{93} = 0.35$	$p = 0.73$
weight	$0.06\pm 0.12$	$t_{92} = 0.56$	$p = 0.58$
<b>(c) late young from mixed paternity broods</b>			
tarsus	$-0.16\pm 0.05$	$t_{113} = -3.18$	$p = 0.002$
weight	$-0.15\pm 0.06$	$t_{112} = -2.38$	$p = 0.02$
<b>(d) late young from uniform paternity broods</b>			
tarsus	$-0.14\pm 0.06$	$t_{104} = -2.45$	$p = 0.02$
weight	$-0.24\pm 0.08$	$t_{103} = -2.91$	$p = 0.004$

### ***Parental response to fledging***

During the entire nestling period the mean parental feeding rate at the nest was  $6.2\pm 0.3$  feeds per nestling per hour (mean $\pm$ SE; average number of feeds at the nest by one parent:  $25 \text{ h}^{-1}$ ). The feeding

rate (expressed as feeds per nestling per day) increased during most of the nestling period from 55 feeds 15 days prior to fledging to 84 feeds 4 days prior to fledging (linear regression:  $t_{696} = 5.04$ ,  $p < 0.0001$ ), but did not change further over the last 4 days (linear regression of day 3 until day 1 prior to fledging: coefficient $\pm$ SE =  $1.21\pm 1.17$ ,  $t_{205} = 1.04$ ,  $p = 0.30$ ). Our feeding rates are within the natural range of rates reported for blue tits (Cowie and Hinsley 1988; Cramp and Perrins 1993), indicating that our measure is reliable. In most (76%) of the 39 broods where the feeding rate of both parents was recorded, they both continued to feed at the nest box after the first young had fledged. In the remaining 9 broods, only one parent visited the nest after the first fledging event ( $N = 8$  broods; male only: 5 broods, female only: 3 broods), or none of the parents still fed at the nest after the start of fledging (one brood with 10 fledglings, which all fledged within 14 min). In both broods where only the male parent was recorded, the male continued to feed nestlings after fledging started.

After fledging had started, parents adjusted their feeding rate to the number of young that remained in the nest. Compared to the last 4 days of the nestling period, they reduced the number of visits to the nest after the first fledging event (linear model: 59.9 vs. 30.8 feeds by both parents per hour,  $t_{75} = -7.54$ ,  $p < 0.0001$ ), but did not change their feeding rate per (remaining) nestling (linear model: 5.7 vs. 5.5;  $t_{75} = -1.72$ ,  $p = 0.09$ ; feeding rate squareroot-transformed). Feeding rate before or after the start of fledging did not depend on the sex of the parent, on the presence of extra-pair young in the brood, or on the sex or paternity status of the first fledgling (Anova; all  $p$ -values  $> 0.20$ ; Fig. 5; feeds per nestling log-transformed).



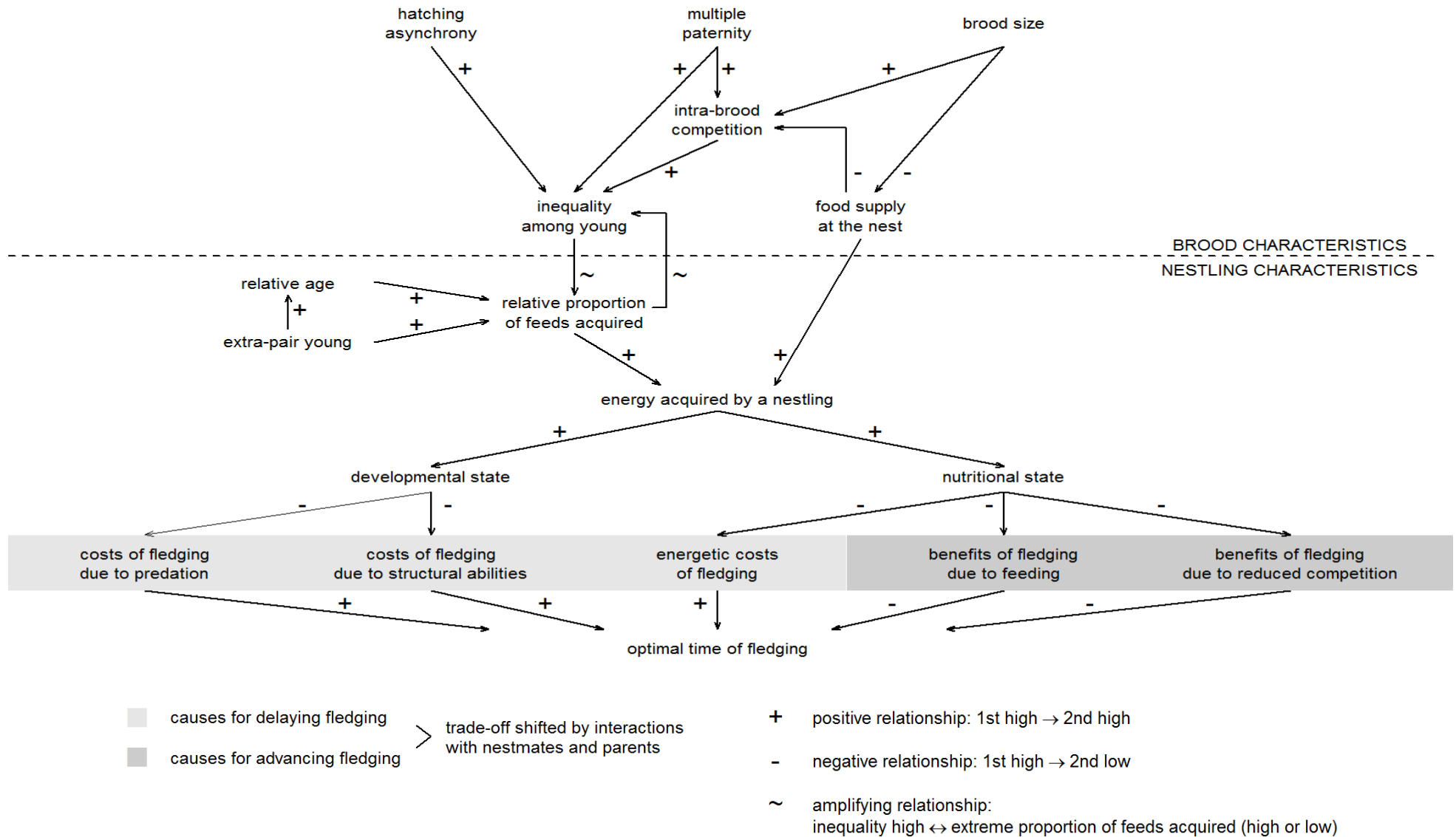
**Fig. 5. Feeding rate, sex, and paternity.** Number of feeds (per nestling per half hour; plus one and log-transformed) by one parent (males *black*, females *grey*) before (left sub-panels) and after fledging start (right sub-panels) for broods with (right panel) and without (left panel) extra-pair young (EPY). All comparisons were non-significant. Shown are mean and SE.

## **DISCUSSION**

We found that body size, mass, and relative mass correlated with fledging order. This correlation differed between early and late fledglings and between broods with and without extra-pair young. Furthermore, when measured for complete broods, the correlation was influenced by brood size, but not by parameters linked to inequality and competition. Although extra-pair young fledged earlier than within-pair young, differences between broods with and without extra-pair young were not caused by individual extra-pair young and there was no effect of paternity when taking into account differences in weight and size. Differences between broods with and without extra-pair young were also not related to parental feeding behaviour. Fledging of a brood could take extended periods of time, although fledging events of individual young were intercorrelated. Most young fledged in the morning. Before discussing these results in detail, we will first present an overview of factors influencing the process of fledging and how they possibly interact.

### ***The process of fledging***

Fledging is a complex behaviour (Johnson et al. 2004), and many different factors may contribute to differential adjustment of fledging times between nestlings. Costs and benefits vary for individual young at each point in time, and since mortality after fledging is high (Magrath 1991; Rush and Stutchbury 2008; Low and Pärt 2009; but see Murphy 1983), optimization of fledging time is expected to be under strong selection. Costs involved in the act of fledging may be increased predation after fledging (especially in cavity-nesting species; Lemel 1989; Naef-Daenzer et al. 2001), energetic demands (flight costs, thermoregulation costs, etc.), or developmental costs (Fig. 6). The latter arise when young leave the nest before they have reached full fledging ability, e.g. fully developed flight muscles and primaries are necessary in order to fly (King and Hubbard 1981; Murphy 1983). Benefits of fledging may consist of additional feeds after fledging. Parents may preferentially feed fledged young (Lemel 1989; Nilsson 1990), and it is clear that at some point feeding at the nest will cease altogether. When nest predation rates are high, leaving the nest may be beneficial also for this reason, since flying young have higher chances of evading attacking predators than young confined to the nest. However, in cavity-nesting species like the blue tit, predation rates in the nest are much lower than outside of the nest (Lemel 1989; Naef-Daenzer et al. 2001), probably because major predators are unable to access young in cavities (e.g. sparrowhawks *Accipiter nisus*; Cramp and Perrins 1993).



**Fig. 6. Factors affecting costs and benefits of fledging.**

Further benefits of fledging arise from other costs associated with staying in the nest, for instance due to a high level of costly competitive interactions (Royle et al. 1999). For an individual young these costs and benefits are likely to vary depending on its nutritional state (e.g. influencing energetic costs of fledging) and its developmental state (e.g. influencing costs of fledging due to structural abilities). The optimal fledging time for the individual results from a trade-off between these costs and benefits and therefore parameters measuring nutritional and developmental state are expected to correlate with fledging order.

Growth of tissues important for structural development (e.g. muscles, bones) or nutritional reserves (e.g. fat stores) is fuelled by the energy acquired by each nestling via food, which depends on two main factors: the overall food availability at the nest and the proportion of this food that can be obtained by an individual nestling in comparison to its nest mates (Fig. 6). Food availability depends on the amount and quality of food brought to the nest by the parents, and on the number of siblings that share this food (brood size). How the food is divided among the nestlings in a brood may also depend on parental behaviour, if they allocate food differentially between young, e.g. in relation to their age or sex (Lessells 2002; Dickens and Hartley 2007; Dickens et al. 2008). Furthermore, the proportion of feeds a nestling can secure against rivaling siblings depends on its relative competitive ability, which in turn is linked to the inequality among nestlings in age and/or in intrinsic assertiveness. Therefore, social interactions among young (e.g. begging scrambles, Parker et al. 2002) and between young and parents (e.g. begging) are important for the energy obtained by individual nestlings, which directly determines the developmental and nutritional state and the resulting optimal fledging time. Of course, for an individual nestling it is difficult to assess this optimum precisely, especially if costs and benefits of fledging are low and the trade-off is weak. Thus, its solution will only define a wider or narrower time interval optimal for fledging. Biologically, this optimal time interval is probably more relevant than an optimal time point for fledging, and we will refer to it as the fledging zone in the following.

If the overlap between fledging zones of young within a brood is low, there will be little noise in the order of fledging, and any pattern of fledging will be clear-cut: correlations between fledging order and parameters of developmental or nutritional state (e.g. tarsus length, weight) will have a steeper slope. If, on the other hand, the overlap is great, then the fledging order will be more arbitrary, patterns will be less clear, and the slope of any correlation for fledging order will be shallower.

The overlap between fledging zones of young within a brood will depend on the size of the differences between young (reflected in their inequality), since the fledging zones will move further



apart the more the young differ. Large differences between young may arise from a high level of competition within the nest, as competition may increase the inequality among the nestlings by redistributing food from bottom to top competitors (Parker et al. 2002). This may especially be true shortly before fledging, when young are large enough to block the entrance of the nest hole (where the parents will arrive with food) from their siblings (Nilsson 1990; Brzęk and Konarzewski 2001; Johnson et al. 2004; Epting and Delotelle 2009). Therefore any factors that enhance inequality or competition among nestlings are expected to decrease the overlap of optimal fledging zones of the young and lead to more pronounced correlations for fledging order.

The optimal time to fledge for one young is shaped by the behaviour of its nest mates not only via competitive interactions. Whether and when siblings have already fledged also influences the costs and benefits of fledging, as for instance, when the family group moves on after some time or when parents focus their care in relation to where the majority of young are located. Independent of cost-benefit considerations, it has to be kept in mind that fledging is not only the decision of the individual young. For instance, in a study on house wrens video recordings of fledging showed that in many cases fledging was not voluntary: some young fell out of the nest, some seemed to be pushed out by parents or siblings (Johnson et al. 2004). In other cases, young are found to block the entrance hole (Nilsson 1990; Brzęk and Konarzewski 2001; Johnson et al. 2004; Epting and Delotelle 2009), and can thereby hinder other young to fledge. Under such circumstances realized fledging time may deviate from the optimal time of fledging. Social interactions other than competition may therefore influence fledging behaviour in unexpected ways.

### **General fledging behaviour**

In our population of blue tits, all nestlings fledged on the same day in 55% of broods, but fledging of the complete brood could take as long as four days (Fig. 1b). Johnson (2004) found similar patterns for house wrens, whereas in marsh tits over 90% of broods completed fledging within a single day (Nilsson 1990). The reduced fledging asynchrony in marsh tits may be explained by the fact that parents reduced feeding rates during the process of fledging, presumably stimulating fledging (Nilsson 1990), while this was not the case in house wrens or blue tits (Johnson et al. 2004, this study). In any case, our finding that fledging asynchrony is often substantial argues against the view that fledging usually takes place in close succession after it has been initiated ('synchronized nest leaving'; Nilsson 1990; Nilsson and Svensson 1993; Nilsson and Gårdmark 2001; but see Johnson et al. 2004).

Fledging asynchrony may simply reflect age differences between siblings if it is correlated with hatching asynchrony. Hatching asynchrony also varied greatly among nests (up to four days), but no correlation with fledging asynchrony was found. For example, two of the three broods where young hatched over four days fledged within two hours, whereas in the brood that fledged over a period of four days all young hatched within a single day. On the other hand, hatching asynchrony was related to variation in body size (intra-brood weight range and tarsus range), as would be expected when age differences lead to a head start in growth. However, within-brood variation in body size was not linked to fledging asynchrony. These results clearly indicate that nestling age and size are not the sole determinants of the time of fledging of individual young. Social interactions also play an important role, which is reflected in the observation that fledging events were intercorrelated and fledging took place in bouts. Even in the absence of synchronized nest leaving, the fledging decisions of individual young therefore depended in part on the fledging times of their siblings. This may have two reasons. Either the nest hole is monopolized by one young (Nilsson 1990; Brzęk and Konarzewski 2001; Johnson et al. 2004; Epting and Delotelle 2009), which leads to queuing and a bout of fledging as soon as the nest hole is opened. Alternatively, optimal fledging time will shift with the fledging behaviour of siblings, for instance because the risk of being abandoned increases when many young have already left (see also below).

In our study, most young fledged in the morning (Fig. 1a). This is consistent with results from studies on other cavity-nesting passerines (Lemel 1989; Johnson et al. 2004; but see Nilsson 1990). Early fledging could be the result of an increased hunger level in the morning. Since parents do not feed during the night, hunger levels are expected to be highest early in the day. Hunger could be an important proximate trigger of fledging for two reasons. First, it has been proposed that parents stimulate young to fledge by reducing their feeding rate at the nest ('parental manipulation hypothesis'; e.g. Bustamante and Hiraldo 1988; Michaud and Leonard 2000), which implies a direct relationship between hunger levels and the timing of fledging. However, we did not find a reduction in the per capita feeding rate at the nest after the start of fledging (see also Nilsson and Svensson 1993; Michaud and Leonard 2000; Johnson et al. 2004; but see Nilsson 1990; Grundel 1987). Still, early fledging young may have gained feeding advantages not measured in our study (see below). Second, if the timing of fledging has evolved as a trade-off between the benefits of additional feeds outside of the nest and costs, such as increased predation risk, individual young that optimize their fledging time should leave the nest when additional feeds are most beneficial, which is probably the case when their hunger is greatest. This idea of a trade-off involving nutrition is supported by the

relationship between indices of condition and fledging order found in this and other studies (see below; Järvinen and Ylimaunu 1986; Lemel 1989). Independent of nutritional state and hunger levels, other possible advantages of fledging early in the day are that it corresponds with general circadian activity patterns (Bednekoff and Houston 1994), that parents can locate and care for newly fledged young immediately, and that fledglings can get accustomed to their new environment, improve their flight skills and search for a suitable and safe roosting place for a longer time period before spending the first night outside of the nest (Perrins 1979, p. 162; Johnson et al. 2004).

### **Between-brood variation in fledging behaviour**

Broods showed considerable variation in almost any aspect of fledging behaviour. This is in line with other studies (Zach 1982; Lemel 1989; Johnson et al. 2004) and probably results from the fact that timing of fledging is a complex trait (Fig. 6). We found several parameters that explained fledging order in general and are related to developmental and nutritional state: tarsus length, weight, and relative weight (Tables 1 and 2). However, the importance of these variables for fledging order varied greatly between broods. We were interested to explain this variation and attempted to link it to different levels of inequality and competition within broods, because the clearest patterns are expected when fledging optima of individual young are not overlapping. This is the case when within-brood variation among young is great or competition high (see above). We tested four nest characteristics associated with inequality or competition for their influence on the relationship between weight (a combined measure of developmental and nutritional state) and fledging order: (a) parental care (measured as feeding rate), (b) brood size, (c) presence of extra-pair young in a brood, and (d) inequality among nestlings (estimated as variance in weight and fledging asynchrony).

(a) Parental care. The quality and amount of parental care could be an important determinant of the strength of the pattern found for individual broods. When less food is available, young are expected to invest more energy into monopolizing feeds, leading to increased competition, a reinforcement of differences among young, and decreasing overlap of fledging zones.

(b) Brood size. The effect of increased intra-brood competition when there is little food may be especially pronounced in large broods, because they are more likely to experience food shortage (Leonard et al. 2000). Brood size manipulations are commonly employed to experimentally change the level of intra-brood competition (e.g. Neuenschwander 2003; Nicolaus et al. 2009a). Indeed,

correlational and experimental evidence suggests that begging intensity increases with the number of competitors also in the absence of brood size manipulations (Leonard et al. 2000). Even if there is no effect of brood size on food shortage – when parents fully compensate for brood size in their per capita feeding rates – competition may still be greater in larger broods, probably because escalated begging scrambles are more common when the number of competitors is high (Leonard et al. 2000; Neuenschwander 2003).

(c) Multiple paternity. It has been proposed that competition among nestlings is higher in mixed paternity broods than in broods without extra-pair young (Briskie et al. 1994; Boncoraglio and Saino 2008). Competition is expected to increase with reduced relatedness in the nest, because the fitness benefits of altruistic behaviour among nestlings decrease when the young are less related (Parker et al. 1989; Royle et al. 1999). Additionally, extra-pair young may have certain characteristics, such as increased competitiveness, that distinguish them from their half-siblings (Foerster et al. 2003). Less altruistic behaviour and distinctive nestling characteristics could therefore increase competitive behaviour within the nest. Furthermore, the presence of extra-pair young in a nest may be associated with specific attributes of the nest, of the feeding male or female parent, or of the territory. For example, males that have perceived cuckoldry may reduce their feeding rate (Møller and Birkhead 1993; Dixon et al. 1994; see also Sheldon 2002), males that have promiscuous mates may hold low-quality territories (Rubenstein 2007), or faithful females may invest more into the breeding attempt, because they have attractive social mates (Burley 1986; Johnsen et al. 2005). These attributes may lead to altered inequality or competition among nestlings. Begging intensity (which increases with the level of competition; Leonard et al. 2000) is higher in broods of mixed parentage than in uniform paternity broods (Boncoraglio and Saino 2008), and higher in species with higher levels of extra-pair paternity (Briskie et al. 1994), in line with the idea that intra-brood competition is higher in multiple paternity broods. This also indicates that higher levels of competition in mixed paternity broods may not only increase inequality by redistributing feeds towards superior competitors (Fig. 6), but may also cause a sharp increase in the benefits of fledging because escalated begging scrambles (Royle et al. 1999) are less likely outside of the nest. Taken together, this should reduce the overlap of fledging zones between consecutive young and strengthen patterns found for correlates of fledging order in multiple paternity broods.

(d) Intra-brood inequality. Any effect of parental care, brood size, or paternity status on the strength of the patterns found presumably works via an increase in inequality among nestlings. We therefore also included two more direct measures of offspring inequality in our test: fledging asynchrony and

the variation in weight among the nestlings of a brood. Fledging asynchrony may reflect inequality among nestlings when the time interval between the fledging events of two consecutive young is related to their difference in age, development, or nutritional state. Variance in weight measures the scatter in developmental and/or nutritional state found within a brood.

Of the tested variables only brood size influenced the between-brood variation in the effect of weight on fledging order. Parental care, brood size, and paternity presumably all influence inequality among young via competition. The effect of parental care and paternity may be too indirect to be picked up in the model. However, variance in weight should be a good measure of inequality among nestlings. It is therefore puzzling that brood size is more influential than variance in weight. Within broods, correlates of fledging order differed between the first half and the second half of a brood: effects of weight and tarsus length (developmental and nutritional state) were stronger for late fledging young (Table 3). As we will discuss below, this may reflect the fact that in large broods late fledging young are under pressure to leave the nest as soon as possible to avoid being left behind by the family group. Thus, if developmental and nutritional thresholds constrain fledging for these young, we expect effects of weight and size on fledging order to be more pronounced for large broods. The fact that brood size differences best explain between-brood variation in fledging order may therefore have other underlying causes than inequality and competition.

We also found a trend for nests with higher fledging asynchrony to show steeper robust regression slopes. As outlined above, fledging asynchrony does not show a particularly strong link to inequality among nestlings, partly because fledging occurs in bouts. The influence of fledging asynchrony may be a statistical artefact only: short fledging asynchrony causes greater overlap between fledging zones for individual young, weakening the effect of any correlates of fledging sequence.

### **Within-brood variation in fledging behaviour**

For individual young, the time interval optimal for fledging depends on the trade-off between costs and benefits of fledging. The realization of this trade-off may be shifted through social interactions (e.g. competition) with nest mates and parents, but two characteristics of a nestling are probably influential: developmental state and nutritional state (Fig. 6). We measured these as, respectively, body size (tarsus length at day 14) and body mass (at day 14) corrected for body size (relative weight). We found that body size was an important determinant of fledging order (Tables 1 and 2),

confirming results from other studies (Zach 1982; Lemel 1989; Nilsson 1990; Nilsson and Svensson 1993; Michaud and Leonard 2000; Johnson et al. 2004): large young fledged earlier than small young. Structural size reaching a certain threshold may therefore be crucial for the timing and initiation of fledging ('threshold size hypothesis'; Nilsson 1990; Johnson et al. 2004). This threshold size may vary between individuals, when it reflects an adjustment for composite morphological traits (e.g. wing load). We found that females – despite being smaller and lighter – did not fledge later than males (Table 1, Fig. 3a), and that females fledged early given their size and weight (Table 2). This indicates that the threshold size may be sex specific and lower for females, as would be expected given that the size difference is maintained in adults (Cramp and Perrins 1993). At least in theory, young may fledge much later than the time at which they reach the developmental threshold that makes fledging structurally possible (Freed 1988; Nilsson 1990). From the trade-off perspective, this depends on the costs and benefits associated with staying in versus leaving the nest. The separate analysis of early and late fledglings revealed that body size influences fledging order only among late fledglings (Table 3). It is likely that costs of staying in the nest sharply increase over time for late fledglings. Because many young have already fledged, parents may shift the focus of care to the young outside (Lemel 1989; Nilsson 1990) or even abandon the remaining nestlings altogether. Sooner or later parents will always cease to provide care at the nest, and late fledglings are at a much greater risk to be left behind by the moving family group than early fledglings. Hence, young that are late in the fledging order should fledge as early as possible, that is, as soon as they have passed the developmental threshold necessary for successful fledging. Young early in the fledging order on the other hand, have lower costs of staying and – being alone or in a smaller group – may be more exposed to predation outside of the nest. They can thus be expected to remain in the nest even after reaching the threshold size. Among them, other factors will then determine the order of fledging.

Patterns found for tarsus length were also present for weight (Tables 1 and 2, Fig. 2, Fig. 4). Additionally, weight had effects on fledging order on top of those found for tarsus length (Table 2). Given two similar sized young, the heavier one fledged earlier than the lighter one. A similar effect has been found for different measures of body condition in other studies (Järvinen and Ylimaunu 1986; Lemel 1989). Thus, our results indicate that fledging depends (a) on reaching a threshold size and (b) on the energetic reserves a nestling carries. This may be a consequence of the energetic costs of fledging, such as flight costs and thermoregulation costs. For young in good condition these energetic demands are easier to fulfil (Naef-Daenzer and Gruebler 2008), which reduces the costs of

fledging, shifts the trade-off, and results in earlier optimal fledging times. Note that nutritional benefits of fledging in the form of additional feeds outside the nest are probably lower for young in good condition. Thus, we suggest that additional parental care (if it occurs) does not trigger fledging in young without sufficient nutritional reserves, because the act of fledging itself is an energetically highly demanding process for the nestling. Still, when the nestling has sufficient energy reserves, additional parental care may act as an immediate incentive for the young to finally leave the nest. The probability of fledging can therefore increase with hunger levels, even when it is inversely related to nestling condition, causing fledging events to take place mainly in the morning (see above). Then effects of condition (energy reserves) on fledging would have two aspects: fat and hungry young fledge earliest.

Again, the more detailed analysis revealed that the effect of weight and relative weight on fledging order was different for early fledging young (Table 3, Fig. 4). For early fledglings from broods without extra-pair young the order of fledging was independent of their nutritional state. As discussed earlier, costs of staying in the nest may be greater for late fledging young due to the risk of being abandoned. Hence, young that are late in the fledging order should fledge immediately, if they possess the necessary structural ability and energetic reserves. This would lead to an effect of tarsus length, weight and relative weight on fledging as shown for late young. Early fledglings from broods without extra-pair young, on the other hand, may delay fledging, even if they fulfil all the structural and energetic requirements. In line with the kin selection hypothesis (Freed 1988; Johnson et al. 2004), fully developed young may delay their fledging until less developed siblings are ready to fledge, thereby increasing their inclusive fitness.

In mixed paternity broods, relative weight did influence fledging order also among early fledglings (Table 3), especially among the first two young. In such broods, increased sibling rivalry may lead to higher costs of staying in the nest and shift the trade-off to fledging earlier. Furthermore, increased sibling competition can lead to higher motor activity of young (Brzęk and Konarzewski 2001) and this muscular exercise may be relevant for fledging by practising flight skills and optimizing wing load (Teather 1993; Wright et al. 2006). This is supported by the observation that the nestling period tended to be reduced in multiple paternity broods compared to broods without extra-pair young. Costs of intra-brood competition may be due to escalated begging scrambles (Neuenschwander 2003) or higher motor activity (Brzęk and Konarzewski 2001). Such energetic demands may be pronounced even for top competitors in a brood, making energetic costs and benefits of fledging more important for all nestlings. This may explain why energy reserves (body

condition), but not structural development (tarsus length), determined fledging order in early fledging young from mixed paternity broods, while neither of these factors were important for early fledglings from broods without extra-pair young. Clearly, our results do not support the nestling competition hypothesis (Lemel 1989; Martins 1997; Johnson et al. 2004), which states that when sibling rivalry is strong, one of the weaker competitors fledges first in order to escape competition. Are extra-pair young responsible for the observed differences between broods with and without extra-pair young? Extra-pair young fledged earlier than within-pair young from the same brood (Table 1b, Fig. 3b). However, extra-pair young were also heavier than their within-pair half-sibs and may therefore have fledged earlier simply because they were heavier. Indeed, there was no effect of paternity on fledging order when variation in body size and mass was taken into account (Table 2). Hence, differences in fledging time between within- and extra-pair young are probably related to differences in age rather than to their different genetic background. Our measure of hatching asynchrony correlated with the range in weight (and tarsus length), so size differences between nestlings present at day 14 post-hatch primarily reflected age differences. In a Dutch population of blue tits, extra-pair young were earlier in the laying order (Magrath et al. 2009; see also Krist et al. 2005; Johnson et al. 2009), which also led to earlier hatching. In our study, extra-pair young may also have hatched earlier and this developmental head start may have caused earlier fledging. Differences in fledging behaviour between broods with and without extra-pair young in our study were not caused by a different behaviour of the extra-pair young per se, because they remained when extra-pair young were removed from the comparison. These differences may be mediated by the behaviour of the male or female or via social interactions among the young. Our analysis of robust regression slopes revealed that between-brood variation in fledging behaviour was best explained by brood size and not by other factors related to the level of intra-brood competition, such as extra-pair paternity. As discussed earlier, this effect of brood size may be a result not so much of competition than of the fact that young in large broods face a greater risk of being left behind by their parents. The pattern found for late fledging young may thus be especially relevant for large broods, causing most of the variation present between broods. A high level of competition in broods with extra-pair young could be more important for the fine-scale timing of fledging within broods, which is lost when patterns are summarized in one variable for the between-brood comparisons.



### **Parental response to fledging**

Although males that are cuckolded or females that have extra-pair young may differ in attributes related to parental care or may modify their care (see above), we did not find differences in feeding behaviour between broods with and without extra-pair young (Fig. 5). Furthermore, there were no obvious differences in feeding behaviour of males and females: in most cases both parents continued to feed at the box after fledging had started (Fig. 5). Thus, parents do not generally split up feeding tasks so that one (e.g. the female) is responsible for the feeding of remaining nestlings whereas the other (e.g. the male) cares for the fledglings.

The parental manipulation hypothesis states that parents stimulate their young to leave the nest, for instance by reducing their feeding rate at the nest (Lemel 1989; Johnson et al. 2004). If this is the case, one would expect lower feeding rates during the fledging process than in the days prior to the start of fledging. In our population, absolute feeding rate at the nest decreased after the first young had fledged. However, per capita feeding rate was not different between the fledging period and the days prior to fledging. Thus, our measure of feeding rate indicates that parents did not reduce the feeding of young remaining in the nest, but simply adjusted their feeding rate to the number of young remaining in the nest. Note, however, that our automated recordings of parental visits do not allow us to differentiate between visits to the nest with and without food. Similarly, it is impossible to control for the size or quality of food brought during a visit. Hence, it is still possible that parents reduced their feeding rate, but continued to visit the nest at the same rate, for instance to induce young to fledge by vocal and optical communication (Meinertzhagen 1954; Rowan 1955; Bustamante and Hiraldo 1988; Michaud and Leonard 2000). In a study of house wrens, visits to the nest without food were rare (2% of visits, Johnson et al. 2004, suggesting that measurements of feeding rate based on visits alone are reliable, at least for single loaders like the blue tit (Cramp and Perrins 1993). Another possibility is that parents do not reduce feeding of nestlings, but that fledglings still benefit from increased parental care. This would be the case if parents increase their feeding rate of fledged young, for example because of reduced foraging costs (fledglings may stay closer to the foraging parents, which would reduce the length of feeding trips). Preferential feeding of particular young and brood division between the parents have been observed in several studies (Lessells 2002, Dickens and Hartley 2007). Such behaviour may also cause advantages for fledged young, for instance when fledglings are always first in row to be fed (Lemel 1989).

Reductions in feeding rate during the fledging process were found in some studies (Grundel 1987; Nilsson 1990), but not in others (Nilsson and Svensson 1993; Michaud and Leonard 2000; Johnson

et al. 2004). Thus, parental control of fledging may vary between species or populations. Our results suggest that it does not generally occur in blue tits, but it would be interesting to examine parental manipulation in more detail in future studies. For instance, its role may vary in relation to differences between nests (e.g. the presence of extra-pair young or fledging asynchrony) or between years (e.g. depending on food availability).

### ***Conclusion***

We found that in our blue tit population both developmental and nutritional state of an individual influenced its fledging decision, which may reflect structural and energetic constraints on fledging. Extra-pair young fledged earlier, but this is probably because they were older, which may in turn result from being earlier in the laying order. We also found differences in fledging behaviour among broods with and without extra-pair young, indicating a role of intra-brood competition. Overall, our results suggest that nestlings adjust their fledging to their intrinsic state, to the time of day, and to the behaviour of their nest mates, while we did not find evidence that parents controlled the fledging of their young.

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## APPENDIX

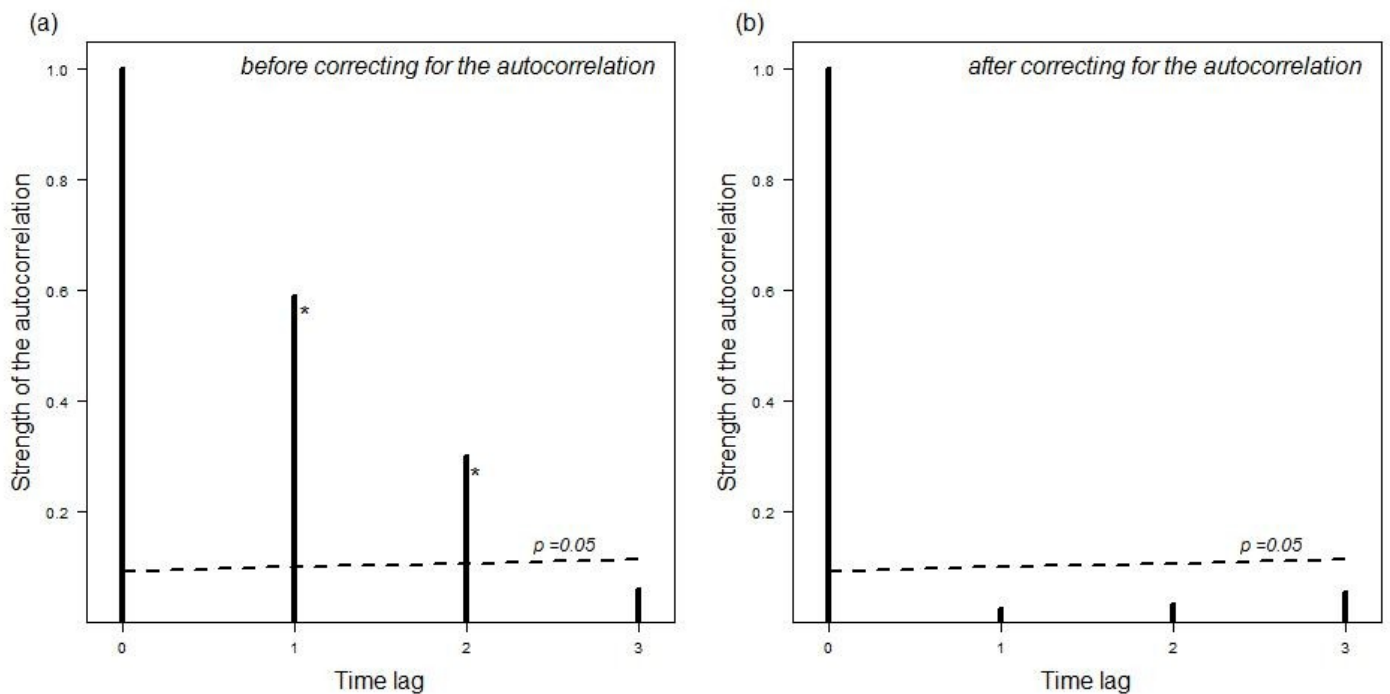
### ***The autocorrelation structure***

We found that the fledging time of a nestling does not only depend on its own characteristics (such as its body mass). It is also related to the timing of fledging events that occurred before: the residuals of fledging events from one brood are correlated in time. This is called an autocorrelation and it is a frequent problem of time-series analyses (Pinheiro and Bates 2000, pp.226-249). In particular, repeated measures of the same individual at different time points are usually not independent data. Not taking into account an existing autocorrelation can therefore lead to effects of pseudo-replication, and overestimation of the t-value. Too much faith will then be placed into the model. Although no repeated measures were used in our analyses (every young was recorded once at the time when it fledged), there is an intra-group dependence in time among the data points of our study, since the fledging events of individual young from one brood (grouping factor) are correlated. Therefore, a model which corrects for the autocorrelation structure has to be used when analysing the data on fledging behaviour.

Time-series autocorrelation models are a one-dimensional counterpart to the two-dimensional spatial autocorrelations (Pinheiro and Bates 2000, pp.226-249). They mostly use discrete time intervals (such as days), to calculate the correlation between observations a certain number of time intervals (or 'lags') apart. In our case, this model for discrete times was adjusted for continuous times, since fledging did not take place in fixed intervals. As can be seen in Fig. A1 a), there was a two-level autocorrelation, and an observation at a certain time (lag 0) influenced the upcoming two observations (lag 1 and lag 2) positively. This means that the fledging of a nestling (lag 0) speeds up fledging of the next two nestlings (lag 1 and lag 2), causing fledging bouts of three. The lag-0-autocorrelation shows a complete dependence, as it is the correlation of an observation with itself. Once the type and strength of the autocorrelation is known, it can be included into the model, which then attaches a weight to each observation, making autocorrelated events (e.g. young that fledge in bouts) less influential than events that are not autocorrelated (e.g. young that fledge outside of bouts). The fitted model includes the autocorrelation coefficient, phi ( $\phi=0.83$  in our model), which ranges between 0 (no autocorrelation) and 1 (complete autocorrelation). Also, after correction, no correlation between lags remains (Fig. A1 b).

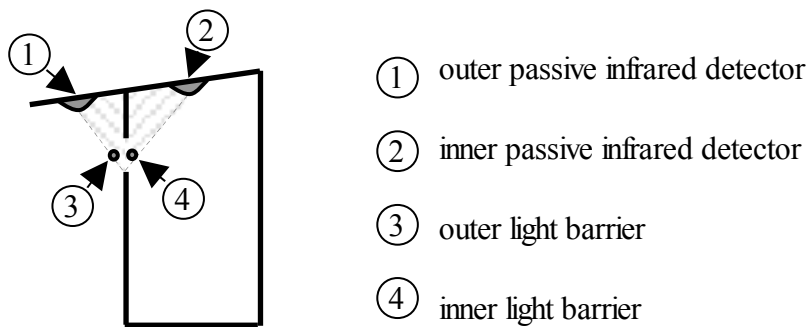
The importance of the autocorrelation structure is also demonstrated in the models of table 1. They show the effects of different variables (size, mass, sex, and paternity status) on fledging order, either

taking into account the autocorrelation structure (a) or not (b). Higher t-values for body size and mass in the uncorrected models (b) suggest an influence of pseudo-replication. This may also be the reason why an effect of paternity status on fledging order is observed only in table 1 (b). Contrary to the other three variables, the t-value for sex increased when the autocorrelation structure was taken into account. This could arise, for instance, if single nestlings that lag behind in the fledging order are more often male than female. When correcting for the autocorrelation single fledging young receive more weight than young fledging in bouts. Thus, any effect of males fledging later than females would be strengthened, if males fledge both later and outside of bouts. Still, there is no effect of sex on fledging order in either the model with or without the autocorrelation structure.



**Fig. A1: The autocorrelation structure.** The strength of the autocorrelation for lag 0 is always 1, since an event is always completely correlated with itself. **(a)** Lag 1 and 2 autocorrelations are significant. This means that the fledging event on one young is correlated with the next two fledging events. **(b)** No autocorrelation remains after correction.

Automatic recording system



**Fig. A2. Setup of passive infra-red detectors and light barriers in nest boxes equipped with the automated recording system.** With this setup we are able to detect which bird enters or leaves the nest at a particular date and time. The transponder reader provides information about the ID of the bird passing through the hole, while the order in which the light barriers and the infra-red detectors are triggered give information about the direction in which the bird is moving. Date and time are supplied by an integrated real-time clock.

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