

# Patterns of female nest attendance and male feeding throughout the incubation period in Blue Tits *Cyanistes caeruleus*

GIULIA BAMBINI, EMMI SCHLICHT & BART KEMPENAERS\* *Department of Behavioural Ecology and Evolutionary Genetics, Max Planck Institute for Ornithology, Eberhard-Gwinner-Straße, 82319 Seewiesen, Germany*

Most bird species exhibit biparental care, but the type of care provided by each sex may differ substantially. In particular, during the incubation phase in passerines, females perform most or all of the incubation, while the male cares for the brood indirectly by feeding the female. However, detailed descriptions of this male investment during the incubation period are missing. Here, we quantitatively describe female nest attendance and male incubation feeding throughout the ~ 14-day incubation period in a population of Eurasian Blue Tits *Cyanistes caeruleus* breeding in nestboxes. Males and females progressively increased their daily activity at the nest over the incubation period. The amount of day-time incubation, measured as the proportion of the active day (time interval between first nestbox exit in the morning and last entry in the evening) a female spent inside the nestbox, varied between 52 and 60% with an average of 55% per day. The frequency of male incubation feeding varied between 0 and 74 times per day with an average of 12 feeds per day. Both male feeding rate and female nest attendance were highest in the morning and declined rapidly throughout the day. Females were more likely to be off the nest during the warmest periods (15–21 °C), as expected based on thermal needs of the developing embryos, but also during the coldest periods (2–5 °C), presumably due to the energetic needs of the female. This was despite the fact that males fed their females more often at the nest when ambient temperatures were low. Females that received more feeds incubated more and their off-nest bouts were shorter after a feed. The observed variation in female incubation and in male feeding rate was not linked to individual age or to variation in measures of reproductive success. However, direct observations showed that in some pairs a substantial amount of feeding by males occurred outside the nestbox. This suggests that the true male investment might have been underestimated, here and in previous studies.

**Keywords:** mate provisioning, parental care, parental investment, sex roles, uniparental incubator.

Most bird species show biparental care, but the type of care provided often differs between males and females (Webb *et al.* 2010). In particular, sex role differentiation exists in ‘uniparental incubators’, where females incubate alone, while males may provide ‘nutritional assistance’ (Matysioková & Remeš 2010). Incubation is energetically costly (Tinbergen & Williams 2002) and food availability is a key limiting factor for all stages of avian

reproduction, including incubation (Tinbergen & Dietz 1994). Incubating females must therefore trade-off their own energetic needs with the thermal needs of developing embryos (Bulla *et al.* 2015) and these opposing demands constrain both daily nest attendance (the proportion of time a bird incubates) and time spent foraging. Male feeding of his incubating female may alleviate the trade-off experienced by females (‘Nutrition hypothesis’, von Haartman 1958).

Among songbird species with uniparental incubation, total nest attendance is higher in species

\*Corresponding author.

Email: b.kempenaers@orn.mpg.de

showing higher levels of male incubation feeding (Matysioková & Remeš 2014). Within species, this relationship is less clear. While experimental food supplementation can increase female nest attendance (Smith *et al.* 1989, Pearse *et al.* 2004, Chalfoun & Martin 2007, Boucaud *et al.* 2016), female nest attendance is not generally associated with the amount of male incubation feeding (for review, see Table S1). Testing this relationship is also not straightforward. Males cannot feed females on the nest unless they are incubating and male feeding rates may be correlated with female attendance simply for this reason. This type of non-functional association cannot be excluded for most studies that found a positive relationship between male incubation feeding and female nest attendance (Matysioková *et al.* 2011, Table S1). Data on the fitness consequences of variation in male incubation feeding or female nest attendance, such as effects on hatching success or offspring traits, are equally mixed (Table S1). In addition, any such association remains difficult to interpret, because parents that perform well during the incubation phase may be superior also in other respects (e.g. territory quality, foraging efficiency, egg quality, quality of chick-rearing). Variation in incubation feeding and incubation attendance has generally been studied in relation to individual-specific traits (primarily age) and environmental traits. While relationships with age have received mixed support (reviewed in Table S2), variation in environmental conditions, such as ambient temperature, habitat quality or predation risk, often explains incubation behaviour in both males and females (Table S2).

A problem with all previous studies is that incubation feeding and nest attendance were only studied during part of the incubation period and part of the day (Table S1). Such a 'snapshot' may not be representative if individuals change their behaviour over time. Here, we studied a population of the Eurasian Blue Tit *Cyanistes caeruleus*, a species with female-only incubation and male incubation feeding (Royama 1966), over the whole incubation period. A previous study of this species (Amininasab *et al.* 2016) estimated male feeding rate based on 8-h recordings inside the nestbox on one specific day (day 6 after incubation onset). We used radio-frequency identification (RFID) technology to record automatically every nestbox visit of each pair member during the entire breeding season.

We quantified the behaviour of both parents (female nest attendance and male feeding rate) and compare our results with patterns described previously. Specifically, we (1) investigated the effects of individual-specific traits (age and clutch size) and environmental factors (precipitation and ambient temperature) on variation in parental behaviour during incubation, (2) considered consequences of between-individual variation in female nest attendance and male feeding rate for breeding success and (3) describe how male feeding rate during incubation relates to female nest attendance at different temporal scales. For a subset of pairs, we directly observed and video-recorded Blue Tits in their nestbox and in the immediate surroundings of the box. We used these data (1) to validate the information obtained from the RFID-based recordings, (2) to confirm that male visits to the nestbox are actual feeding visits and (3) to assess how often males feed their female outside the nestbox.

## METHODS

### Study area and species

We studied a population of Blue Tits in a 40-ha oak-rich plot within a mixed-deciduous forest close to Landsberg am Lech, Germany ('Westerholz', 48°08'26"N, 10°53'29"E) during the breeding seasons of 2013–16. The study area has contained 277 nestboxes since 2007. Blue Tits are small (c. 10–12 g) cavity-nesting passerines that are socially monogamous with occasional social polygyny. In our population, the mean clutch size is nine eggs (Table S3). Females usually initiate incubation soon after clutch completion, but they may also start incubating before the clutch is complete or delay incubation for more than a week after clutch completion (Cramp *et al.* 1993, Glutz von Blotzheim & Bauer 1993, this study).

### Field procedures

Each year we monitored breeding activity in all nestboxes from early March until early June. We visited every nestbox at least weekly and recorded the stage of nest-building. When nests were complete (lining), we checked them daily until the start of egg-laying. We recorded clutch size and determined the start and end of hatching based on daily nest checks starting 2 days before the

expected hatch date. Thus, the assigned hatch date is at most 1 day late (when eggs hatched after a nest was checked on a given day). After hatching was complete, we checked nests at least weekly to determine fledging success. All parents included in this study were captured before the start of the breeding season, and ringed, measured, sexed and aged (yearling or older). We also took a ~30- $\mu$ L blood sample and implanted a transponder under the skin on the back. We ringed nestlings and took a blood sample when they were 13–14 days old. For a more detailed description of field procedures and ethical implications, see Schlicht *et al.* (2012, 2015). Permits were obtained from the Bavarian government and the Bavarian regional office for forestry (LWF).

We monitored bird activity at all nestboxes using a transponder-based system. Each nestbox is permanently equipped with an RFID antenna installed inside the front panel around the nest hole and with two light barriers (one on the outside of the box and one on the inside). Each Blue Tit carrying a transponder is automatically recorded when it passes through the nest-hole (bird identity, date and time and box entry or exit based on information from the light barriers). For this study, we only included data from active nestboxes where both pair members carried a transponder during the entire incubation period. Data on hourly precipitation and ambient temperatures were obtained from a nearby weather station (Methods S1 in Appendix S1). We investigated whether the presence of extra-pair young (young not sired by the male that provisioned the female and the offspring) influenced incubation behaviour (for details on paternity analysis, see Methods S2 in Appendix S1).

### Direct behavioural observations and video recordings

In 2016, we performed direct observations and made video recordings inside and outside the nestbox during the incubation period at 32 nests. Because diurnal nest attendance increased gradually from 'partial' to 'full' incubation (see Results), we checked female presence at the nest based on the RFID data. We chose nestboxes for recording and observation such that we obtained data evenly covering the early, middle and late period of full incubation (Table S2). At these nestboxes, we installed an infra-red camera (CCD IR board

camera module, Conrad Electronic SE) on the inside of the lid. We also put up a camouflaged hide about 15 m from the nestbox. At nine nests, we additionally put a tripod with a hard-disk camcorder (GZ – MG77E, JVC) inside the hide, focused on the entrance hole with a field of view covering the front of the nestbox.

On the day following camera installation, one of us (G.B.) performed direct observations from the hide ( $n = 28$  nests) or started the outside video recorder ( $n = 9$  nests of which 5 were also observed) from 06:00 to 09:00 h or from 10:00 to 13:00 h. We started observations as soon as birds did not show any sign of alarm. We recorded all events at the nest and all behaviours of one or both pair members outside the nestbox that could be observed from the hide. We particularly focused on males feeding their female outside the nestbox.

### Data compilation

From the videos inside the box ( $n = 29$  nests, three cameras malfunctioned), we discarded the first 30 min of recordings after camera installation because all birds returned to the box and resumed normal behaviour within that period. We extracted the times of all entries and exits, together with bird identity and noted whether the male brought food. From the direct observations, we additionally noted whenever the male fed the female outside the nestbox. From the video recordings outside the nestbox, we additionally extracted whether the male vocalized before entering the nestbox. When multiple sources of information were available, we used data based on the lid cameras, because these were the most accurate. Data from direct observations and from video recordings outside and inside the nestbox closely matched each other (Methods S3 in Appendix S1).

From the transponder-based data we removed the nights for all analyses because, during the night, incubating females always roosted inside the nestbox. We defined 'active time' as the period between the first and last registration of a female at the nestbox on a given day. Because males visited the nestbox almost exclusively within the female's active time (on 1689 of 1694 days), active time best represents the time used by males for feeding. We measured incubation as female presence in the nestbox during the incubation

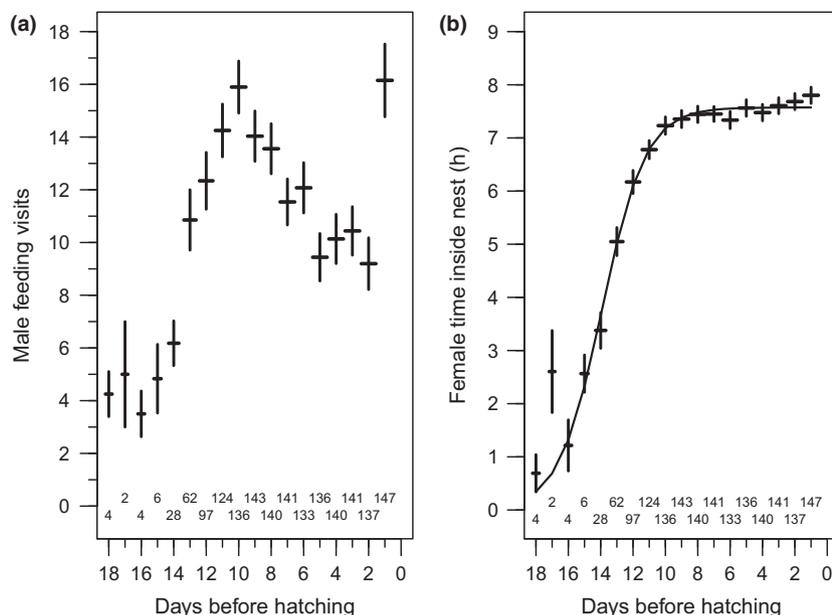
period (Martin 2002) because earlier work showed that the latter coincides with constant high egg temperatures (Haftorn & Reinertsen 1985, Matysioková & Remeš 2010, Vedder *et al.* 2012, Bueno-Enciso *et al.* 2017a).

Except when examining the seasonal progression of incubation (Fig. 1), we only included days of full incubation in the analysis. During full incubation, females usually spent about half of their active time on the nest each day. However, some females showed large variation in attendance between days, even a few days before hatching (see Results). The start of full incubation was therefore defined arbitrarily as the first of two consecutive days during which the female spent at least 4 h in the nestbox during its active time. In total, we collected data for 1632 days of full incubation at 171 nests (average number of days per nest:  $10 \pm 3$  sd). To describe the seasonal progression of incubation behaviour we also included all days after clutch completion and before the start of full incubation, as long as data were available for the complete day (89 additional days). Hereafter, incubation or incubation period refer to days of full incubation, except when stated otherwise.

## Statistical analyses

Female investment in incubation was measured as the proportion of active time spent on the nest (*nest attendance*). Using alternative measurements gave qualitatively identical results (see Methods S4 in Appendix S1). Male incubation behaviour was estimated as the number of male visits over the active time of the female (*feeding visit rate*). We also performed analyses using the number of visits across the time the female was on the nest (*feeding visit intensity*). Because results were qualitatively identical, we only present the results based on visit rate. The frequency of male feeding sharply increased the day before hatching. Because the assigned hatch day can be 1 day late (see above), this could be an artefact: the sudden increase may represent the start of nestling feeding. Hence, we performed all tests excluding the day before hatching (including it did not affect the conclusions).

Statistical analyses were performed with R version 3.2.2 (R Core Team 2015). Female presence in the nestbox over the incubation period showed a sigmoid pattern. We therefore tested for a logistic relationship of the form



**Figure 1.** (a) Number of male feeding visits to the nest (total number per day) in relation to day relative to hatching (=day 0). The peak on the day before hatching may be the result of imprecision in the assignment of hatching date (see Methods). (b) Female time on the nest (total time, non-active time excluded) in relation to day relative to hatching. Shown are means (horizontal bars) with standard errors (whiskers). In (b) the line shows the fitted logistic curve (see Methods). Numbers above the x-axis denote sample size (number of males or females; total  $n = 1721$  nest-days from 171 nests). Sample sizes differ because of variation in the number of days of full incubation and the number of days before incubation available for each nest.

$$I = \frac{a}{e^{(-b(D-c))}}$$

where  $I$  is the time the female spent incubating on day  $D$ , and  $D$  is the number of days before hatching, by calculating non-linear least-squares estimates for the parameters  $a$ ,  $b$  and  $c$  using the 'nls'-function in R.

We used linear (LMMs) or generalized linear mixed models (GLMMs: R-packages lme4, Bates *et al.* 2014, and nlme, Pinheiro *et al.* 2015) to perform analyses at four levels: data compiled for each nest over the entire incubation period (nest-wise models N1–7), data separated by days (daily models D1–2) or by hours (hourly models H1–3) and data based on single events (event-based model E1). Model details are summarized in Table S4. We checked assumptions of normality and homogeneity of variance by visual inspection of the residuals. Confidence intervals (95% CI) shown in figures were calculated using the package 'effects' (following Fox 2003). We report either estimates with 95% CI or mean  $\pm$  sd.  $P$ -values for GLMMs were obtained using  $t$ -tests with Satterthwaite approximations to calculate degrees of freedom (package lmerTest; Kuznetsova *et al.* 2016). Daily and hourly analyses (models D1–2 and H1–3) include data from successive days and hours. To account for non-independence of these data points, we included a temporal autocorrelation structure in these models (autoregressive-moving average; package nlme), following the methods described in Pinheiro and Bates (2000, p. 226–249). Our dataset includes multiple breeding events of some individuals or pairs in successive years (females:  $n = 109$ , 28 and 2 over 1, 2 and 3 years, respectively; males:  $n = 111$ , 27 and 2 over 1, 2 and 3 years, respectively; pairs:  $n = 155$  and 8 over 1 and 2 years, respectively). Thus, in the nest-wise analyses, we included male, female or pair identity as random effects. In daily, hourly and event-based analyses, each male, female or pair was used only once (the last nesting attempt for each,  $n = 120$  nests, 1061 nest-day combinations, 12 782 nest-day-hour combinations). In nest-wise, daily and hourly analyses, we also included year as a random factor.

Female nest attendance and male incubation feeding rate may correlate simply because females with low nest attendance cannot be visited as much by their mate (non-functional relationship, Fig. S1a,b). Thus, we need to correct for the time

the female is absent from the nest. In principle, male feeding visit intensity would serve this purpose (Matysioková *et al.* 2011). However, female attentive time is part of this variable (the denominator) and relating it to female attendance is therefore statistically problematic (Fig. S1e). An operationally equivalent test that solves this issue checks for a square-root relationship between female nest attendance and male feeding visit rate (Fig. S1c,d). We therefore included male feeding rate as linear and as square-root term in these tests (models N2, D2, using 'poly'-function in R).

When analysing effects of ambient temperature on daily male feeding rate and female nest attendance (models D1–2), temperature was used as a quadratic term (using 'poly'-function), because preliminary analyses indicated a non-linear relationship (see also Conway & Martin 2000a, Camfield & Martin 2009).

In the event-wise analysis (model E1), we tested whether a male feeding visit during an incubation bout shortened the duration of the succeeding incubation recess (exit duration), assuming that a male feeding visit would reduce the female's need to forage and thus allow her to return to the nest faster. To do this, we considered a sequence of two incubation bouts and recesses: on1  $\rightarrow$  off1  $\rightarrow$  on2  $\rightarrow$  off2. We coded two variables: male feed during the first on-bout (on1-feed: yes/no) and male feed during the second on-bout (on2-feed: yes/no). As response variable we calculated the difference in the two exit durations ( $\Delta$  exit duration = off2-duration – off1-duration). If a male feeding visit reduces the consecutive female exit duration,  $\Delta$  exit duration should be positive when the male feeds during the first but not during the second incubation bout, and negative when the male feeds during the second but not during the first incubation bout. If the male feeds during neither incubation bout or during both incubation bouts,  $\Delta$  exit duration should be zero. Comparing two successive female exits with or without a preceding male feeding visit allows us to control for temporal variation in exit duration, for example due to changing environmental conditions. The distribution of the response variable ( $\Delta$  exit duration) was roughly symmetrical around zero, but with a tail of very long exit durations (up to 8 h, see Fig. S2). Here, we restricted the data to  $\Delta$  exit durations between  $-12$  and  $12$  min ( $n = 16\,435$ , 70% of all data, Fig. S2). We only included each incubation recess once, either as off1 or as off2

( $n = 8217$ ). To verify our results, we also conducted the complementary test where the off1-intervals from the first model became off2-intervals and vice versa ( $n = 8218$ ). Results were similar and we only report the first test. Note that male visits may allow females not only to shorten incubation recesses but also to lengthen incubation bouts. However, this is difficult to test. Whether male visits should lengthen the bout during which they occur depends on when the visits occur during the bout. This precludes using the type of pairwise comparison described above.

## RESULTS

### Male incubation feeding

#### *General description*

Direct observations and video recordings showed that males brought food during all their nestbox visits throughout the incubation period. In only two of 359 cases was it unclear whether the female accepted the food or whether the male left with it (Table S5). During most feeding events, males vocalized before feeding their incubating female (Table S5). The frequency of incubation feeding inside the nestbox varied strongly between males and between days in the incubation period (for examples see Figs S3 & S4). Across the entire incubation period, males fed their incubating female on average 119 times ( $sd = 84$ , range 2–390 times).

#### *Feeding in the nestbox: seasonal and daily variation*

The median time of the first daily feed by males was 07:13 ( $sd = 139$  min; range 05:42–19:40) or 66 min after the female's first exit in the morning (range –26 to 816 min; there was only one instance of a male visit before his female's first exit). The median time of the last daily feed by males was 17:15 ( $sd = 196$  min; range 06:16–20:10) or 129 min before the female's last entry in the evening (range –35 to 828 min; there were four instances of a male visit performed after his female's last entry). On average, males fed their incubating females  $12 \pm 12$  times per day (range 0–74,  $n = 171$  nests). Daily feeding rate increased progressively up to 10 days before hatching (Fig. 1a), coinciding with the increase in female incubation (Fig. 1b). After that, the daily visit rate declined slowly (Fig. 1a, Table S6). Male feeding visits were most frequent in the morning and

declined rapidly throughout the day (Fig. 2a, Table S7). This daily decline was not present for feeding visit intensity (the frequency of male feeds measured across the time the female was actually in the nestbox; Table S7), suggesting that male feeding visits may simply follow patterns of female nest attendance.

#### *Feeding outside the nestbox*

Direct observations showed that some males also fed their female while she was off the nest (range 0–1.5 events/h,  $n = 26$  nests). This behaviour was highly variable among pairs: for a third, such events were never observed, whereas for six nests, males exclusively fed their mate outside the nestbox (Fig. S5). Off-nest feeds were preceded by a male vocalization in 16 of 26 cases (62%). The male vocalized when the female was still in the box, then the female left the nestbox and flew towards the male. Based on the outside video recordings, 29% of 171 male vocalizations were followed by a female exit. Females did not return to the nest faster when the male had been observed feeding her outside the box (Fig. S6). We observed 21 cases where the female flew off together with the male after he approached the nestbox (vocalizing in 10 cases), mostly after a feed inside ( $n = 9$ ) or outside the nestbox ( $n = 6$ ).

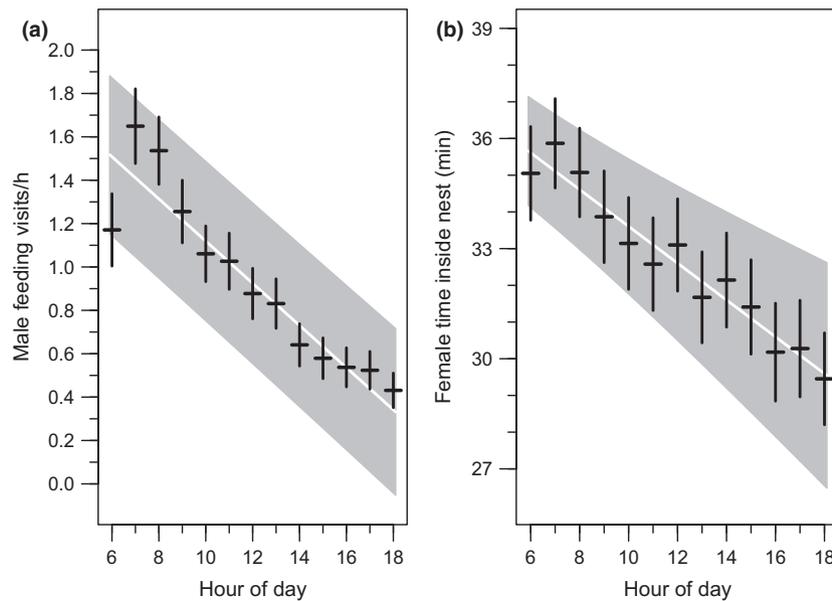
#### *Causes and consequences of variation in male feeding rate*

The observed variation in male feeding rate (inside the nestbox) across the entire incubation period did not depend on clutch size, male or female age, or paternity loss or gain (Table 1). Daily nest visit rate depended on ambient temperature (quadratic effect; Fig. 3a, Table 2). Specifically, male feeding rate stayed more or less constant at lower mean daily temperatures, but then decreased with increasing mean daily temperature. Males also reduced feeding with increasing rainfall, both on a daily and on an hourly basis (Fig. 3b, Table 2 and Table S7). The frequency of male feeding visits to the nestbox across the incubation period did not affect the duration of the incubation period or any of the four measures of reproductive success (Table S8).

### Female nest attendance

#### *Seasonal and daily variation*

Full incubation started 1–11 days after clutch completion (mean  $\pm$   $sd = 4 \pm 3$ ), lasted 8–14 days



**Figure 2.** (a) Frequency of male feeding visits to the nest (total number per hour) in relation to time of day. (b) Female time on the nest (in minutes) for each hour of the day (non-active time excluded). Shown are means (horizontal bars) with standard errors (whiskers) and model fits (white lines) with 95% CI (shading). See Table S6 for model output.  $n = 12\,782$  nest-day-hour combinations from 120 nests.

(mean  $\pm$  sd =  $12 \pm 1$  days) and there were 12–24 days (mean  $\pm$  sd =  $16 \pm 3$  days) between clutch completion and hatching. Across all females, time spent in the nestbox closely followed a logistic curve until the onset of full incubation around 11 days before hatching (Fig. 1b;  $a = 7.8$ , 95% CI 7.7–8.0;  $b = -0.7$ , 95% CI  $-0.9$  to  $-0.6$ ;  $c = 13.7$ , 95% CI 13.4–14.0; all significantly different from zero:  $P < 0.001$ ; see Methods). After day  $-11$ , female nest attendance increased slowly until hatching (Fig. 1b, Table S6). Patterns for individual females varied substantially (examples in Figs S3 & S4).

During the period of full incubation, the median time for the first exit was 06:05 (sd = 16 min; range 05:20–07:00) or 49 min after dawn (range  $-5$  to 118 min) and the median time for the last entry was 19:26 (sd = 27 min; range 17:41–20:32) or 105 min before dusk (range 38–218 min). In sum, females were active on average  $13.2 \pm 0.4$  h/day (range 12–14 h/day), of which they spent on average  $7.2 \pm 1.4$  h/day on the nest (range 1.5–12.3 h/day). Across the entire period of full incubation, females spent approximately 60% of the day inside the nest (mean =  $59 \pm 8\%$ , range 43–80%,  $n = 75$  nests; nests were only included if data from all days of incubation were available). These

values are based on the automated recordings (RFID data), but direct observations or video recordings inside the nestbox gave similar estimates: females spent on average  $62 \pm 15\%$  of the day on the nest (range 21–85%,  $n = 28$  females). Females also showed strong variation in the way they partitioned incubation within days (Fig. S3). Overall, however, female nest attendance declined throughout the day (Fig. 2b, Table S7). Females left their nestbox on average  $2.0 \pm 0.6$  times per hour and median exit duration was 7 min (mean =  $15 \pm 25$  min, range 10 s to 8.5 h; Fig. S7).

#### *Causes and consequences of variation in female nest attendance*

Female nest attendance across the entire incubation period did not depend on clutch size or on female or male age (Table 1). Daily female nest attendance was related to ambient temperature, with the highest nest attendance on days with intermediate temperatures (Fig. 3c, Table 2), and increased slowly throughout the period of full incubation (Fig. 1b, Table 2 and Table S6). Rainfall had no effect on female nest attendance (Fig. 3d, Table 2 and Table S7). Female nest attendance across the incubation period did not

**Table 1.** Potential causes of variation in male feeding visit rate (number of feeding visits per hour of female active time) and female nest attendance (proportion of active time spent inside the nestbox) during incubation. Male visit rate and female nest attendance are calculated across the period of full incubation and each nest represents one data point ( $n = 171$ ). Shown are results from linear mixed models with male, female and pair identity as well as year as random factors. In the second model, removal of the non-significant square-root term gave qualitatively similar results. Paternity gain: whether a male sired extra-pair offspring. Paternity loss: whether an extra-pair male sired offspring in the male's nest.

Fixed effect	Estimate	95% CI	<i>t</i>	<i>P</i>
Response: Male feeding visit rate <sup>a</sup>				
Intercept	1.1	0.3–1.7		
Clutch size	0.002	–0.05 to 0.06	0.1	0.93
Male age	–0.14	–0.33 to 0.08	–1.5	0.13
Female age	0.08	–0.08 to 0.3	0.9	0.38
Paternity gain (yes/no)	–0.15	–0.3 to 0.03	–1.7	0.09
Paternity loss (yes/no)	0.007	–0.2 to 0.2	0.1	0.95
Response: Female nest attendance <sup>b</sup>				
Intercept	0.60	0.46–0.72		
Clutch size	–0.001	–0.01 to 0.01	–0.2	0.84
Male age	0.003	–0.03 to 0.04	0.2	0.81
Female age	–0.004	–0.03 to 0.03	–0.3	0.80
Male feeding visit rate	0.02	–0.15 to 0.21	1.1	0.25
$\sqrt{(\text{male feeding visit rate})}$	0.11	–0.08 to 0.30	0.3	0.79

<sup>a</sup>Variance explained by random effects: pair ID = 21%; male ID = 27%; female ID = 13%; year = 13%. <sup>b</sup>Variance explained by random effects: pair ID < 0.1%; male ID < 0.1%; female ID = 31%; year = 30%.

affect the duration of the incubation period or any of the four measures of reproductive success (Table S8).

### Relationship between male incubation feeding rate and female nest attendance

Female nest attendance across the complete incubation period was unrelated to her partner's feeding visit rate (Table 1). However, male feeding visit rate did explain variation in daily female nest attendance (Table 2). Male feeding visit rate increased faster than expected if it had followed female nest attendance (indicated by the significant square-root term in Table 2; Fig. 4). High female nest attendance was thus associated with a higher frequency of male feeding during the time when the female was in the box (male feeding

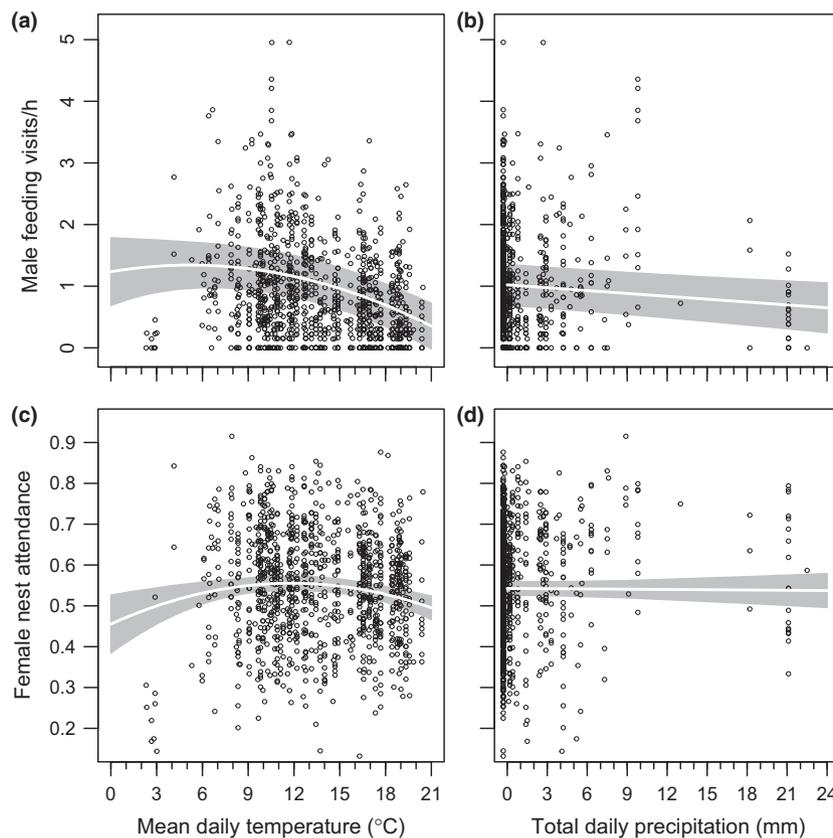
visit intensity), suggesting a functional relationship between male and female behaviour (Fig. S1). On the time scale of single events, if the male fed his incubating female in the nestbox, her subsequent exit duration was on average about 20 s shorter than when the male did not feed her (Fig. 5, Table S9). This suggests that increased male feeding can lead to higher female nest attentiveness, at least in the short-term.

## DISCUSSION

### Male feeding behaviour during the incubation period

We examined patterns of male nest visits and female nest attendance during the entire incubation period in a population of Blue Tits. Direct observations showed that males visiting the nest during incubation always bring food to the incubating female, confirming another recent study of Blue Tits (Amininasab *et al.* 2017). In contrast to previous studies (Hinde 1952, Nilsson & Smith 1988, Pearse *et al.* 2004, Klatt *et al.* 2008, Lloyd *et al.* 2009, Matysioková & Remeš 2010, Amininasab *et al.* 2016, but see Gibb 1950), we observed that for most pairs, a substantial amount (up to 100%) of male feeds of females occurred outside the nestbox (Table S5). Male incubation feeding away from the nest may be more frequent than hitherto assumed because most previous studies collected data in such a way that only feeding events occurring at the nest or directly next to it could be detected (Tables S1 & S10). We also observed considerable variation among pairs in the amount of feeding outside the nestbox. This may be an observational artefact related to varying vegetation density. However, most males were either observed feeding at or away from the nest (Fig. S5), suggesting genuine differences between pairs. Such differences may be partly determined by female behaviour in response to male vocalizations.

Male Blue Tits usually vocalized just before incubation feeding took place and sometimes the female left the box in response and was fed outside. If the female did not leave, the male typically entered with the food. When the female left the box, this was often preceded by a male vocalization. If the female was not fed, she sometimes flew off together with the male, perhaps being led to foraging spots (*cf.* Dixon 1949, p. 123). Notes on



**Figure 3.** Relationship between environmental variables (a, c: mean daily temperature; b, d: total daily rainfall) and (a, b) daily male feeding visit rate (number of feeding visits per hour of female active time) and (c, d) daily female nest attendance (proportion of active time spent inside the nestbox). Shown are the model fit (solid line) with 95% CI (shading). See Table 2 for model output.  $n = 1061$  nest-days from 120 nests. In (b) and (d) 1 day with extreme precipitation (38.2 mm) is not shown (included in model – model results are almost identical when excluding this day).

similar behaviour are available for other Paridae (Brewer 1961, Royama 1966, McLaren 1975).

### Seasonal and daily patterns of female incubation

The sigmoidal increase in female nest attendance from 18 to 11 days before hatching (Fig. 1b) reflects partly the gradual onset of full incubation for individual females and partly the between-female variation in the time at which they started full incubation. Female nest attendance was highest in the morning hours (around 60%) and dropped gradually in the afternoon (Fig. 2b). This may reflect daily variation in temperature (Haftorn 1979). During full incubation, female nest attendance reached daily means of  $> 7$  h (Fig. 1b), which is roughly 55% of the active time of a female (time between a female's first exit in the

morning and her last nestbox entry in the evening). This value is lower than that reported in other studies of Paridae (range 67–82%), even when differences in measuring intervals and potential lower attendance early in incubation are taken into account (Table S10). However, in most of these studies data are less complete than in our study. Days of low female attendance are then difficult to interpret and extended incubation recesses are commonly considered outliers (MacDonald *et al.* 2013, Bueno-Enciso *et al.* 2017b). In our population such extended recesses (exit durations  $> 60$  min, definition following Bueno-Enciso *et al.* 2017b) represent approximately 10% of all exits (Fig. S7). Excluding days with such exits from our data, nest attendance is at least 64% (Table S10). This suggests that the nest attendance patterns we observed are not fundamentally different from those in other populations. The huge range of exit

**Table 2.** Effects of total daily rainfall, mean daily temperature and day in the incubation period on daily male feeding visit rate (number of feeding visits per hour of active female time) and daily female nest attendance (proportion of active time spent inside the nest-box). The effect of daily male feeding visit rate on female nest attendance is also reported. Male visit rate and female nest attendance are calculated for every day during the period of full incubation ( $n = 1061$  data points from 120 nests). Shown are results from linear mixed models (models D1 and D2) with nest identity and year as random factors and a temporal autocorrelation structure.

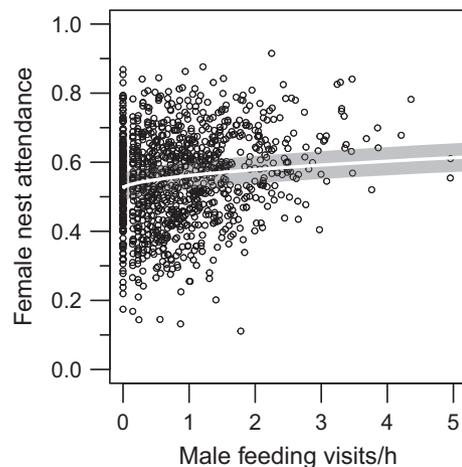
Fixed effect	Estimate	95% CI	<i>t</i>	<i>P</i>
Response: Male feeding visit rate <sup>a</sup>				
Intercept	1.1	0.7–1.4		
Total daily rain (mL)	−0.02	−0.03 to −0.01	−3.4	< 0.001
Temperature ( <i>T</i> ) in °C	−8.7	−10.2 to −7.1	−11.0	< 0.001
$T^2$	−1.8	−3.1 to −0.5	−2.7	0.006
Day of full incubation	−0.01	−0.03 to 0.01	−1.1	0.29
Response: Female nest attendance <sup>b</sup>				
Intercept	0.49	0.45–0.53		
Total daily rain (mL)	0.0002	−0.002 to 0.001	−0.3	0.75
Temperature ( <i>T</i> ) in °C	−0.28	−0.54 to −0.02	−2.1	0.03
$T^2$	−0.36	−0.57 to −0.16	−3.5	< 0.001
Day of full incubation	0.01	0.008–0.01	8.1	< 0.001
Male feeding visit rate	0.40	0.19–0.61	7.4	< 0.001
$\sqrt{(\text{male feeding visit rate})}$	0.99	0.73–1.25	3.8	< 0.001

<sup>a</sup>Variance explained by random effects: nest ID = 21%, year = 31%. <sup>b</sup>Variance explained by random effects: nest ID = 14%, year = 32%.

durations (10 s to 8.5 h) reflects large between-female variation in nest attendance (from 40 to 80%) and its partitioning within and between days (e.g. Figs S3e–h & S4c,d), and supports the notion that incubation behaviour is highly flexible within and between individuals (Morosinotto *et al.* 2013, Cantarero *et al.* 2014).

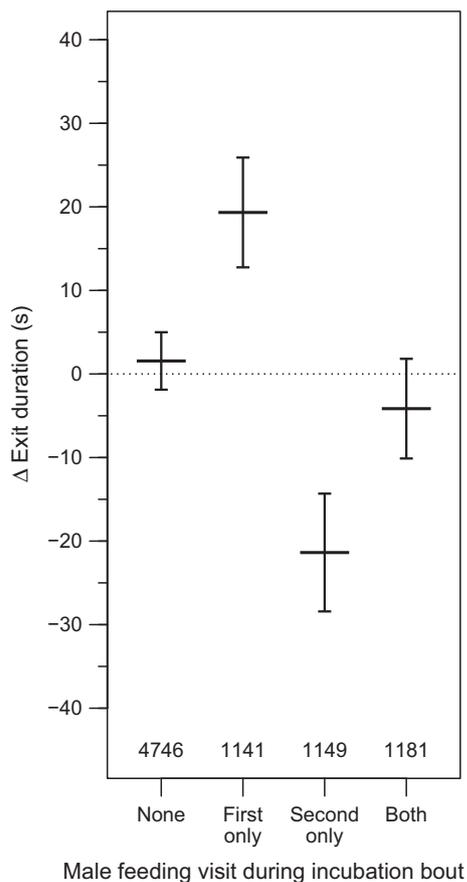
### Seasonal and daily patterns of male incubation feeding

Overall, males fed their incubating female up to 74 times on a single day and up to 390 times across the period of full incubation (between day 13 and day 1 before hatching). On average, the frequency of male nest visits followed the pattern of female incubation in the early incubation stages, but slowly decreased after day 10 pre-hatch (Fig. 1a). In line with female attendance, male feeding visits during full incubation peaked in the early morning (with an average of about one feed every 40 min) and then gradually decreased to about one feed every 2 h in the evening (Fig. 2a; see Cowie & Novak 1990 for a similar result). This decline was not present when considering male visit rate relative to female time spent in the nest-box (Table S7). Thus, males did not decrease feeding intensity over the day, but followed the pattern of female presence in the nest-box.



**Figure 4.** Relationship between daily male feeding visit rate in the nestbox (number of feeding visits per hour of female active time) and daily female nest attendance (proportion of active time spent inside the nestbox). Shown are the model fit (solid line) with 95% CI (shading). See Table 1 for model output.  $n = 1061$  nest-days from 120 nests.

The average rate at which males fed their incubating female may seem relatively low (e.g. compared with nestling feeding). However, caterpillars are the main food delivered by the male during female incubation (Betts 1955, Perrins 1991, Matysioková & Remeš 2010, Amininasab *et al.*



**Figure 5.** Effect of a male feeding visit during a female's incubation bout on the duration of her subsequent incubation recess. Shown are means (horizontal bars) and standard errors (whiskers) of the difference in the length of two subsequent recesses ( $\Delta$  exit duration = off2-duration – off1-duration) for all four scenarios of male feeding visits during the preceding incubation bouts. Male feeds can occur during neither bout, during the first or the second bout only or during both bouts. Sample sizes (number of paired exit bouts compared) are indicated at the bottom. See Table S6 for model output.  $n = 16\,434$  bouts (8217 comparisons) from 120 nests.

2017). Secondly, the peak of caterpillar abundance is typically narrow (Gibb & Betts 1963, Naef-Daenzer & Keller 1999, Tremblay *et al.* 2005, Visser *et al.* 2006) and such that caterpillar biomass available during the incubation period is on average less than half of that experienced during chick-feeding (Naef-Daenzer & Keller 1999, Visser *et al.* 2006, Matysioková & Remeš 2010). Thirdly, the duration of foraging trips (search time) decreases exponentially with caterpillar biomass (Naef-Daenzer & Keller 1999, Stauss *et al.* 2005, Tremblay *et al.* 2005). Thus, the 23 males we observed feeding their mate at least eight times

per hour in April (maximum of 12 times per hour on April 20) may have worked at least as hard as observed during provisioning of chicks (approximately 16 male feeds/h in mid-May or 4 feeds/h by both parents to each chick; see also Royama 1966).

The incubation feeding rate reported here is in the lower range of that found in the Paridae (Table S10). However, precision of estimates in most of these studies is low due to small sample sizes and large variation among males (Table S10). In line with previous studies (Lyon & Montgomerie 1985, Lifjeld & Slagsvold 1986, Halupka 1994, Cantarero *et al.* 2014) we observed remarkable between-male variation in patterns of incubation feeding: some males fed their female regularly and frequently throughout the incubation period (e.g. Fig. S3a), whereas others visited the nest only rarely, and not at all on some days (e.g. Fig. S3b). In still other cases, male incubation feeding became frequent only in the last days of incubation (e.g. Fig. S3c). Further, some males switched between days of high and low provisioning at the nest (e.g. Fig. S3d).

## Causes of variation in female incubation and male feeding behaviour

### Effects of individual characteristics

Female nest attendance and the frequency of male incubation feeding were unrelated to clutch size (Matysioková & Remeš 2010, Amininasab *et al.* 2017, but see Martin & Wiebe 2000, Kötél *et al.* 2016) and did not differ between yearling and older males or females (as reported in previous studies: Table S2). We also found no effect of extra-pair paternity on a male's feeding behaviour during incubation. These results suggest that observed variation in female nest attendance and male feeding behaviour is not primarily a consequence of investment decisions based on the own or the partner's state but may be related to the fluctuating environment (e.g. variation in temperature or food availability). In line with this, the most consistent predictors of male incubation feeding and female nest attendance in previous studies were local ecological factors (Table S2).

### Effects of ambient temperature

Ambient temperature is expected to have a direct influence on incubation behaviour and on male feeding because at lower temperatures females

expend more energy during incubation (Haftorn & Reinertsen 1985, Tinbergen & Williams 2002, Cresswell *et al.* 2004) and eggs cool faster during an incubation break, which may negatively affect embryo development (Olson *et al.* 2006). Previous studies tested for linear associations and reported a variety of relationships between ambient temperature and male incubation feeding or female nest attendance (Table S2). However, a non-linear association of attendance and temperature is likely (Conway & Martin 2000a). For example, when days with low temperatures necessitate neglect of eggs to ensure female survival or when high temperatures make prolonged incubation superfluous, a negative quadratic relationship is expected. Accordingly, we found lower nest attendance at both low and at high temperatures and peak attendance at intermediate temperatures (10–13 °C, Fig. 3b).

We also found a quadratic relationship between temperature and male feeding rate, but males fed most often during days with the lowest temperatures (4–8 °C), with a rapid decline in feeding rate at higher temperatures (Fig. 3a). Rainfall can have strong effects on nestling feeding rates (Öberg *et al.* 2015). Similarly, we found that males fed females less with increasing daily rainfall (Fig. 3c) and this pattern was detectable also on an hourly basis (Table S7), suggesting that males respond quickly to precipitation, perhaps due to reduced availability of caterpillars (Zandt *et al.* 1990). Female incubation attendance, however, was not affected by rainfall (Fig. 3d). Previous findings suggest that rainfall affects incubation behaviour primarily in aerial feeders (where rainfall strongly reduces foraging efficiency; Coe *et al.* 2015) and in species where eggs are exposed when the female is absent (Fu *et al.* 2017).

### Relationship between male and female behaviour during incubation

Male feeding during incubation may enable females to spend more time on the nest, because the trade-off with self-maintenance is alleviated. Indeed, some studies report that female nest attendance increased with increasing male feeding rate, although this is by no means a universal finding (Table S1). When considering the entire incubation period, we found no relationship between overall male incubation feeding rate and overall female nest attendance. However, on a daily basis, male provisioning rate was positively correlated with female nest

attendance. This could reflect a non-functional relationship arising because successful incubation feeding necessitates some coordination among parents in the time budget spent at the nest.

Our results show that on days the female spent more time in the nest, she obtained more feeds per unit time than on days she spent less time in the nest. This provides evidence for a functional process linking male and female investment during incubation; that is, females may be able to spend more time incubating as a direct consequence of the feeds provided by the male. However, other explanations cannot be ruled out. First, such a link may be driven by other factors such as assortative mating between individuals capable of investing a lot or variation in territory quality (food availability). In that case, we would have expected a relationship between male and female behaviour over the complete incubation period, which we did not find. Yet, the ability to invest more or less may covary temporally among parents because they are exposed to the same environment (e.g. fluctuations in predation risk or adverse weather). Further, male and female behaviour may be linked causally (in either direction), when investment decisions by one member of the pair affect the motivation of the partner.

Previous studies measured incubation feeding during 1 day or during a few hours over 1–7 days (Table S1). Thus, previous findings of a positive relationship between male incubation feeding and female nest attendance (Table S1) may only reflect short-term correlations rather than showing any overall relationship across the incubation period. Indeed, our analysis shows that females interrupted incubation for a shorter period when they had been fed by the male during the preceding incubation bout. Mate provisioning thus plays a role in determining how long the female stays outside the nest at the level of single visits. Overall, our results suggest that pairs do not show a consistent investment strategy during the incubation phase, but instead adjust their behaviour to the immediate ecological circumstances (Conway & Martin 2000a,b, Boulton *et al.* 2010, Matysioková *et al.* 2011, Amininasab *et al.* 2016).

### Consequences of variation in female incubation and male feeding behaviour

Higher female nest attendance is often postulated to improve hatching and fledging success, as well

as offspring quality (Stein *et al.* 2010, DuRant *et al.* 2013, Amininasab *et al.* 2016, Kötél *et al.* 2016). Similarly, one could expect that a higher male incubation feeding rate enhances reproductive success. However, the empirical results on fitness consequences of male and female behaviour are mixed (Table S1, Zimmerling & Ankney 2005, Blackman *et al.* 2006, Wang & Beissinger 2009). We found that neither overall female nest attendance nor overall male incubation feeding rate explained variation in incubation duration, hatching success or offspring survival (Table S8). However, the results of correlational studies are difficult to interpret because the analyses cannot control for confounding effects of other parental behaviours or traits that may influence reproductive success (e.g. quality of individuals, eggs, offspring care). In addition, environmental variation (e.g. food availability, predation risk) may influence offspring survival and modulate male nest visit rate as well as female nest attendance.

### Limitations of this study

We assessed male incubation feeding based on feeding frequency. This may be misleading if there is considerable variation in prey type or size. However, caterpillars are the main food delivered by the male during female incubation (Betts 1955, Perrins 1991, Matysioková & Remeš 2010, Amininasab *et al.* 2017), the size of these caterpillars varies mostly seasonally, and Blue Tits rarely bring more than one food item per visit (Naef-Daenzer & Keller 1999). The occurrence of male feeding outside the nestbox provides an obvious limitation to the exact quantification of male feeding effort and its effects on female behaviour and reproductive success (Cowie & Novak 1990). Our observations show that nest visit rates provide an incomplete picture of the true male investment in feeding his female during the incubation period. The high variation in male feeding rate between males, but also between days for the same male we observed (e.g. Figs S3 & S4) may then represent not only variation in investment patterns but also variation in the location of feeding. Nevertheless, across the complete dataset, male provisioning inside the nest appears to represent an important component of total male investment: on a daily basis, females that stayed longer on the nest not only received more

feeds overall but were fed at higher rates while they were on the nest (Fig. 4). This result would not be affected by unregistered feeds of females outside the nest. The same holds for the analysis of single events (i.e. shorter female exit durations after male visits, Fig. 5).

### CONCLUSIONS

Our data suggest that in Blue Tit pairs, male feeding allows females to spend more time incubating (short-term effect), in line with the idea that a key function of male incubation feeding is nutritional support of the female. Our data suggest that males and females modulate their behaviour in relation to time of day, daily variation in ambient temperature and rainfall, and date relative to hatching. Some males invested heavily during the incubation phase, but it is unclear whether this reflects a consistent paternal trait. Our finding that (some) males frequently feed their incubating female outside the nest indicates that data on male nest visitation need to be interpreted cautiously. Finally, the fitness benefits of high female nest attendance and of high male incubation feeding rates remain unresolved.

We thank A. Türk, A. Wittenzellner and all members of the field team for collecting data on the birds over the years. We are grateful to P. Loës and P. Skripky for technical support, L. Schlicht, P.B. D'Amelio, P. Santema and C. Gilshan for constructive discussions and feedback. Arie van Noodwijk and one anonymous reviewer provided comments that greatly improved the manuscript. This work was funded by the Max Planck Society.

### REFERENCES

- Amininasab, S.M., Kingma, S.A., Birker, M., Hildenbrandt, H. & Komdeur, J. 2016. The effect of ambient temperature, habitat quality and individual age on incubation behaviour and incubation feeding in a socially monogamous songbird. *Behav. Ecol. Sociobiol.* **70**: 1591–1600.
- Amininasab, S.M., Birker, M., Kingma, S.A., Hildenbrandt, H. & Komdeur, J. 2017. The effect of male incubation feeding on female nest attendance and reproductive performance in a socially monogamous bird. *J. Ornithol.* **158**: 687–696.
- Bates, D., Maechler, M., Bolker, B.M. & Walker, S. 2014. *lme4: Linear Mixed-Effects Models Using Eigen and S4. R Package Version 1.1-7*. Available at: <http://CRAN.R-project.org/package=lme4> (accessed 17 May 2018).
- Betts, M.M. 1955. The behaviour of a pair of Great Tits at the nest. *Br. Birds* **48**: 77–82.
- Blackman, R., Deeming, D.C., Eady, P.E. & Barton, S. 2006. Egg cooling in nests and attentiveness during

- incubation in British Passerines. *Avian Poult. Biol. Rev.* **17**: 57–76.
- Boucaud, I.C.A., Aguirre Smith, M.L.N., Valère, P.A. & Vignal, C.** 2016. Incubating females signal their needs during intrapair vocal communication at the nest: a feeding experiment in Great Tits. *Anim. Behav.* **122**: 77–86.
- Boulton, R.L., Richard, Y. & Armstrong, D.P.** 2010. The effect of male incubation feeding, food and temperature on the incubation behaviour of New Zealand Robins. *Ethology* **116**: 490–497.
- Brewer, R.** 1961. Comparative notes on the life history of Carolina Chickadees. *Wilson Bull.* **73**: 348–373.
- Bueno-Enciso, J., Barrientos, R. & Sanz, J.J.** 2017a. Incubation behaviour of Blue *Cyanistes caeruleus* and Great Tits *Parus major* in a Mediterranean habitat. *Acta Ornithol.* **52**: 21–34.
- Bueno-Enciso, J., Barrientos, R., Ferrer, E.S. & Sanz, J.J.** 2017b. Do extended incubation recesses carry fitness costs in two cavity-nesting birds? *J. Field Orn.* **88**: 146–155.
- Bulla, M., Stich, E., Valcu, M. & Kempenaers, B.** 2015. Off-nest behaviour in a biparentally incubating shorebird varies with sex, time of day and weather. *Ibis* **157**: 575–589.
- Camfield, A. & Martin, T.E.** 2009. The influence of ambient temperature on Horned Lark incubation behaviour in an alpine environment. *Behaviour* **146**: 1615–1633.
- Cantarero, A., López-Arrabé, J., Palma, A., Redondo, A.J. & Moreno, J.** 2014. Males respond to female begging signals of need: a handicapping experiment in the Pied Flycatcher, *Ficedula hypoleuca*. *Anim. Behav.* **94**: 167–173.
- Chalfoun, A.D. & Martin, T.E.** 2007. Latitudinal variation in avian incubation attentiveness and a test of the food limitation hypothesis. *Anim. Behav.* **73**: 579–585.
- Coe, B.H., Beck, M.L., Chin, S.Y., Jachowski, C.M.B. & Hopkins, W.A.** 2015. Local variation in weather conditions influences incubation behavior and temperature in a passerine bird. *J. Avian Biol.* **46**: 385–394.
- Conway, C.J. & Martin, T.E.** 2000a. Effects of ambient temperature on avian incubation behavior. *Behav. Ecol.* **11**: 178–188.
- Conway, C.J. & Martin, T.E.** 2000b. Evolution of passerine incubation behavior: influence of food, temperature, and nest predation. *Evolution* **54**: 670–685.
- Cowie, R.J. & Novak, J.A.** 1990. Incubation patterns of Blue Tits (*Parus caeruleus*). In Blondel, J., Gosler, A., Lebreton, J.-D. & McCleery, R. (eds) *Population Biology of Passerine Birds: An Integrated Approach*: 345–356. Berlin: Springer.
- Cramp, S., Perrins, C.M. & Brooks, D.J. (eds)** 1993. *The Birds of the Western Palearctic*. Vol. 7: 225–255. Oxford: Oxford University Press.
- Cresswell, W., Holt, S., Reid, J.M., Whitfield, D.P., Mellanby, R.J., Norton, D. & Waldron, S.** 2004. The energetic costs of egg heating constrain incubation attendance but do not determine daily energy expenditure in the Pectoral Sandpiper. *Behav. Ecol.* **15**: 498–507.
- Dixon, K.L.** 1949. Behavior of the Plain Titmouse. *Condor* **51**: 110–136.
- DuRant, S.E., Hopkins, W.A., Hepp, G.R. & Walters, J.R.** 2013. Ecological, evolutionary, and conservation implications of incubation temperature-dependent phenotypes in birds. *Biol. Rev.* **88**: 499–509.
- Fox, J.** 2003. Effect displays in R for generalised linear models. *J. Stat. Softw.* **8**: 1–27.
- Fu, Y., Dai, B., Wen, L., Chen, B., Dowell, S. & Zhang, Z.** 2017. Unusual incubation behavior and embryonic tolerance of hypothermia in the Sichuan Partridge (*Arborophila rufipectus*). *J. Ornithol.* **158**: 707–715.
- Gibb, J.** 1950. The breeding biology of the Great and Blue Titmice. *Ibis* **92**: 507–539.
- Gibb, J.A. & Betts, M.M.** 1963. Food and food supply of nestling tits (Paridae) in Breckland Pine. *J. Anim. Ecol.* **32**: 489–533.
- Glutz von Blotzheim, U.N. & Bauer, K.M.** 1993. *Handbuch der Vögel Mitteleuropas*. Vol. 13/1: 579–662. Wiesbaden: Aula-Verlag.
- von Haartman, L.** 1958. The incubation rhythm of the female Pied Flycatcher (*Ficedula hypoleuca*) in the presence and absence of the male. *Ornis Fenn.* **35**: 71–76.
- Haftorn, S.** 1979. Incubation and regulation of egg temperature in the Willow Tit *Parus montanus*. *Ornis Scand.* **10**: 220–234.
- Haftorn, S. & Reinertsen, R.E.** 1985. The effect of temperature and clutch size on the energetic cost of incubation in a free-living Blue Tit (*Parus caeruleus*). *Auk* **102**: 470–478.
- Halupka, K.** 1994. Incubation feeding in Meadow Pipit *Anthus pratensis* affects female time budget. *J. Avian Biol.* **25**: 251–253.
- Hinde, R.A.** 1952. The behaviour of the Great Tit (*Parus Major*) and some other related species. *Behav. Suppl.* **2**: 1–201.
- Klatt, P.H., Stutchbury, B.J.M. & Evans, M.L.** 2008. Incubation feeding by male Scarlet Tanagers: a mate removal experiment. *J. Field Orn.* **79**: 1–10.
- Kötél, D., Laczi, M., Török, J. & Hegyi, G.** 2016. Mutual ornamentation and the parental behaviour of male and female Collared Flycatchers *Ficedula albicollis* during incubation. *Ibis* **158**: 796–807.
- Kuznetsova, A., Brockhoff, P.B. & Christensen, R.H.B.** 2016. *lmerTest: Tests in Linear Mixed Effects Models. R package Version 2.0-32*. Available at: <http://CRAN.R-project.org/package=lmerTest> (accessed 17 May 2018).
- Lifjeld, J.T. & Slagsvold, T.** 1986. The function of courtship feeding during incubation in the Pied Flycatcher *Ficedula hypoleuca*. *Anim. Behav.* **34**: 1441–1453.
- Lloyd, P., Taylor, W.A., du Plessis, M.A. & Martin, T.E.** 2009. Females increase reproductive investment in response to helper-mediated improvements in allo-feeding, nest survival, nestling provisioning and post-fledging survival in the Karoo scrub-Robin *Cercotrichas coryphaeus*. *J. Avian Biol.* **40**: 400–411.
- Lyon, B.E. & Montgomerie, R.D.** 1985. Incubation feeding in Snow Buntings: female manipulation or indirect male parental care? *Behav. Ecol. Sociobiol.* **17**: 279–284.
- MacDonald, E.C., Camfield, A.F., Jankowski, J.E. & Martin, K.** 2013. Extended incubation recesses by alpine-breeding Horned Larks: a strategy for dealing with inclement weather? *J. Field Orn.* **84**: 58–68.
- Martin, T.E.** 2002. A new view of avian life-history evolution tested on an incubation paradox. *Proc. R. Soc. Lond. B* **269**: 309–316.
- Martin, K. & Wiebe, K.L.** 2000. The use of incubation behavior to adjust avian reproductive costs after egg laying. *Behav. Ecol. Sociobiol.* **48**: 463–470.
- Matysioková, B. & Remes, V.** 2010. Incubation feeding and nest attentiveness in a socially monogamous songbird: role

- of feather colouration, territory quality and ambient environment. *Ethology* **116**: 596–607.
- Matysioková, B. & Remeš, V.** 2014. The importance of having a partner: male help releases females from time limitation during incubation in birds. *Front. Zool.* **11**: 24.
- Matysioková, B., Cockburn, A. & Remeš, V.** 2011. Male incubation feeding in songbirds responds differently to nest predation risk across hemispheres. *Anim. Behav.* **82**: 1347–1356.
- McLaren, M.A.** 1975. Breeding biology of the Boreal Chickadee. *Wilson Bull.* **87**: 344–354.
- Morosinotto, C., Thomson, R.L. & Korpimäki, E.** 2013. Plasticity in incubation behaviour under experimentally prolonged vulnerability to nest predation. *Behaviour* **150**: 1767–1786.
- Naef-Daenzer, B. & Keller, L.F.** 1999. The foraging performance of Great and Blue Tits (*Parus major* and *P. caeruleus*) in relation to caterpillar development, and its consequences for nestling growth and fledging weight. *J. Anim. Ecol.* **68**: 708–718.
- Nilsson, J.-Å. & Smith, H.G.** 1988. Incubation feeding as a male tactic for early hatching. *Anim. Behav.* **36**: 641–647.
- Öberg, M., Arlt, D., Pärt, T., Laugen, A.T., Eggers, S. & Low, M.** 2015. Rainfall during parental care reduces reproductive and survival components of fitness in a passerine bird. *Ecol. Evol.* **5**: 345–356.
- Olson, C.R., Vleck, C.M. & Vleck, D.** 2006. Periodic cooling of bird eggs reduces embryonic growth efficiency. *Physiol. Biochem. Zool.* **79**: 927–936.
- Pearse, A.T., Cavitt, J.F. & Cully, J.F.** 2004. Effects of food supplementation on female nest attentiveness and incubation mate feeding in two sympatric wren species. *Wilson Bull.* **116**: 23–30.
- Perrins, C.M.** 1991. Tits and their caterpillar food supply. *Ibis* **133**(s1): 49–54.
- Pinheiro, J. & Bates, D.** 2000. *Mixed-Effects Models in S and S-Plus*. New York, NY: Springer.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team** 2015. *nlme: Linear and Nonlinear Mixed Effects Models. R Package Version 3.1-120*. Available at: <http://CRAN.R-project.org/package=nlme> (accessed 17 May 2018).
- R Core Team** 2015. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. Available at: <http://www.R-project.org> (accessed 17 May 2018).
- Royama, T.** 1966. A re-interpretation of courtship feeding. *Bird Study* **13**: 116–129.
- Schlicht, L., Girg, A., Loës, P., Valcu, M. & Kempenaers, B.** 2012. Male extrapair nestlings fledge first. *Anim. Behav.* **83**: 1335–1343.
- Schlicht, L., Valcu, M. & Kempenaers, B.** 2015. Male extraterritorial behavior predicts extrapair paternity pattern in Blue Tits, *Cyanistes caeruleus*. *Behav. Ecol.* **26**: 1404–1413.
- Smith, H.G., Källander, H., Hultman, J. & Sanzén, B.** 1989. Female nutritional state affects the rate of male incubation feeding in the Pied Flycatcher *Ficedula hypoleuca*. *Behav. Ecol. Sociobiol.* **24**: 417–420.
- Stauss, M.J., Burkhardt, J.F. & Tomiuk, J.** 2005. Foraging flight distances as a measure of parental effort in Blue Tits *Parus caeruleus* differ with environmental conditions. *J. Avian Biol.* **36**: 47–56.
- Stein, L.R., Oh, K.P. & Badyaev, A.V.** 2010. Fitness consequences of male provisioning of incubating females in a desert passerine bird. *J. Ornithol.* **151**: 227–233.
- Tinbergen, J.M. & Dietz, M.W.** 1994. Parental energy expenditure during brood rearing in the Great Tit (*Parus major*) in relation to body mass, temperature, food availability and clutch size. *Funct. Ecol.* **8**: 563–572.
- Tinbergen, J.M. & Williams, J.B.** 2002. Energetics of incubation. *Oxford Ornithol. Ser.* **13**: 299–313.
- Tremblay, I., Thomas, D., Blondel, J., Perret, P. & Lambrechts, M.M.** 2005. The effect of habitat quality on foraging patterns, provisioning rate and nestling growth in Corsican Blue Tits *Parus caeruleus*. *Ibis* **147**: 17–24.
- Vedder, O., Magrath, M.J.L., Niehoff, D.L., van der Velde, M. & Komdeur, J.** 2012. Declining extra-pair paternity with laying order associated with initial incubation behavior, but independent of final clutch size in the Blue Tit. *Behav. Ecol. Sociobiol.* **66**: 603–612.
- Visser, M.E., Holleman, L.J.M. & Gienapp, P.** 2006. Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. *Oecologia* **147**: 164–172.
- Wang, J.M. & Beissinger, S.R.** 2009. Variation in the onset of incubation and its influence on avian hatching success and asynchrony. *Anim. Behav.* **78**: 601–613.
- Webb, T.J., Olson, V.A., Székely, T. & Freckleton, R.P.** 2010. Who cares? Quantifying the evolution of division of parental effort. *Methods Ecol. Evol.* **1**: 221–230.
- Zandt, H.S., Strijkstra, A.M., Blondel, J. & van Balen, J.H.** 1990. Two Mediterranean Blue tit populations: are differences in the timing of breeding associated with caterpillar availability? In Blondel, J., Gosler, A., Lebreton, J.-D. & McCleery, R. (eds) *Population Biology of Passerine Birds: An Integrated Approach*: 145–155. Berlin: Springer.
- Zimmerling, J.R. & Ankney, C.D.** 2005. Variation in incubation patterns of Red-Winged Blackbirds nesting at lagoons and ponds in Eastern Ontario. *Wilson Bull.* **117**: 280–290.

Received 24 September 2017;  
revision accepted 30 April 2018.  
Associate Editor: Luc Lens.

## SUPPORTING INFORMATION

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

**Appendix S1.** Supplementary Methods.

**Table S1.** Overview of sampling methods used in previous studies of male incubation feeding and female nest attendance and summary of effects of these behaviours on reproductive success.

**Table S2.** Results from studies examining correlates of male incubation feeding and female nest attendance.

**Table S3.** Summary of variables reflecting reproductive success of Blue Tit pairs used in this study.

**Table S4.** Summary of statistical models used in this study.

**Table S5.** Summary of the behavioural variables collected in 2016 using either direct observation, or video recordings inside or outside the nestbox.

**Table S6.** Effect of the time before hatching (in days; hatch day = 0) on the daily number of male feeding visits and on the daily amount of time spent in the nestbox by the female.

**Table S7.** Effect of time of day and hourly rainfall on the number of male feeding visits and on female incubation time.

**Table S8.** Effects of male feeding visit rate (number of feeding visits per hour of female active time) and female nest attendance (proportion of active time spent inside the nestbox) on the duration of the incubation period and on measures of breeding success.

**Table S9.** Effect of a male feeding visit during the female's incubation bout on the length of the subsequent incubation recess (exit duration).

**Table S10.** Incubation feeding and nest

attendance in Paridae species (overview).

**Figure S1.** Theoretical implications of examining the association between male feeding and female incubation behaviour.

**Figure S2.** Frequency distribution of  $\Delta$  exit duration.

**Figure S3.** Actograms showing variation in male nest visit behaviour and in female nest attendance.

**Figure S4.** Examples of daily variation in feeding visits to the nestbox for two males (a, b) and in time spent inside the nestbox for two females (c, d).

**Figure S5.** Frequency distribution of the proportion of male feeds observed outside the nestbox among all observed male feeds.

**Figure S6.** Female exit duration with or without a male feed observed outside the nestbox.

**Figure S7.** Frequency distribution of female exit durations.

## SUPPORTING INFORMATION

G. Bambini, E. Schlicht & B. Kempenaers: Patterns of female nest attendance and male feeding throughout the incubation period in Blue Tits *Cyanistes caeruleus*. Ibis 2018

### APPENDIX S1: SUPPLEMENTARY METHODS

#### Methods S1

Data on hourly precipitation and ambient temperatures were obtained from a nearby weather station (Landsberg am Lech, [http://www.am.rlp.de/Internet/AM/NotesBAM.nsf/MainFrame\\_Web?OpenFrameSet&Frame=mitte&Src=%2FInternet%2FAM%2FNotesBAM.nsf%2Fbamweb%3FOpenView%26AutoFramed](http://www.am.rlp.de/Internet/AM/NotesBAM.nsf/MainFrame_Web?OpenFrameSet&Frame=mitte&Src=%2FInternet%2FAM%2FNotesBAM.nsf%2Fbamweb%3FOpenView%26AutoFramed)). From these data, we extracted for each bird the measurements from those hours, in which the female was active (see Methods for definition). We then calculated the mean and minimum daily temperature across the hourly measurements from the active period of a given day. For rainfall, we additionally calculated the total daily precipitation. Analyses with minimum and mean temperature gave qualitatively similar results, so we only report the results for mean temperature. Total daily rainfall and mean daily temperature were moderately negatively correlated (Pearson's  $r = -0.32$ ).

In 2016, we also measured hourly temperature locally at ground level at each nestbox. Hourly temperature averaged across all nestboxes correlated strongly with hourly temperature data from the weather station:  $R^2_{\text{marginal}} = 0.87$ ,  $P < 0.001$ ,  $n = 174$  hours on 24 days (linear mixed model including an hourly temporal autocorrelation structure as in model H1, Table S4; marginal  $R^2$ -value obtained with the methods implemented in the R-package piecewiseSEM (Lefcheck 2015)).

#### Methods S2

Molecular analysis with microsatellite markers (Delhey *et al.* 2003, Schlicht *et al.* 2012) showed that 64 of the 171 monitored

nests (37%) contained extra-pair young, i.e. at least one offspring was not sired by the male that provisioned the female and the offspring. We analysed the effects of paternity loss (the presence of extra-pair young in the nest, yes/no) and of paternity gain (siring at least one extra-pair young in the population in the same year, yes/no) on male visit behaviour. Using the proportion of extra-pair young in the nest or the total number of extra-pair young sired gave similar results (not shown).

#### Methods S3

Data from direct observations and from the video recordings outside and inside the nestbox closely matched each other: all feeds observed or filmed outside the nestbox could be identified from the recordings inside the nestbox and all events recorded inside the nestbox matched those recorded outside. We observed 94.5% of 147 male entry events filmed with the nestbox cameras. At two nests where all three methods were used simultaneously, 97% of events were in accordance. Data from direct observations and video recordings were also consistent with RFID data: 94% of the 1590 recorded or observed events were also unequivocally identified via the automated RFID and light barrier system.

#### Methods S4

A female's active time is the time between her first exit in the morning and her last entry in the evening. To exclude days with incomplete data (e.g. due to recorder malfunctioning), we only accepted cases (days) where the first female exit was between 05:00 and 07:00 h and the last entry

between 18:00 and 21:30 h. These intervals were established from daily events known to be correct based on technical information (functioning recording device at the box) and on observed behavioural patterns. We here measure female investment in incubation as the proportion of active time spent on the nest (*nest attendance*; see Table S10 for studies using similar definitions). However, differences among females in when they stop incubating in the morning or start incubating in the evening may reflect genuine investment decisions, whereby a prolongation of the nightly 'incubation bout' may influence the duration spent on the nest during the active time (Zerba & Morton 1983). We therefore also calculated, for each day, the earliest and latest activity observed across the entire population and used this

time interval ('longest time') instead of the female's active time for calculating the proportion of time spent on the nest. Finally, the lighted part of the day ('lighted time') is shorter early in the season and limits the time available for activity (mean  $\pm$  SD time between civil dawn and dusk:  $15.9 \pm 0.3$  h; range = 14.8-17.1 h;  $n = 1632$  days). Hence, we further calculated the proportion of time spent on the nest between dawn and dusk (Shaw & Cresswell 2014). Because results were qualitatively identical when using active, longest or lighted time to calculate nest attendance, we here present the results based on active time only. For males results also did not change qualitatively when using longest or lighted instead of active time for the calculation of feeding visit rate (not shown).

## **SUPPLEMENTARY TABLES**

**Table S1.** Overview of sampling methods used in previous studies of male incubation feeding and female nest attendance and summary of effects of these behaviours on reproductive success. Shown are sampling duration (video recording or direct observation), number of days on which observations were made, whether feeds away from the nest (external feeds) were known to occur (yes / no) and if and how they were assessed. Shown are also, whether there was a significant relationship between male incubation feeding and female nest attendance (yes or no), and whether either male incubation feeding or female nest attendance significantly affected hatching success, fledging success or measures of offspring quality (yes or no).

Species	Duration [h]	Method		♂ feeding ~ ♀ attendance	♂: feeding / ♀: attendance			Source
		No. of observation days	External feeds occurrence / assessment <sup>1</sup>		Hatching	Fledging	Offspring traits	
19 songbird species	6	-	- / No	Yes	-	-	-	Martin & Ghalambor 1999 <sup>2</sup>
12 songbird species	4–6	2	- / No	No	-	-	-	Fontaine & Martin 2006 <sup>2</sup>
78 songbird species	/	/	- / No	Yes	-	-	-	Matysioková <i>et al.</i> 2011 <sup>2</sup>
156 songbird species	/	/	- / No	Yes	-	-	-	Matysioková & Remeš 2014 <sup>2</sup>
Karoo Prinia	8	1	- / -	Yes	-	-	-	Chalfoun & Martin 2007 <sup>5f</sup>
Eastern Yellow Robin	0.75	1-3	Yes / No	Yes	-	-	♂: Yes	Zanette <i>et al.</i> 2000
New Zealand Robin	8.3	1-2	Yes / fi	No <sup>3</sup>	-	♂ & ♀: No <sup>4</sup>	-	Boulton <i>et al.</i> 2010
Pied Flycatcher	0.5	1	Yes / su	Yes	♂: No	♂: No	♂: No	Lifjeld & Slagsvold 1986
Pied Flycatcher	1	1	Yes / su	Yes	♂: No	-	-	Lifjeld <i>et al.</i> 1987
Pied Flycatcher	0.5	2 - 3	Yes / su	No	-	-	-	Lifjeld & Slagsvold 1989
Pied Flycatcher	1	1	- / -	Yes	♀: No	♀: No	-	Moreno & Carlson 1989
Pied Flycatcher	1	3	Yes / su	Yes	-	-	-	Smith <i>et al.</i> 1989 <sup>5f</sup>
Pied Flycatcher	1.5–2	1	Yes / an	Yes	♀: No	♀: No	-	Moreno <i>et al.</i> 2011 <sup>5h</sup>
Pied Flycatcher	1.7	1	- / No	Yes	♂: No	♂: No	♂: No	Cantarero <i>et al.</i> 2014 <sup>5h</sup>
Collared Flycatcher	5	1	- / No	Yes	♂: Yes <sup>6</sup>	-	-	Kötél <i>et al.</i> 2016
Eastern Bluebird	4	1	Yes / an	Yes	♂: No	-	-	Siefferman & Hill 2005
Meadow Pipit	1.6 (1.25–1.9)	1	Yes / an	Yes	♂: No	♂: No	-	Hałupka 1994
House Finch	1.5-2	1	- / No	No	♀: No	-	-	Stein <i>et al.</i> 2010
Yellow Warbler	5	1	- / No	Yes	-	-	-	Tewksbury <i>et al.</i> 2002 <sup>5p</sup>
Yellow Warbler	~7	1	- / No	Yes	-	-	-	Moore & Rohwer 2012

(Table S1 continued)								
Scarlet Tanager	1	2	Yes / fi	Yes	-	-	-	Klatt <i>et al.</i> 2008 <sup>5r</sup>
Northern Cardinal	1	5	Yes / an	No	-	♂: No	-	Jawor & Breitwisch 2006
Snow Bunting	1	>1	- / No	Yes	♂: Yes <sup>7</sup>	♂: No	♂: No	Lyon & Montgomerie 1985 <sup>5r</sup>
Marsh Tit, Blue Tit	1	1	Yes / fi	-	♂: Yes	♂: No	-	Nilsson & Smith 1988 <sup>5f</sup>
Blue Tit	7.5 ± 1.3	1	Yes / No	Yes	♀: No	No	♀: Yes	Amininasab <i>et al.</i> 2017
Great Tit	1.5	1	Yes / No	No	♂ & ♀: No	-	-	Matysioková & Remeš 2010
Great Tit	8.3	2	- / No	Yes	-	-	-	Boucaud <i>et al.</i> 2016 <sup>5f</sup>
Mountain Chickadee, Pygmy Nuthatch, Red- breasted Nuthatch, Brown Creeper	1.5	1	- / -	No	-	-	-	Ghalambor & Martin 2002
Nuthatch	1.5	1	- / No	No <sup>8</sup>	♂: No	♂: No	♂: No	Cantarero <i>et al.</i> 2016
Bewick's Wren, House Wren	2-4	2	- / No	Yes	♂: No	-	-	Pearse <i>et al.</i> 2004 <sup>5f</sup>
Green Woodhoopoe	2	1-3	Yes / an	Yes <sup>9</sup>	-	-	-	Radford 2004

<sup>1</sup> assessment of outside feeds via observation of surroundings (su), via observation of area directly next to nest (an), via following individuals (fi)

<sup>2</sup> comparative study: interspecific relationship

<sup>3</sup> Y for female incubation rhythm

<sup>4</sup> nest survival

<sup>5</sup> experimental: female handicapping (h), brood ectoparasites (p), male removal (r), food supplementation (s)

<sup>7</sup> also for early chick mortality

<sup>8</sup> Y for female recess length

<sup>6</sup> in interaction with time of hatching

<sup>9</sup> provisioning of male helpers included

**Table S2.** Results from studies examining correlates of male incubation feeding and female nest attendance.

Factor and species	Male incubation feeding	Female nest attendance
Age - Positive relationship		
Pied Flycatcher	Lifjeld & Slagsvold 1986 <sup>a</sup>	
Age - Negative relationship		
Rook	Røskaft et al. 1983	
Age - No relationship		
Blue Tit	Amininasab et al. 2016	Amininasab et al. 2016
Great Tit	Matysioková & Remeš 2010	Matysioková & Remeš 2010
Eastern Bluebird	Siefferman & Hill 2005	
Rook		Røskaft et al. 1983
Ambient Temperature – Positive relationship		
Pied Flycatcher	Lifjeld & Slagsvold 1986 <sup>a</sup>	
White-crowned Sparrow		Zerba & Morton 1983
Dusky Flycatcher		Morton & Pereyra 1985
Yellow-eyed Junco		Weathers & Sullivan 1989
Tree Swallow		Ardia et al. 2009, Coe et al. 2015
House Wren		Voss et al. 2006
Ambient Temperature - Negative relationship		
Blue Tit	Amininasab et al. 2016	Amininasab et al. 2016
Great Tit	Matysioková & Remeš 2010	
Pied Flycatcher	Lifjeld & Slagsvold 1986 <sup>a</sup> , Lifjeld et al. 1987, Smith et al. 1989	
Bewick's Wren	Pearse et al. 2004	
Black-capped Chickadee		Voss et al. 2006
Carolina Chickadee		Walters et al. 2016
Ambient temperature - No relationship		
House Wren	Pearse et al. 2004	Pearse et al. 2004
Meadow Pipit	Hałupka 1994	Hałupka 1994
Long-tailed Tit	Hatchwell et al. 1999	Hatchwell et al. 1999
Bewick's Wren		Pearse et al. 2004
Tree Swallow		Voss et al. 2006
Habitat Quality		
Eastern Yellow Robin	Zannette et al. 2000	
Great Tit	Matysioková & Remeš 2010	
Blue Tit	Amininasab et al. 2016	
Water Pipit		Rauter & Reyer 1997
Red-winged Blackbird		Zimmerling & Akney 2005
Predation Risk		
19 songbird species	Martin & Ghalambor 1999 <sup>b</sup>	Martin & Ghalambor 1999 <sup>b</sup>
170 songbird species	Galván & Sanz 2011 <sup>b</sup>	
78 songbird species	Matysioková et al. 2011 <sup>b</sup>	
12 songbird species	Fontaine & Martin 2006	Fontaine & Martin 2006

(Table S2 continued)	
5 songbird species	Ghalambor & Martin 2002

<sup>a</sup> in one of two study years

<sup>b</sup> comparative study: interspecific relationship

**Table S3.** Summary of variables reflecting reproductive success of Blue Tit pairs used in this study (individual years and all years combined).

	Mean $\pm$ SD (range)				
	2013 <i>n</i> = 4	2014 <i>n</i> = 16	2015 <i>n</i> = 74	2016 <i>n</i> = 77	Total <i>n</i> = 171
Laying date <sup>a</sup>	116.8 $\pm$ 1.7 (115–119)	97.1 $\pm$ 2.0 (95–103)	109.4 $\pm$ 2.1 (106–116)	107.5 $\pm$ 4.8 (100–135)	107.5 $\pm$ 5.1 (95–135)
Clutch size	11.0 $\pm$ 0.8 (10–12)	11.1 $\pm$ 1.3 (8–13)	9.8 $\pm$ 1.5 (5–13)	9.7 $\pm$ 1.7 (5–13)	9.9 $\pm$ 1.6 (5–13)
Incubation length	11.3 $\pm$ 1.5 (10–13)	11.8 $\pm$ 1.4 (9–13)	11.4 $\pm$ 1.4 (8–14)	11.7 $\pm$ 1.4 (8–14)	11.6 $\pm$ 1.4 (8–14)
Number of hatched	10.8 $\pm$ 1.0 (10–12)	8.4 $\pm$ 2.5 (3–12)	9.2 $\pm$ 2.0 (2–12)	8.6 $\pm$ 2.3 (2–13)	8.9 $\pm$ 2.2 (2–13)
Number of fledged	6.8 $\pm$ 4.7 (0–10)	8.3 $\pm$ 2.5 (3–12)	7.7 $\pm$ 3.2 (0–12)	7.3 $\pm$ 3.0 (0–13)	7.5 $\pm$ 3.0 (0–13)
Proportion of hatchlings that were alive on day 5 <sup>b</sup>	1.0 $\pm$ 0.04 (0.9–1.0)	1.0 $\pm$ 0.04 (0.9–1.0)	1.0 $\pm$ 0.08 0.6 $\pm$ 1.0	1.0 $\pm$ 0.06 (0.7–1.0)	1.0 $\pm$ 0.07 (0.6–1.0)
Proportion of nestling alive on day 5 that fledged <sup>c</sup>	0.7 $\pm$ 0.5 (0–1)	1.0 $\pm$ 0.03 (0.9–1)	0.9 $\pm$ 0.3 (0–1)	0.9 $\pm$ 0.3 (0–1)	0.9 $\pm$ 0.3 (0–1)

<sup>a</sup> 90 = 1<sup>st</sup> of April (in non-leap years)

<sup>b</sup> 2013: *n* = 4; 2014: *n* = 14; 2015: *n* = 70; 2016: *n* = 73; Total: *n* = 161

<sup>c</sup> 2013: *n* = 4; 2014: *n* = 14; 2015: *n* = 71; 2016: *n* = 73; Total: *n* = 162

**Table S4.** Summary of statistical models used in this study.

Model	Response	Explanatory	Random	Error structure <sup>a</sup>	R-package, function
Nest-wise analyses					
N1	Overall male feeding visit rate	clutch size, male age, female age, paternity loss, paternity gain,	male identity, female identity, pair identity, year	Gaussian	lme4, lmer
N2	Overall female nest attendance	clutch size, male age, female age, male feeding rate, $\sqrt{\text{male feeding rate}}$ <sup>b</sup>	male identity, female identity, pair identity, year	Gaussian	lme4, lmer
N3	Duration of incubation period	overall male feeding rate, overall female nest attendance	male identity, female identity, pair identity, year	Gaussian	lme4, lmer
N4	Hatching success	overall male feeding rate, overall female nest attendance	male identity, female identity, pair identity, year	binomial	lme4, glmer
N5	Early nestling survival	overall male feeding rate, overall female nest attendance	male identity, female identity, pair identity, year	binomial	lme4, glmer
N6	Late nestling survival	overall male feeding rate, overall female nest attendance	male identity, female identity, pair identity, year	binomial	lme4, glmer
N7	Fledging success	overall male feeding rate, overall female nest attendance	male identity, female identity, pair identity, year	binomial	lme4, glmer

(Table S4 continued)

Daily analyses <sup>c</sup>					
D1	Daily male feeding rate	day of incubation <sup>d</sup> , daily ambient temperature, (daily ambient temperature) <sup>2</sup> , daily rainfall	nest identity, year	Gaussian	nlme, lme
D2	Daily female nest attendance	day of incubation <sup>d</sup> , daily ambient temperature, (daily ambient temperature) <sup>2</sup> , daily rainfall, daily male feeding rate, $\sqrt{\text{daily male feeding rate}}$	nest identity, year	Gaussian	nlme, lme
D3	$\sqrt{\text{Daily number of male visits}}$	day before hatching	nest identity, year	Gaussian	lme4, lmer
D4	Daily time female inside nest	day before hatching	nest identity, year	Gaussian	lme4, lmer
Hourly analyses <sup>c</sup>					
H1	$\sqrt{\text{Hourly male visit number}}$	hour of day, hourly rainfall	nest identity, year	Gaussian	nlme, lme
H2	Hourly male visit number / hourly female incubation time	hour of day, hourly rainfall	nest identity, year	Gaussian	nlme, lme
H3	Hourly female incubation time	hour of day, hourly rainfall	nest identity, year	Gaussian	nlme, lme
Event-based analysis					
E1	$\Delta$ exit duration = off2-duration - off1-duration	on1-feed: yes/no, on2-feed: yes/no	nest identity <sup>e</sup>	Gaussian	lme4, lmer

<sup>a</sup> Gaussian error structure: linear mixed model (LMM) with identity-link function; binomial error structure: generalized linear mixed model (GLMM) with logit-link function.

<sup>b</sup> Model reduction by removal of the non-significant square-root term does not alter results qualitatively (not shown).

<sup>c</sup> Models include a temporal auto-correlation structure (see Methods in main text).

<sup>d</sup> Results and model fit are almost identical when absolute date is used instead of incubation day (not shown).

<sup>e</sup> Results are similar when including male visit as random slope to allow the effect of male feeding visits on  $\Delta$  exit duration to differ between nests (not shown).

**Table S5.** Summary of the behavioural variables collected in 2016 using either direct observation, or video recordings inside or outside the nestbox.

	Events total count (range)	Events/h mean $\pm$ SD (range)
Observations <sup>a</sup> ( $n = 28$ nests; mean $\pm$ SD duration per nest = 2.1 h $\pm$ 0.6, range = 0.7 - 3)		
Male outside feeds	26 (0 - 3)	0.4 $\pm$ 0.5 (0 - 1.5)
Male entries	138 (0 - 62)	2.1 $\pm$ 4.2 (0 - 21.9)
Inside recordings <sup>b</sup> ( $n = 29$ nests; mean $\pm$ SD duration per nest = 13.5 h $\pm$ 4.0, range = 4.7 - 25.8)		
Male entries	359 (0 - 43)	0.9 $\pm$ 0.9 (0 - 3.6)
Male inside feeds	357 (0 - 43)	0.9 $\pm$ 0.9 (0 - 3.6)
Female exits	786 (7 - 64)	2.0 $\pm$ 0.7 (0.4 - 3.5)
Outside recordings <sup>c</sup> ( $n = 9$ nests; mean $\pm$ SD duration per nest = 3.3 h $\pm$ 1.2, range = 1.9 - 5)		
Male entries	127 (0 - 73)	4.0 $\pm$ 5.1 (0 - 15.8)
Proportion of male entries preceded by male call	0.86 (0.64 - 1.00) <sup>d</sup>	
Female exits	84 (4 - 17)	3 $\pm$ 0.8 (2 - 4.4)
Proportion of female exits preceded by male call	0.57 (0.18 - 1) <sup>e</sup>	

<sup>a</sup> 26 April-14 May, day 1-15 of full incubation, 1-12 days before hatching

<sup>b</sup> 26 April-14 May, day 1-15 of full incubation, 1-12 days before hatching

<sup>c</sup> 28 April-14 May, day 4-11 of full incubation, 1-10 days before hatching

<sup>d</sup> mean  $\pm$  SD among nests: 0.89  $\pm$  0.13

<sup>e</sup> mean  $\pm$  SD among nests: 0.61  $\pm$  0.22

**Table S6.** Effect of the time before hatching (in days; hatch day = 0) on the daily number of male feeding visits and on the daily amount of time spent in the nestbox by the female (non-active time excluded;  $n = 1061$  data points from 120 nests). Shown are results from linear mixed models with nest identity and year as random factors and a temporal autocorrelation structure. The number of male visits was square-root-transformed to approach normality. Note that positive estimates indicate a decrease, negative values an increase in incubation behaviour as hatching approaches.

Fixed effect	Estimate	95% CI	t	P
Response: $\sqrt{\text{Number of male visits}}$ <sup>a</sup>				
Intercept	2.5	1.9 to 3.2		
Day before hatching (2 to 14)	0.09	0.05 to 0.12	4.6	< 0.001
Response: Female h inside nest <sup>b</sup>				
Intercept	8.3	7.7 to 8.9		
Day before hatching (1 to 14)	-0.12	-0.16 to -0.09	-6.6	< 0.001

<sup>a</sup> Variance explained by random effects: nest ID = 17%, year = 31%

<sup>b</sup> Variance explained by random effects: nest ID = 16%, year = 31%

**Table S7.** Effect of time of day and hourly rainfall on the number of male feeding visits and on female incubation time. The number of male visits and the time spent in the nest by the female are calculated for each hour from 06:00 to 18:00 for every day during the period of full incubation ( $n = 12782$  data points from 120 nests). The number of male visits was also calculated per hour of female presence in the box. Shown are results from linear mixed models (models H1-3) with nest identity and year as random factors and a temporal autocorrelation structure. The number of male visits was square-root-transformed to approach normality.

Fixed effect	Estimate	95% CI	t	P
Response: $\sqrt{\text{Number of male visits}}$ <sup>a</sup>				
Intercept	0.7	0.3 to 1.0		
Hourly rainfall (ml)	-0.04	-0.07 to -0.002	-2.1	0.04
Time of day	-0.04	-0.05 to -0.03	-8.7	< 0.001
Response: Number of male visits / female time inside nest [h] <sup>b</sup>				
Intercept	2.7	1.7 to 3.7		
Hourly rainfall (ml)	-0.8	-1.4 to -0.1	-2.3	0.02
Time of day	-0.1	-0.3 to 0.03	-1.6	0.11
Response: Female time inside nest [min] <sup>c</sup>				
Intercept	31.7	30.2 to 33.2		
Hourly rainfall (ml)	0.2	-0.6 to 1.1	0.5	0.61
Time of day	-0.7	-0.9 to -0.5	-7.2	< 0.001

<sup>a</sup>Variance explained by random effects: nest ID = 20%, year = 29%

<sup>b</sup>Variance explained by random effects: nest ID = 2%, year = < 0.1%

<sup>c</sup>Variance explained by random effects: nest ID = 0.2%, year = 13%

**Table S8.** Effects of male feeding visit rate (number of feeding visits per hour of female active time) and female nest attendance (proportion of active time spent inside the nestbox) on the duration of the incubation period and on measures of breeding success. Male visit rate and female nest attendance are calculated across the period of full incubation and each nest represents one data point. Hatching success: proportion of eggs hatched ( $n = 171$  nests), early survival: proportion of hatchlings alive on day 5 ( $n = 161$ ), late survival: proportion of nestling alive on day 5 that fledged ( $n = 161$ ), fledging success: proportion of hatchlings that fledged ( $n = 170$ ). We differentiated between early and late survival, because incubation efficiency and male feeding of the incubating female might have stronger effects on events that happen immediately after hatching. Sample sizes vary because not all variables were available for all nests (see Results). Shown are results from a linear mixed model (for the duration of the incubation period,  $n = 171$ , model N3) and generalized linear mixed models with binomial error structure (logit link function; for the four measures of breeding success, models N4-7). All models include male, female, pair identity and year as random factors. For the analyses of breeding success, the fixed effects are mean-centred to obtain meaningful intercept values.

Fixed effect	Estimate	95% CI	z	P
Response: Duration of incubation period <sup>a</sup>				
Intercept	10.8	9.6 to 12.0		
Male visit rate	-0.2	-0.6 to 0.2	-1.1	0.28
Female nest attendance	1.8	-0.3 to 3.9	1.8	0.08
Response: Hatching success <sup>b</sup>				
Intercept	2.7	1.7 to 4.0		
Male visit rate	0.2	-0.4 to 0.8	0.7	0.46
Female nest attendance	1.3	-1.7 to 4.3	0.8	0.40
Response: Early survival <sup>c</sup>				
Intercept	3.6	3.2 to 4.1		
Male visit rate	0.5	-0.1 to 1.1	1.5	0.13
Female nest attendance	2.4	-0.5 to 5.4	1.5	0.12
Response: Late survival <sup>d</sup>				
Intercept	10.5	8.3 to 13.7		
Male visit rate	0.3	-1.8 to 3.0	0.3	0.78
Female nest attendance	7.5	-4.2 to 21.5	1.2	0.22
Response: Fledging success <sup>e</sup>				
Intercept	4.4	3.4 to 6.1		
Male visit rate	0.6	-0.6 to 1.9	1.0	0.31
Female nest attendance	6.5	0.1 to 14.1	1.9	0.06

<sup>a</sup>Variance explained by random effects: pair ID = 20%; male ID = 1%; female ID = 23%; year = 5%

<sup>b</sup>Variance explained by random effects: pair ID = 31%; male ID = 0.4%; female ID = 35%; year = 34%

<sup>c</sup>Variance explained by random effects: pair ID = 16%; male ID < 0.1%; female ID = 38%; year = 46%

<sup>d</sup>Variance explained by random effects: pair ID = 74%; male ID = 0.1%; female ID = 19%; year = 7%

<sup>e</sup>Variance explained by random effects: pair ID = 53%; male ID < 0.1%; female ID = 31%; year = 16%

**Table S9.** Effect of a male feeding visit during the female's incubation bout on the length of the subsequent incubation recess (exit duration). Considered are two subsequent incubation bouts and recesses of the female (on1 → off1 → on2 → off2), where the male could bring food during the first (on1-feed) and/or the second incubation-bout (on2-feed). The response variable is the difference in length of the two incubation recesses ( $\Delta$  exit duration = off2-duration-off1-duration). Results are from a linear mixed model (model E1) with nest identity and year as random factors ( $n = 8217$  data points from 120 nests). Variance explained by random effects: nest ID = < 0.1%, year = < 0.1%.

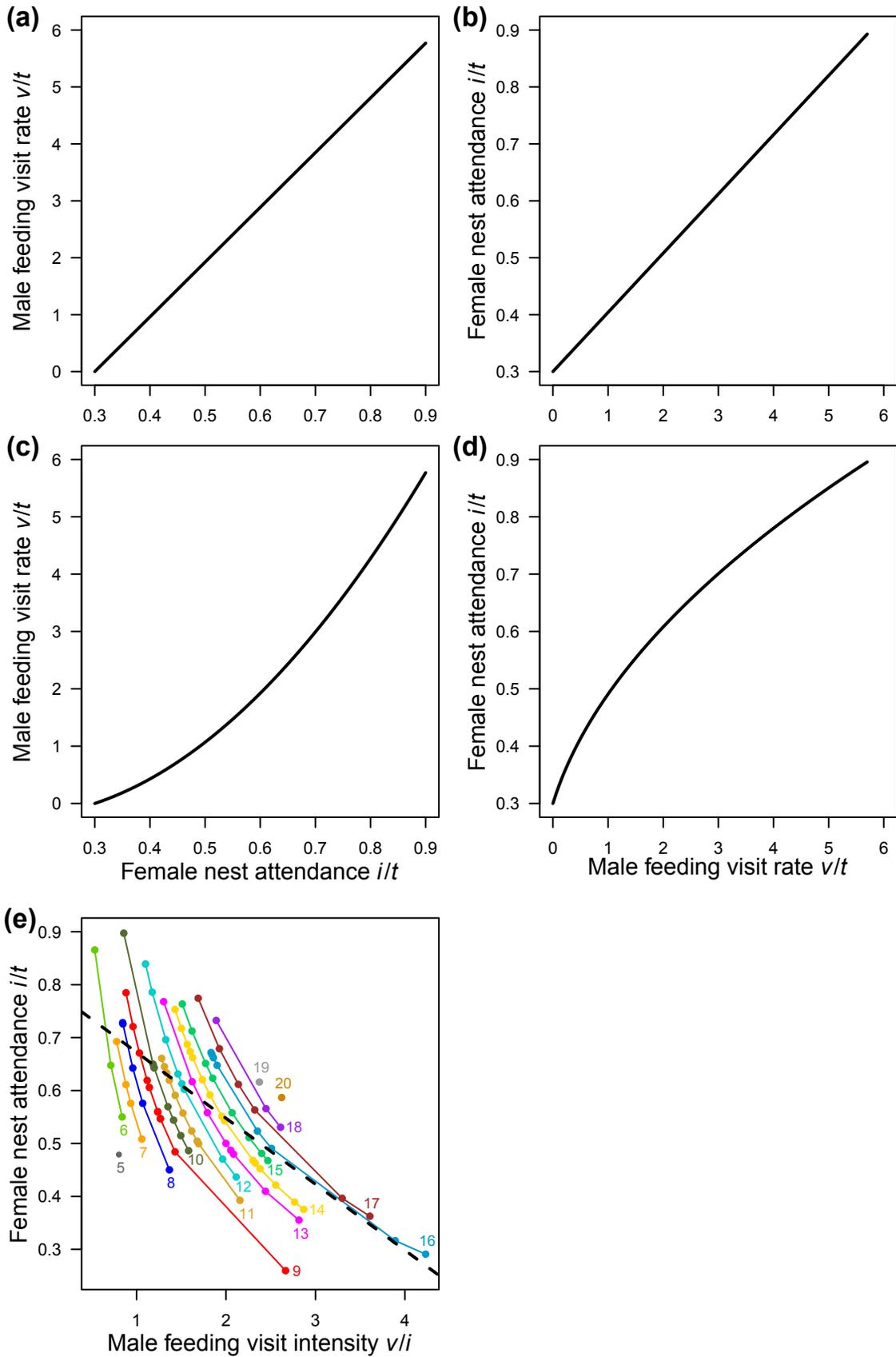
Fixed effect	Estimate	95% CI	t	P
Intercept	1.1	-5.4 to 11.0	0.3	0.74
on1-feed (yes vs. no)	18.0	6.8 to 30.2	3.1	0.002
on2-feed (yes vs. no)	-22.4	-34.2 to -10.7	-3.7	<0.001

**Table S10.** Incubation feeding and nest attendance in Paridae species (overview).

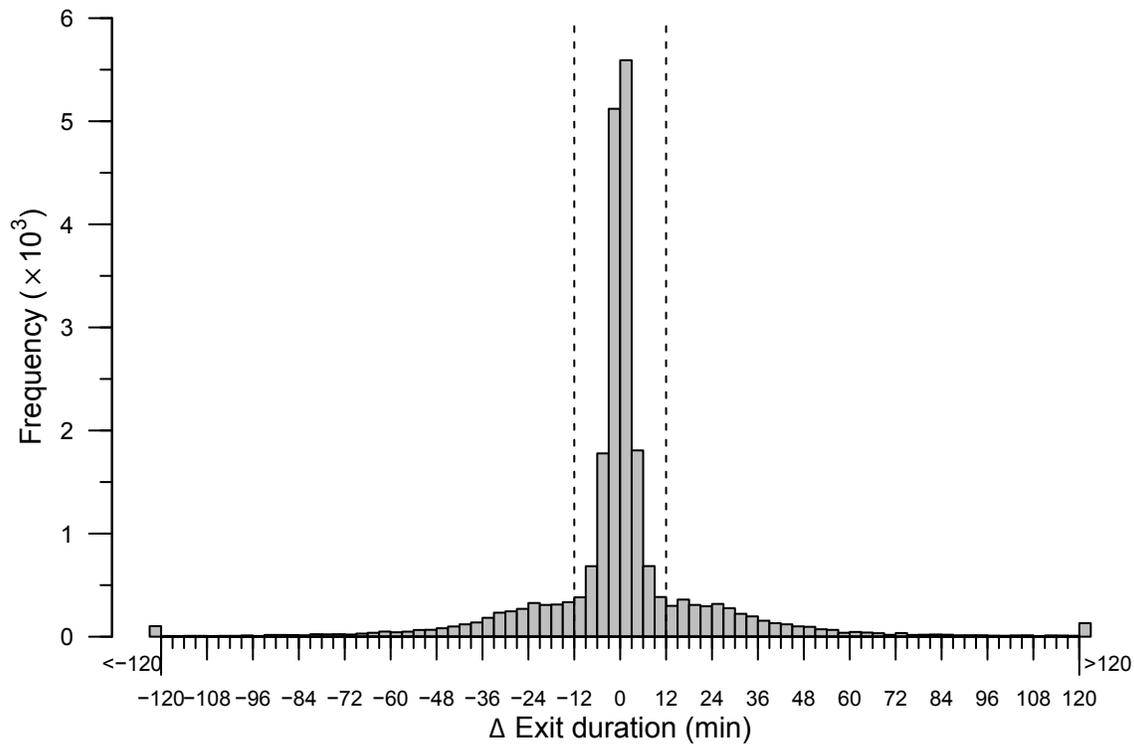
Factor and Species	Mean	SD	N	Source
Male incubation feeding rate (feeds / h)				
Blue Tit	1.7 <sup>a</sup>	1.7 <sup>a</sup>	171	<i>This study</i>
Blue Tit	1.8 <sup>a</sup>	1.9 <sup>a</sup>	63	Amininasab <i>et al.</i> 2017
Blue Tit	1.4	0.2	7	Cowie & Nowak 1990
Great Tit	0.9	1.2	90	Matysioková & Remeš 2010
Marsh Tit	2.5 <sup>a</sup>	1.5 <sup>a</sup>	10	Nilsson & Smith 1988, Figure 4
Mountain Chickadee	3.5	-	13	Ghalambor & Martin 2002, Figure 1; Martin & Ghalambor 1999
Tufted Titmouse	2.5	-	3	Offutt 1965
Black-capped Chickadee	1.6	0.9	32	Otter <i>et al.</i> 1999
Boreal Chickadee	0.7	-	8	McLaren 1975
Carolina Chickadee	2.2 <sup>a</sup>	-	<6	Brewer 1961
Female nest attendance (%)				
Blue Tit	59 <sup>b</sup>	8	171	<i>This study</i>
Blue Tit	60 <sup>c</sup>	12	171	<i>This study</i>
Blue Tit	58 <sup>b,d</sup>	13	171	<i>This study</i>
Blue Tit	63 <sup>c,d</sup>	12	171	<i>This study</i>
Blue Tit	64 <sup>b,e</sup>	10	171	<i>This study</i>
Blue Tit	68 <sup>c,e</sup>	9	171	<i>This study</i>
Blue Tit	73 <sup>c</sup>	6	63	Amininasab <i>et al.</i> 2017
Blue Tit	82 <sup>f1</sup>	-	7	Cowie & Nowak 1990
Blue Tit	67 <sup>b</sup>	1	157	Bueno-Enciso <i>et al.</i> 2016, 2017
Blue Tit	75 <sup>u</sup>	-	-	Deeming & Gray 2016, Table 1
Great Tit	>60 <sup>b</sup>	-	25	de Heij <i>et al.</i> 2008
Great Tit	82 <sup>f2</sup>	-	12	Boucaud <i>et al.</i> 2016
Great Tit	77 <sup>f3</sup>	5	77	Matysioková & Remeš 2010
Great Tit	76 <sup>c</sup>	-	7	Shaw & Cresswell 2014
Stripe-breasted Tit	68 <sup>c</sup>	-	51	Shaw & Cresswell 2014
Willow Tit	80 <sup>b</sup>	-	2	Haftorn 1979, Figures 11 and 12
Marsh Tit	74 <sup>g</sup>	11	10	Nilsson & Smith 1988, Figure 2
Four Paridae species	80 <sup>h</sup>	4	-	Chalfoun & Martin, 2007 Figure 2

<sup>a</sup> feeds per female attentive hour<sup>b</sup> Percentage of female active time (see Methods for definition).<sup>c</sup> Percentage of time between sunrise and sunset.<sup>d</sup> only last three days pre-hatching included ( $n = 438$  days).<sup>e</sup> Days with extended recesses excluded (resulting  $n = 761$  days).<sup>f</sup> Percentage of fixed recording interval:<sup>1</sup> Recording interval 06.00–19.00. <sup>2</sup> Recording interval 05.30–14.00. <sup>3</sup> Recording interval 05.00–22.30.<sup>g</sup> Percentage of 1-hour observation period.<sup>h</sup> Percentage of undefined interval.

## **SUPPLEMENTARY FIGURES**

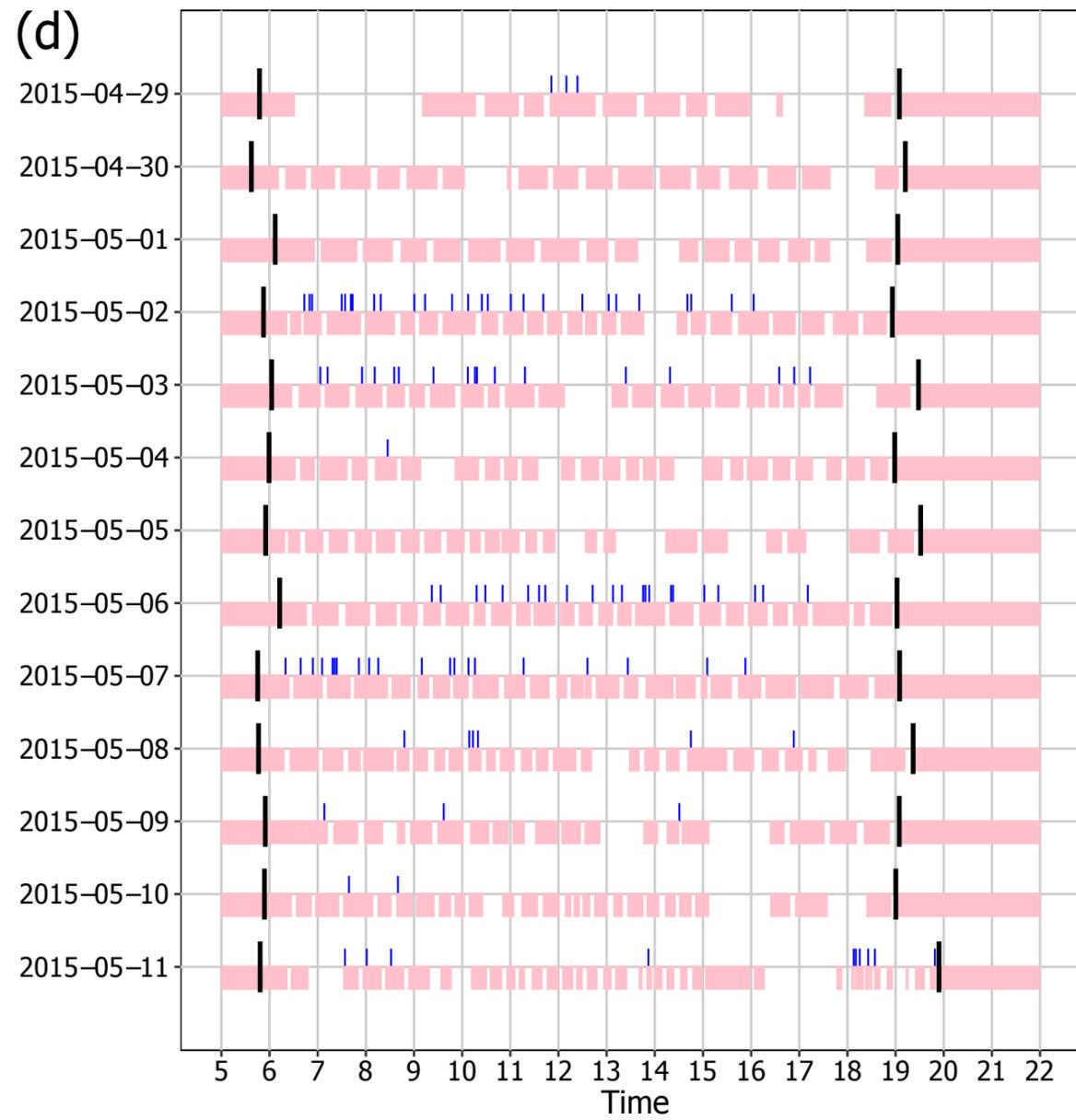
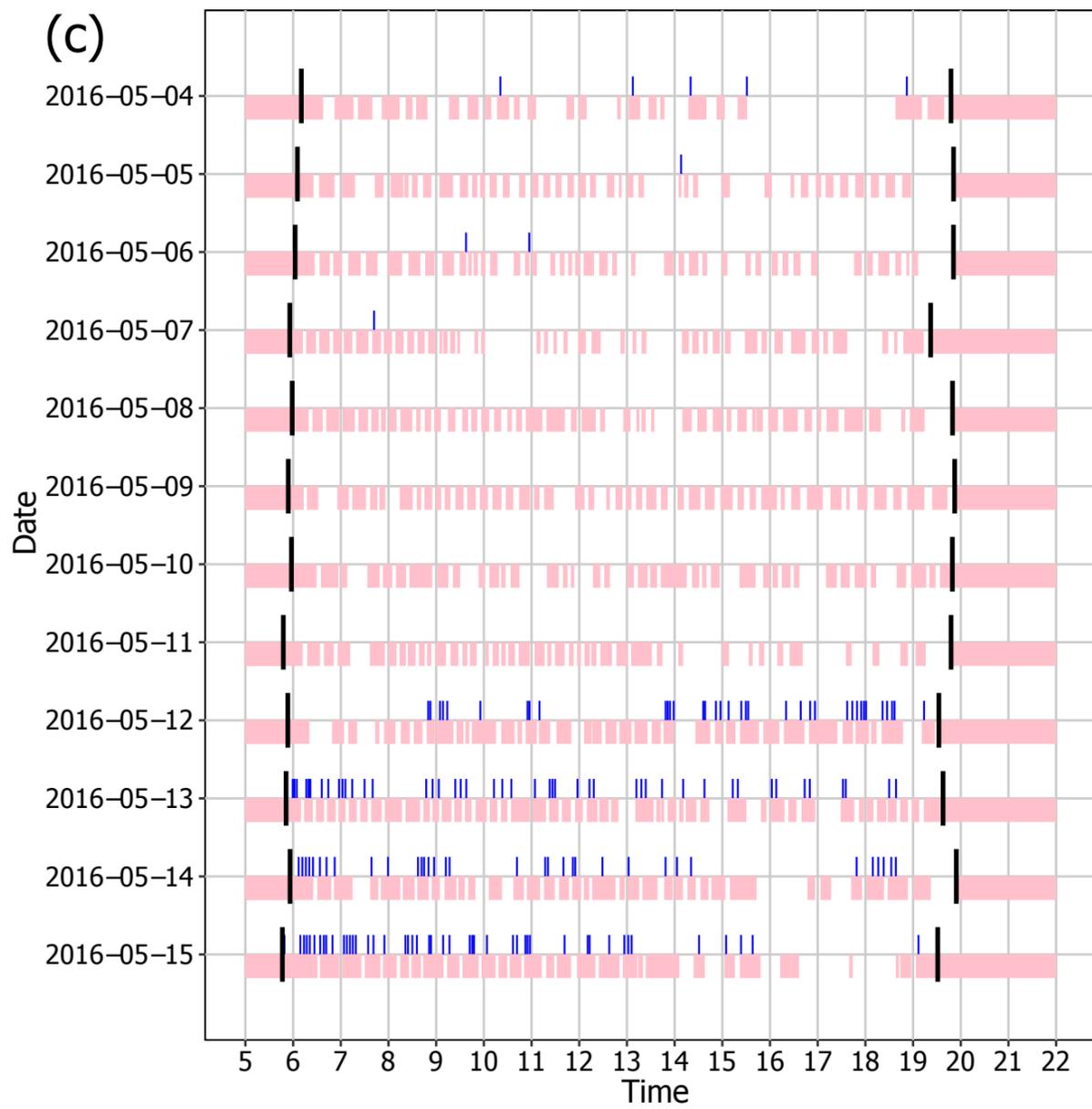
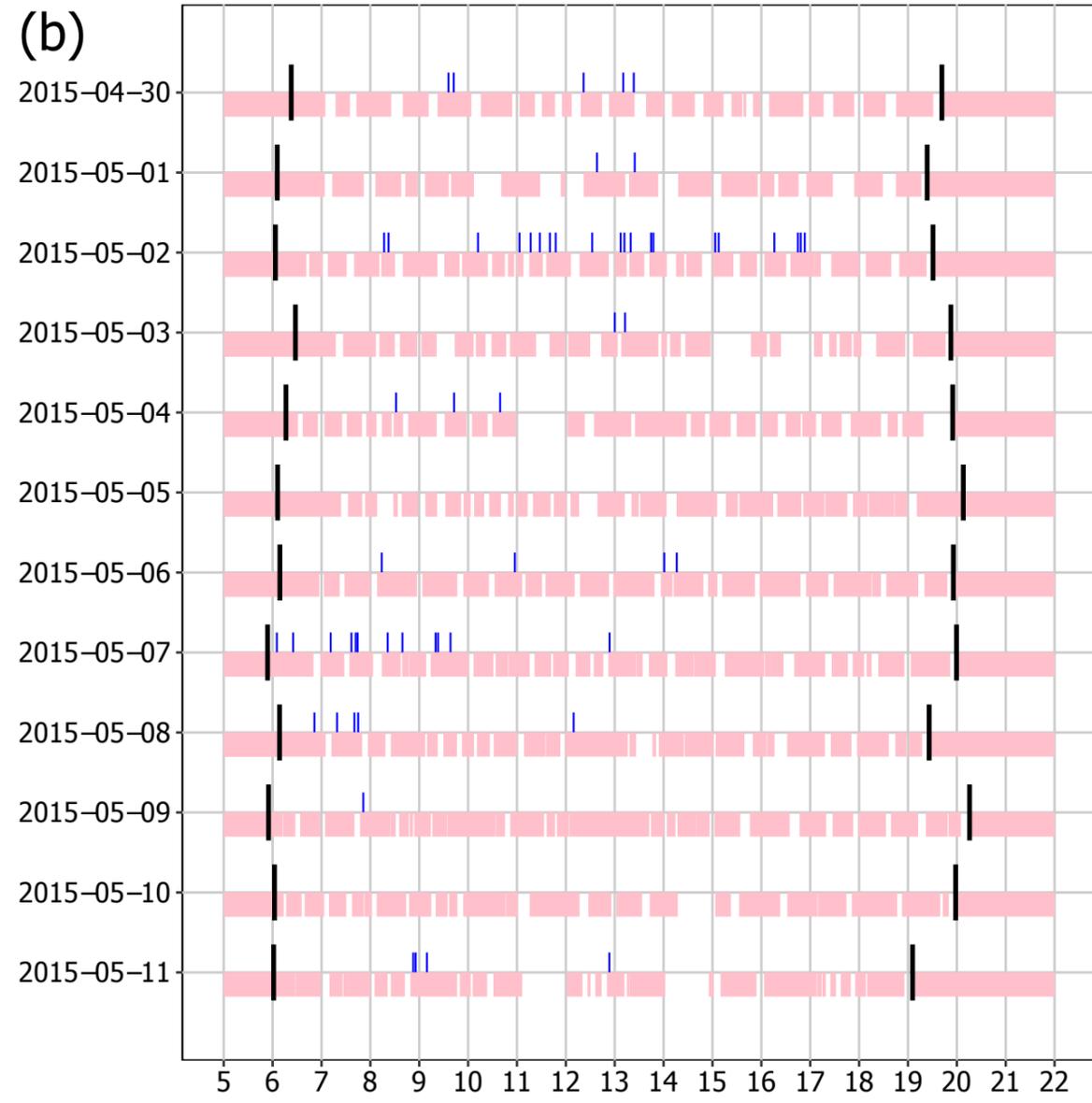
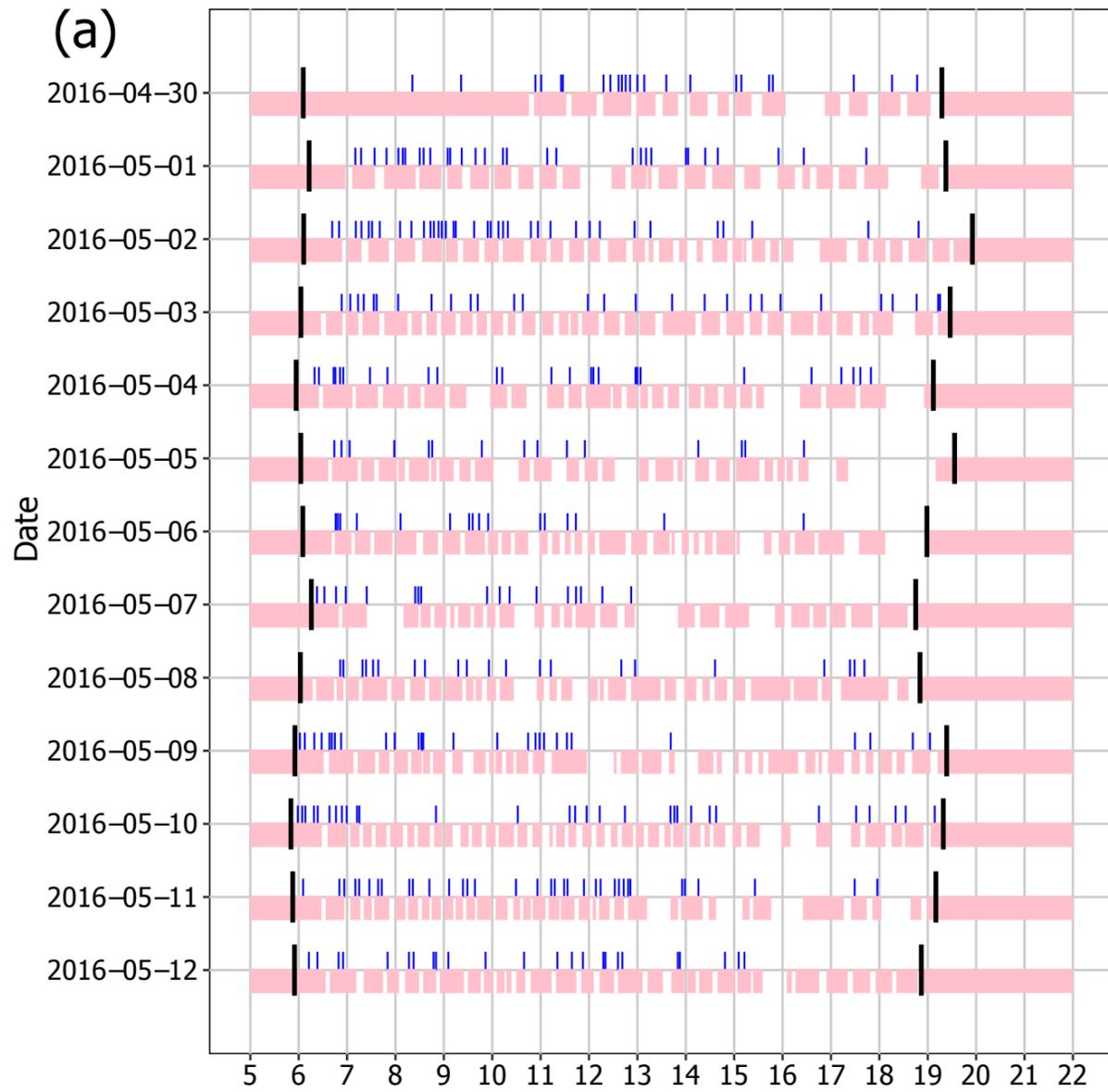


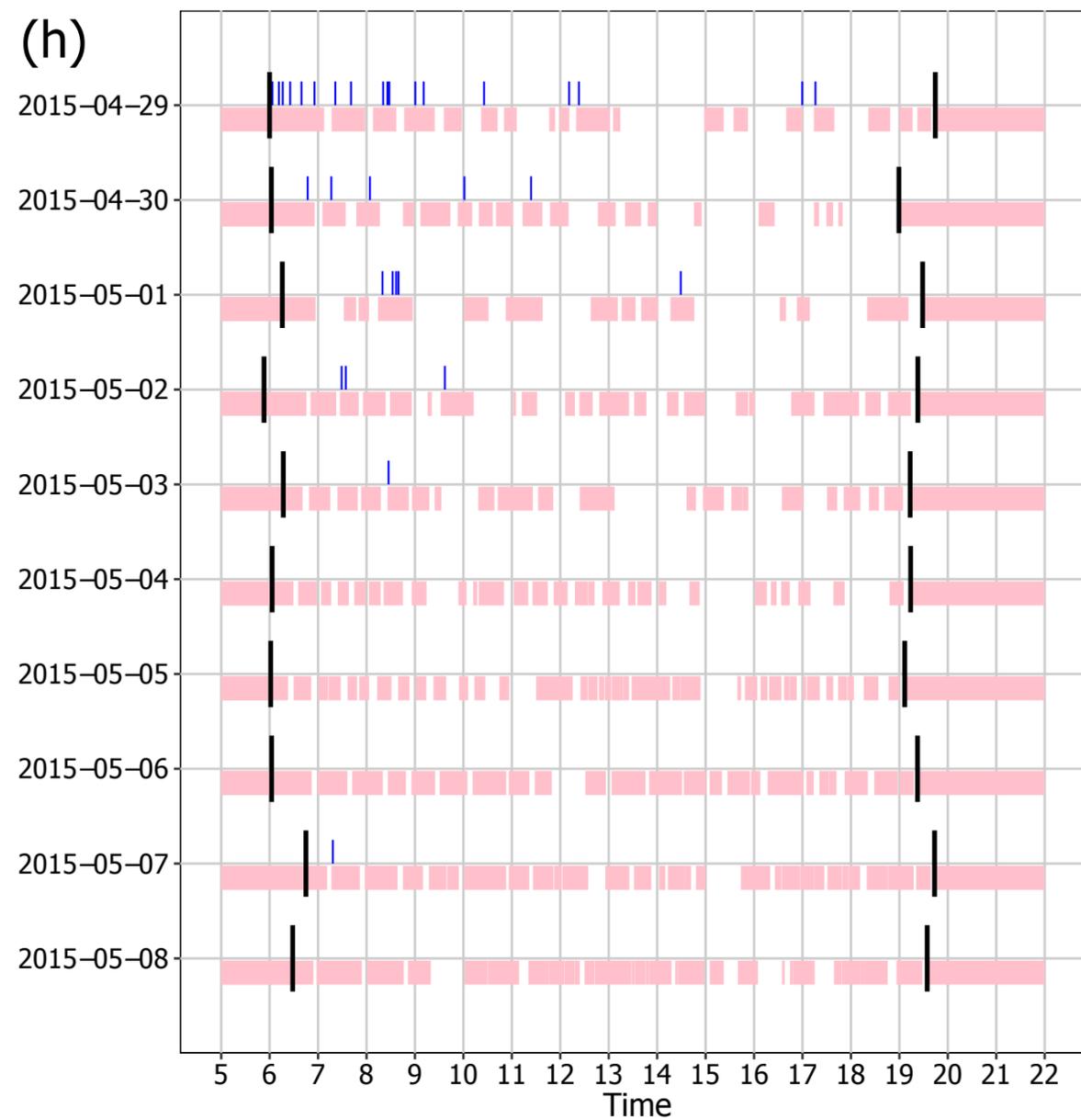
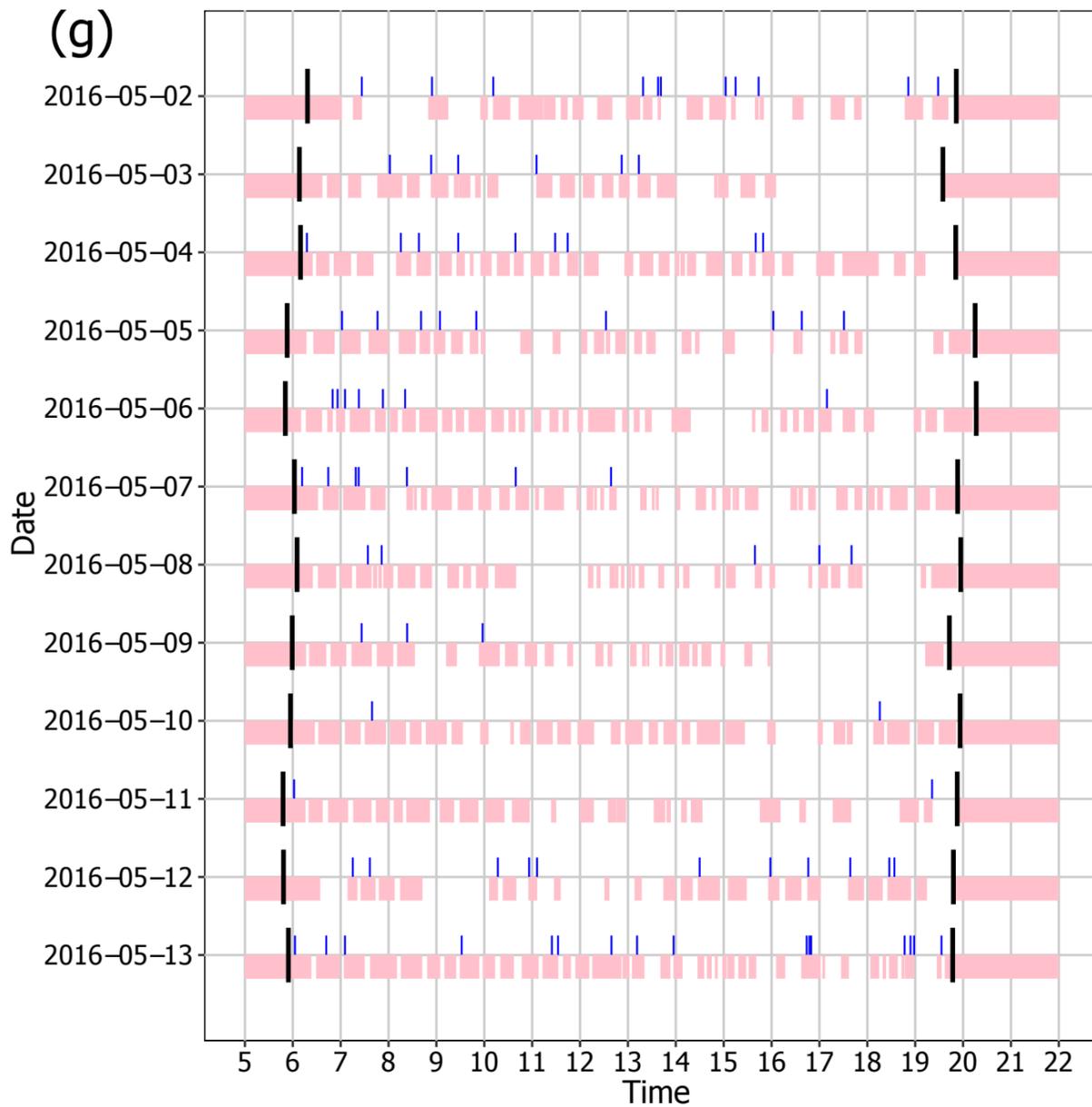
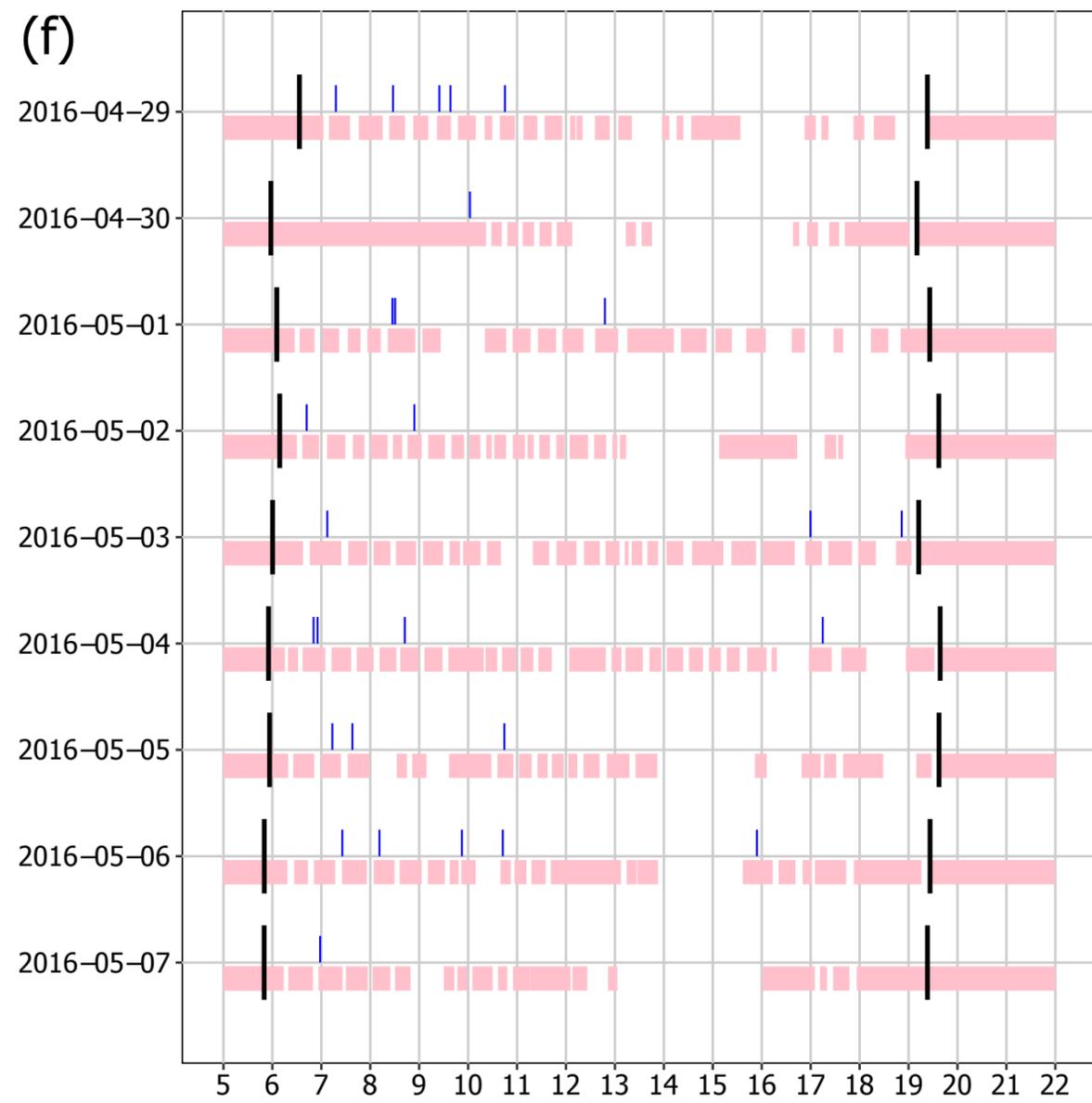
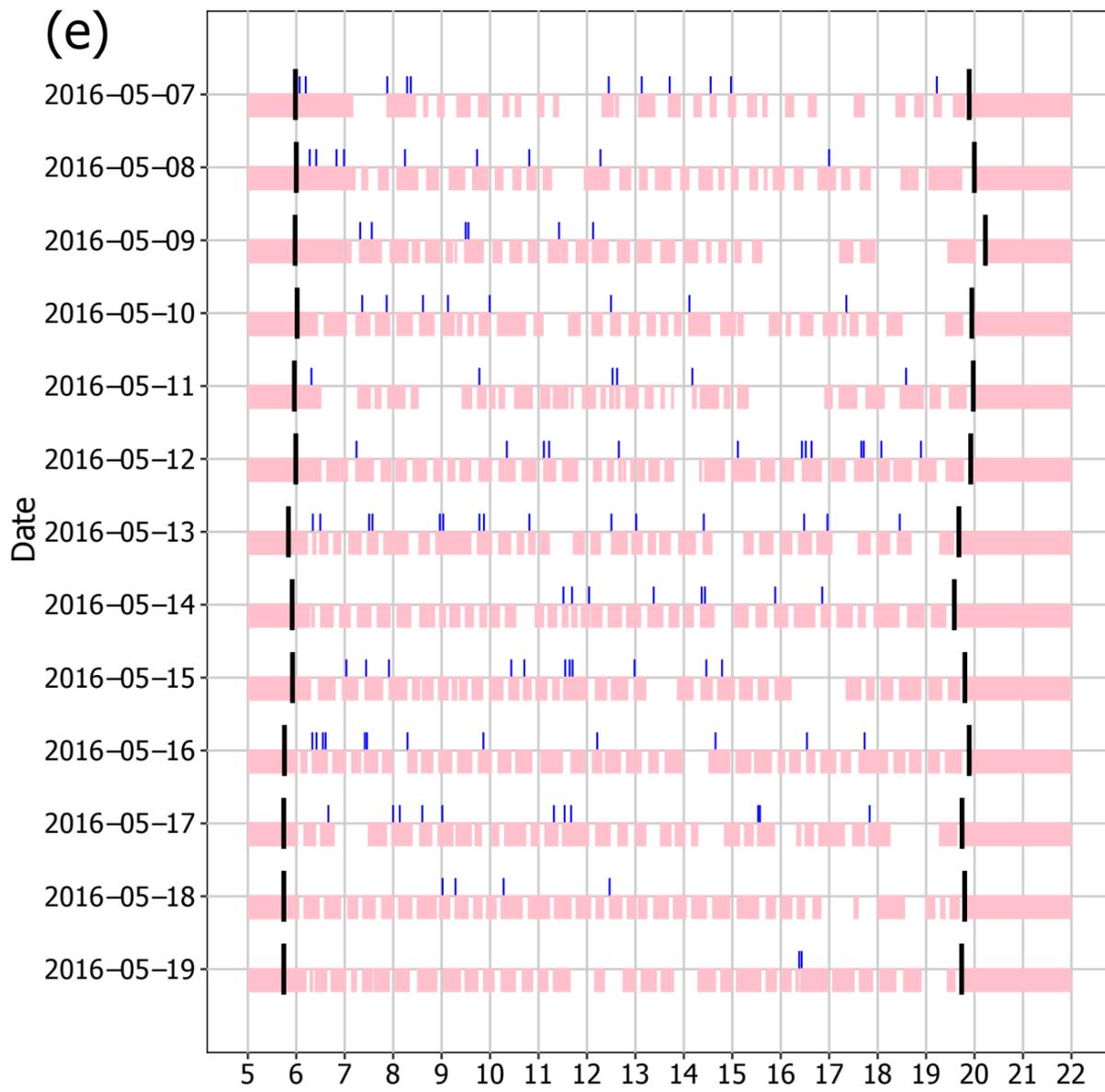
**Figure S1.** Theoretical implications of examining the association between male feeding and female incubation behaviour. Female incubation behaviour is represented by nest attendance, which is the time the female spends incubating,  $i$ , divided by her active time,  $t$ . Male feeding behaviour is computed in two ways: (i) as male feeding visit rate: the number of feeding visits,  $v$ , performed over the female's active time,  $t$ ; (ii) as male feeding visit intensity: the number of feeding visits,  $v$ , performed over the female's attentive time (i.e. the time the female is in the nestbox, i.e. the time available to the male for feeding visits),  $i$ . **(a, b)** Linear association (schematic) of female nest attendance,  $\frac{i}{t}$ , and male feeding visit rate,  $\frac{v}{t}$  (a) and the inverse relation (b). This relationship may arise if females receive a fixed amount of feeds per unit time (on or off the nest, a) or if males are limited in their feeding visits by female presence at the nestbox (b). Thus, a linear relationship provides limited evidence for a behavioural mechanism linking investment of males and females (Matysioková *et al.* 2011). A non-linear relationship on the other hand would suggest the action of an additional process. **(c, d)** Non-linear association (schematic) of female nest attendance,  $\frac{i}{t}$ , and male feeding visit rate,  $\frac{v}{t}$  (c) and the inverse relation (d). With quadratic growth,  $\left(\frac{i}{t}\right)^2 \sim \frac{v}{t}$ , male feeding visits increase faster than predicted by female attendance alone (c). Female nest attendance increases more slowly than predicted from a fixed rate of male feeding visits throughout (d), in this case in a square-root relationship  $\frac{i}{t} \sim \sqrt{\frac{v}{t}}$ . Note that this can be rearranged to  $\frac{i}{t} \sim \frac{v}{i}$ , i.e. a linear relationship between male feeding visit intensity and female nest attendance. This association has been tested in previous studies (Hałupka 1994, Hatchwell *et al.* 1999, Matysioková *et al.* 2011, Amininasab *et al.* 2017). **(e)** Testing the association of male feeding visit intensity,  $\frac{v}{t}$ , and female nest attendance,  $\frac{i}{t}$ . Illustrated is an example of 100 randomly generated data points. Data for female incubation lengths,  $i$ , were drawn from a normal distribution (mean = 7.4, SD = 1.8). Data for male visit numbers,  $v$ , were drawn from a Poisson distribution ( $\lambda = 12.1$ ). For simplicity, female active time,  $t$ , was assumed to be constant at 13 h. Colours indicate data based on the same number of male feeding visits,  $v$  (value indicated by number). Because changes in  $i$  affect nest attendance and feeding visit intensity in opposite directions, identical visit numbers come with lower feeding intensity for longer female incubation lengths. The dashed line indicates the regression line for the complete data set, which is declining although data were randomly generated (intercept:  $a = 0.8$  (0.7 to 0.8),  $t = 32.8$ ,  $P < 0.001$ ; slope:  $b = -0.1$  (-0.2 to -0.1),  $t = -9.6$ ,  $P < 0.001$ ): the null-hypothesis for this test is a negative relationship, which makes interpretation of statistical results difficult.

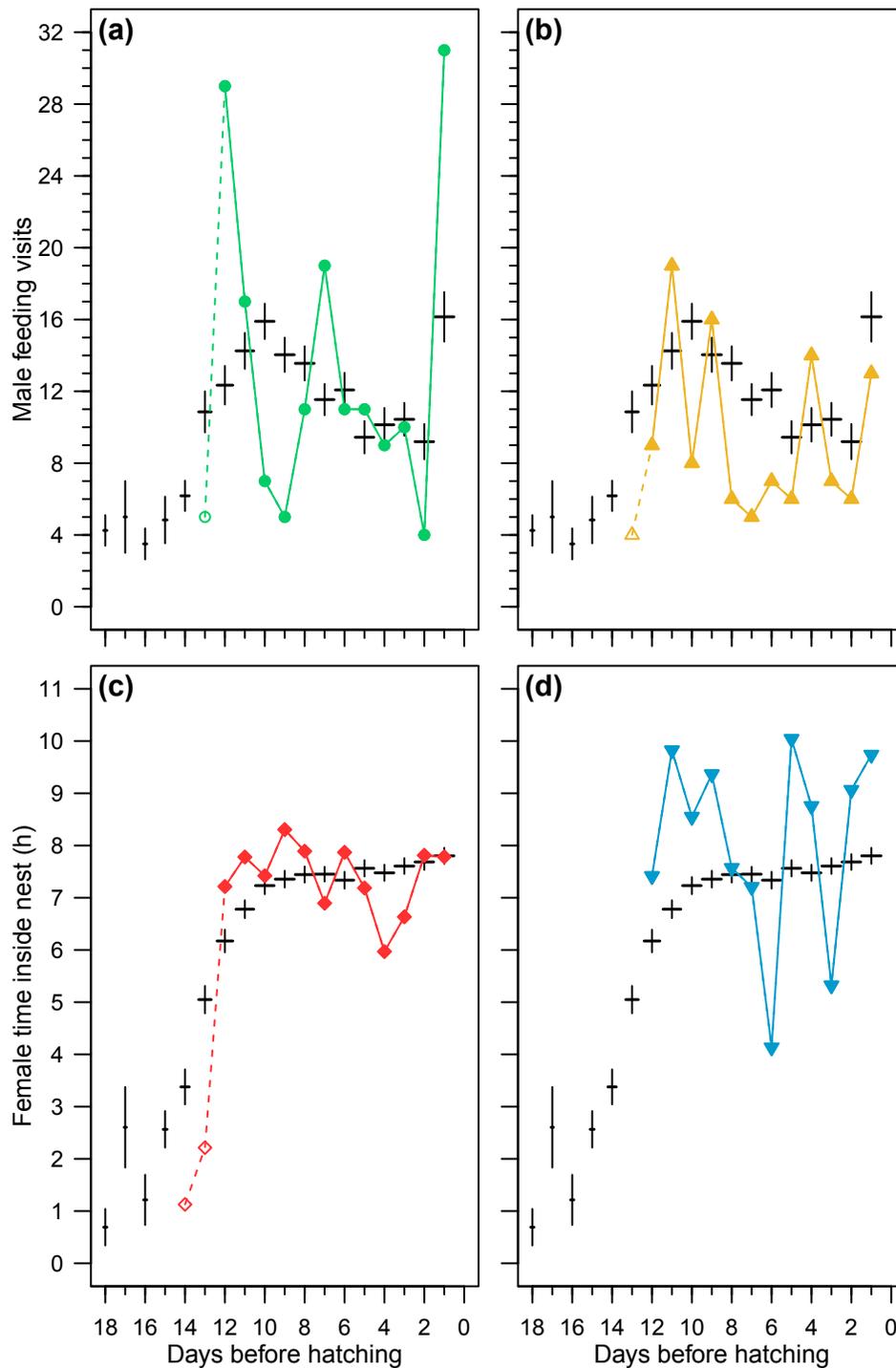


**Figure S2.** Frequency distribution of  $\Delta$  exit duration: mean  $\pm$  SD =  $44 \pm 1834$  s; 1<sup>st</sup>, 2<sup>nd</sup>, and 3<sup>rd</sup> quartile = -3, 0.2, and 4 min, respectively; range = -7.9 to 8.4 h;  $n = 23312$ .  $\Delta$  exit durations between -12 and 12 min were included in the analysis (indicated by dashed lines,  $n = 16435$ , 70% of all data).

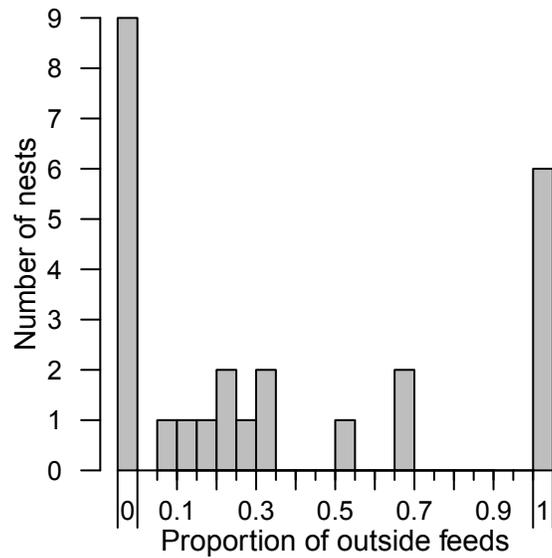
**Figure S3 (below).** Actograms showing variation in male nest visit behaviour and in female nest attendance. Each actogram shows one pair with the pattern of male visits (blue lines) and female presence in the nestbox (pink area) during the period of full incubation. Black lines indicate the first female exit in the morning and the last female entry in the evening (the period in between is considered the female's 'active period'). Examples illustrate: variation among males in the number of visits (a, b), and in the way male visit patterns change between days (c, d), and variation among females in the amount of time spent on the nest (e, f) and in the way female nest attendance varies between days (g, h).



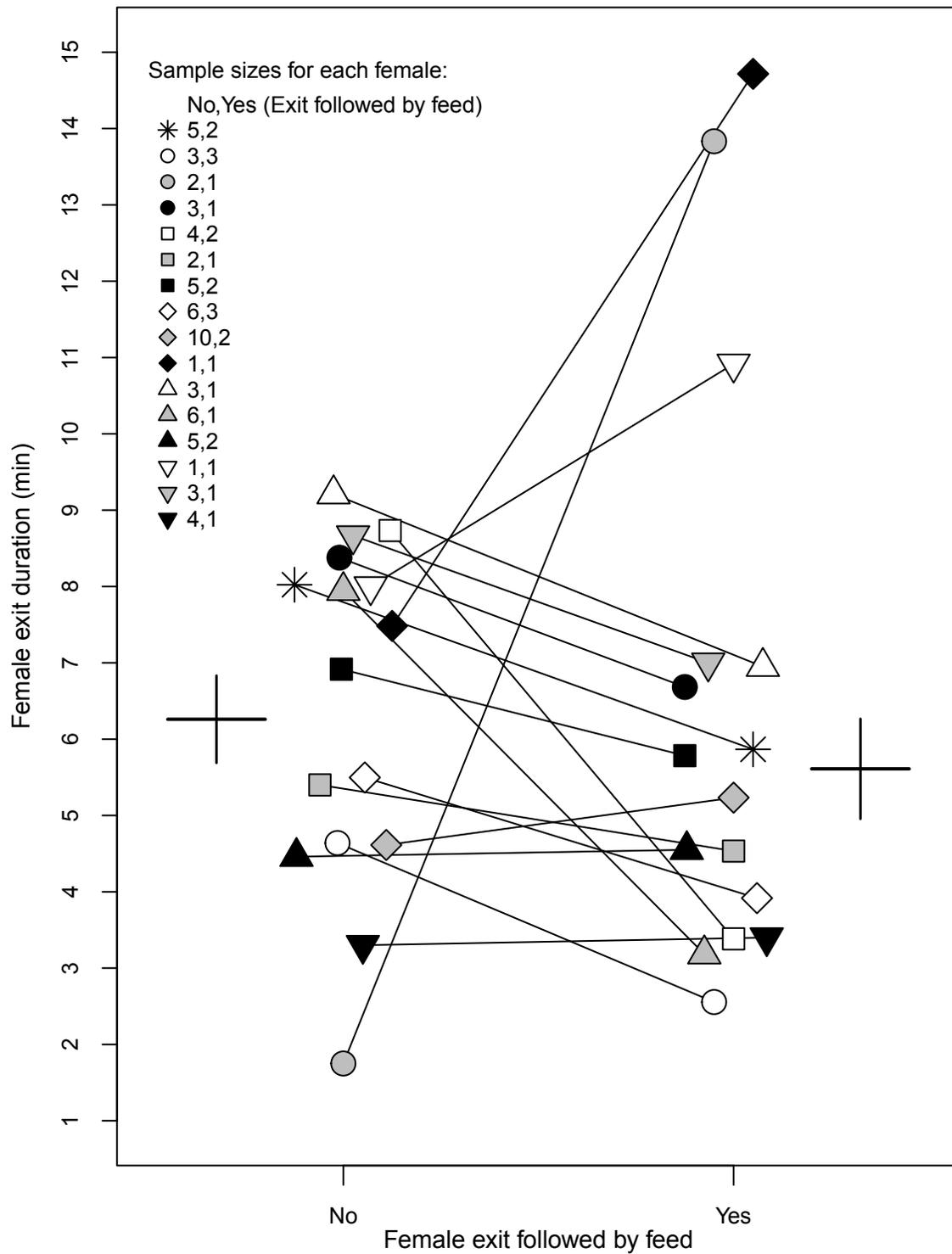




**Figure S4.** Examples of daily variation in feeding visits to the nestbox for two males (a, b) and in time spent inside the nestbox for two females (c, d). The population pattern is shown in black as comparison (see Fig. 1 for details). Dashed lines and open symbols are days before the start of full incubation (see Methods section for definition).

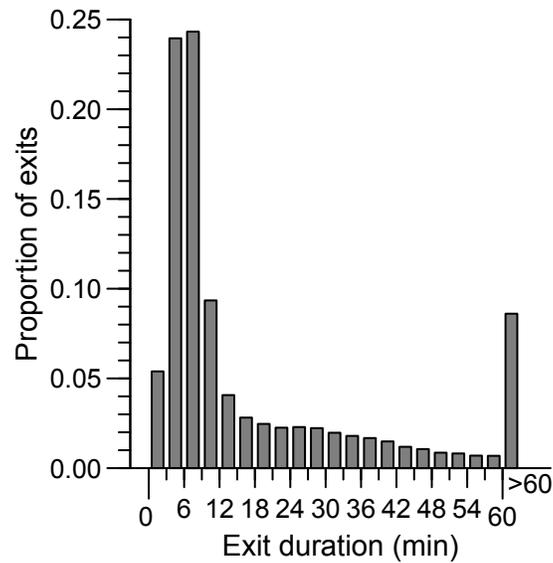


**Figure S5.** Frequency distribution of the proportion of male feeds observed outside the nestbox among all observed male feeds ( $n = 175$ ). Data based on direct observations of nestboxes where at least one feeding event (outside or inside the nest) was observed ( $n = 26$  pairs).



**Figure S6.** Female exit duration with or without a male feed observed outside the nestbox. Shown are for each of 16 females for which at least one outside feed was observed the mean exit duration, either without an outside feed (no,  $n = 63$ ) or with a feed (yes,  $n = 25$ ) after the exit. The black horizontal bars

and whiskers indicate the mean and standard errors for all females combined. Exit durations were somewhat shorter when the male fed the female, but the difference was not significant (linear mixed model with nest identity as a random factor: difference: 0.7 (95% CI: -2.6, 1.3);  $P = 0.52$ ;  $n = 88$ ; nest identity explained 19% of the variation).



**Figure S7.** Frequency distribution of female exit durations ( $n = 51215$  exits from 171 nests).

## SUPPLEMENTARY REFERENCES

- Amininasab, S. M., Birker, M., Kingma, S. A., Hildenbrandt, H. & Komdeur, J.** 2017. The effect of male incubation feeding on female nest attendance and reproductive performance in a socially monogamous bird. *J. Ornithol.* **158**: 687–696.
- Amininasab, S. M., Kingma, S. A., Birker, M., Hildenbrandt, H. & Komdeur, J.** 2016. The effect of ambient temperature, habitat quality and individual age on incubation behaviour and incubation feeding in a socially monogamous songbird. *Behav. Ecol. Sociobiol.* **70**: 1591–1600.
- Ardia, D. R., Pérez, J. H., Chad, E. K., Voss, M. A. & Clotfelter, E. D.** 2009. Temperature and life history: experimental heating leads female Tree Swallows to modulate egg temperature and incubation behaviour. *J. Anim. Ecol.* **78**: 4–13.
- Boucaud, I. C. A., Aguirre Smith, M. L. N., Valère, P. A. & Vignal, C.** 2016. Incubating females signal their needs during intrapair vocal communication at the nest: a feeding experiment in Great Tits. *Anim. Behav.* **122**: 77–86.
- Boulton, R. L., Richard, Y. & Armstrong, D. P.** 2010. The effect of male incubation feeding, food and temperature on the incubation behaviour of New Zealand Robins. *Ethology* **116**: 490–497.
- Brewer, R.** 1961. Comparative notes on the life history of Carolina Chickadees. *Wilson Bull.* **73**: 348–373.
- Bueno-Enciso, J., Barrientos, R. & Sanz, J. J.** 2017. Incubation behaviour of Blue *Cyanistes caeruleus* and Great Tits *Parus major* in a Mediterranean habitat. *Acta Ornithol.* **52**: 21–34.
- Bueno-Enciso, J., Ferrer, E. S., Barrientos, R. & Sanz, J. J.** 2016. Effect of nestbox type on the breeding performance of two secondary hole-nesting passerines. *J. Ornithol.* **157**: 759–772.
- Cantarero, A., López-Arrabé, J., Palma, A., Redondo, A. J. & Moreno, J.** 2014. Males respond to female begging signals of need: A handicapping experiment in the Pied Flycatcher, *Ficedula hypoleuca*. *Anim. Behav.* **94**: 167–173.
- Cantarero, A., López-Arrabé, J., Plaza, M., Saavedra-Garcés, I. & Moreno, J.** 2016. Males feed their mates more and take more risks for nestlings with larger female-built nests: an experimental study in the Nuthatch *Sitta europaea*. *Behav. Ecol. Sociobiol.* **70**: 1141–1150.
- Chalfoun, A. D. & Martin, T. E.** 2007. Latitudinal variation in avian incubation attentiveness and a test of the food limitation hypothesis. *Anim. Behav.* **73**: 579–585.
- Coe, B. H., Beck, M. L., Chin, S. Y., Jachowski, C. M. B. & Hopkins, W. A.** 2015. Local variation in weather conditions influences incubation behavior and temperature in a passerine bird. *J. Avian Biol.* **46**: 385–394.
- Cowie, R.J. & Novak, J.A.** 1990. Incubation patterns of Blue tits (*Parus caeruleus*). In Blondel, J., Gosler, A., Lebreton, J.-D., McCleery, R. (eds) *Population biology of Passerine birds: An integrated approach*: 345–356. Berlin, Germany: Springer.
- Deeming, D. C. & Gray, L. A.** 2016. Incubation attentiveness and nest insulatory values correlate in songbirds. *Avian Biol. Res.* **9**: 32–36.
- Delhey, K., Johnsen, A., Peters, A., Andersson, S. & Kempenaers, B.** 2003. Paternity analysis reveals opposing selection pressures on crown coloration in the Blue Tit (*Parus caeruleus*). *Proc. R. Soc. Lond. B* **270**: 2057–2063.
- Fontaine, J. J. & Martin, T. E.** 2006. Parent birds assess nest predation risk and adjust their reproductive strategies. *Ecol. Lett.* **9**: 428–434.
- Galván, I. & Sanz, J. J.** 2011. Mate-feeding has evolved as a compensatory energetic strategy that affects breeding success in birds. *Behav. Ecol.* **22**: 1088–1095.
- Ghalambor, C. K. & Martin, T. E.** 2002. Comparative manipulation of predation risk in incubating birds reveals variability in the plasticity of responses. *Behav. Ecol.* **13**: 101–108.
- Haftorn, S.** 1979. Incubation and regulation of

- egg temperature in the Willow Tit *Parus montanus*. *Ornis Scand.* **10**: 220–234.
- Hałupka, K.** 1994. Incubation feeding in Meadow Pipit *Anthus pratensis* affects female time budget. *J. Avian Biol.* **25**: 251–253.
- Hatchwell, B., Fowlie, M., Ross, D. & Russell, A.** 1999. Incubation behavior of Long-tailed Tits: why do males provision incubating females? *Condor* **101**: 681–686.
- de Heij, M. E., Ubels, R., Visser, G. H. & Tinbergen, J. M.** 2008. Female Great Tits *Parus major* do not increase their daily energy expenditure when incubating enlarged clutches. *J. Avian Biol.* **39**: 121–126.
- Jawor, J. M. & Breitwisch, R.** 2006. Is mate provisioning predicted by ornamentation? A test with Northern Cardinals (*Cardinalis cardinalis*). *Ethology* **112**: 888–895.
- Klatt, P. H., Stutchbury, B. J. M. & Evans, M. L.** 2008. Incubation feeding by male Scarlet Tanagers: a mate removal experiment. *J. Field Orn.* **79**: 1–10.
- Kötél, D., Laczi, M., Török, J. & Hegyi, G.** 2016. Mutual ornamentation and the parental behaviour of male and female Collared Flycatchers *Ficedula albicollis* during incubation. *Ibis* **158**: 796–807.
- Lefcheck, J. S., Byrnes, J. E. K., Isbell, F., Gamfeldt, L., Griffin, J. N., Eisenhauer, N., Hensel, M. J. S., Hector, A., Cardinale, B. J. & Duffy, J. E.** 2015. Biodiversity enhances ecosystem multifunctionality across trophic levels and habitats. *Nature Comm.* **6**: 6936.
- Lifjeld, J. T. & Slagsvold, T.** 1986. The function of courtship feeding during incubation in the Pied Flycatcher *Ficedula hypoleuca*. *Anim. Behav.* **34**: 1441–1453.
- Lifjeld, J. T. & Slagsvold, T.** 1989. Female nutritional state influences the allocation of incubation feeding by polygynous Pied Flycatcher males. *Anim. Behav.* **38**: 903–904.
- Lifjeld, J. T., Slagsvold, T. & Stenmark, G.** 1987. Allocation of incubation feeding in a polygynous mating system: a study on Pied Flycatchers *Ficedula hypoleuca*. *Anim. Behav.* **35**: 1663–1669.
- Lyon, B. E. & Montgomerie, R. D.** 1985. Incubation feeding in Snow Buntings: female manipulation or indirect male parental care? *Behav. Ecol. Sociobiol.* **17**: 279–284.
- Martin, T. E. & Ghalambor, C. K.** 1999. Males feeding females during incubation. I. Required by microclimate or constrained by predation? *Am. Nat.* **153**: 131–139.
- Matysioková, B. & Remeš, V.** 2010. Incubation feeding and nest attentiveness in a socially monogamous songbird: role of feather colouration, territory quality and ambient environment. *Ethology* **116**: 596–607.
- Matysioková, B., Cockburn, A. & Remeš, V.** 2011. Male incubation feeding in songbirds responds differently to nest predation risk across hemispheres. *Anim. Behav.* **82**: 1347–1356.
- Matysioková, B. & Remeš, V.** 2014. The importance of having a partner: male help releases females from time limitation during incubation in birds. *Front. Zool.* **11**: 24.
- McLaren, M. A.** 1975. Breeding biology of the Boreal Chickadee. *Wilson Bull.* **87**: 344–354.
- Moore, S. D. & Rohwer, V. G.** 2012. The functions of adult female begging during incubation in sub-Arctic breeding Yellow Warblers. *Anim. Behav.* **84**: 1213–1219.
- Moreno, J. & Carlson, A.** 1989. Clutch size and the costs of incubation in the Pied Flycatcher *Ficedula hypoleuca*. *Ornis Scand.* **20**: 123–128.
- Moreno, J., Redondo, A. J., Cantarero, A., Ruiz-de-Castañeda, R. & González-Braojos, S.** 2011. Handicapped females receive more feedings during incubation from their mates: support for the female nutrition hypothesis. *Acta Ethol.* **14**: 85–89.
- Morton, M. L. & Pereyra, M. E.** 1985. The regulation of egg temperatures and attentiveness patterns in the Dusky Flycatcher (*Empidonax oberholseri*). *Auk* **102**: 25–37.
- Nilsson, J.-Å. & Smith, H. G.** 1988. Incubation feeding as a male tactic for early hatching. *Anim. Behav.* **36**: 641–647.
- Offutt, G. C.** 1965. Behavior of the Tufted Titmouse before and during the nesting season. *Wilson Bull.* **77**: 382–387.
- Otter, K., Ramsay, S. M. & Ratcliffe, L.** 1999. Enhanced reproductive success of female Black-capped Chickadees mated to high-

- ranking males. *Auk* **116**: 345–354.
- Pearse, A. T., Cavitt, J. F. & Cully, J. F.** 2004. Effects of food supplementation on female nest attentiveness and incubation mate feeding in two sympatric wren species. *Wilson Bull.* **116**: 23–30.
- Radford, A. N.** 2004. Incubation feeding by helpers influences female nest attendance in the Green Woodhoopoe, *Phoeniculus purpureus*. *Behav. Ecol. Sociobiol.* **55**: 583–588.
- Rauter, C. & Reyer, H.-U.** 1997. Incubation pattern and foraging effort in the female Water Pipit *Anthus spinoletta*. *Ibis* **139**: 441–446.
- Røskoft, E., Espmark, Y. & Järvi, T.** 1983. Reproductive effort and breeding success in relation to age by the Rook *Corvus frugilegus*. *Ornis Scand.* **14**: 169–174.
- Schlicht, L., Girg, A., Loës, P., Valcu, M. & Kempenaers, B.** 2012. Male extrapair nestlings fledged first. *Anim. Behav.* **83**: 1335–1343
- Shaw, P. & Cresswell, W.** 2014. Latitudinal variation in day length and working day length has a confounding effect when comparing nest attentiveness in tropical and temperate species. *J. Ornithol.* **155**: 481–489.
- Siefferman, L. & Hill, G. E.** 2005. Blue structural coloration of male eastern bluebirds *Sialia sialis* predicts incubation provisioning to females. *J. Avian Biol.* **36**: 488–493.
- Smith, H. G., Källander, H., Hultman, J. & Sanzén, B.** 1989. Female nutritional state affects the rate of male incubation feeding in the pied flycatcher *Ficedula hypoleuca*. *Behav. Ecol. Sociobiol.* **24**: 417–420.
- Stein, L. R., Oh, K. P. & Badyaev, A. V.** 2010. Fitness consequences of male provisioning of incubating females in a desert passerine bird. *J. Ornithol.* **151**: 227–233.
- Tewksbury, J. J., Martin, T. E., Hejl, S. J., Kuehn, M. J. & Jenkins, J. W.** 2002. Parental care of a cowbird host: caught between the costs of egg-removal and nest predation. *Proc. R. Soc. Lond. B* **269**: 423–429.
- Voss, M. A., Reed Hainsworth, F. & Ellis-Felege, S. N.** 2006. Use of a new model to quantify compromises between embryo development and parental self-maintenance in three species of intermittently incubating passerines. *J. Therm. Biol.* **31**: 453–460.
- Walters, L. A., Webber, J. A., Jones, B. A. & Volker, C. L.** 2016. Taking a break: the relationship between ambient temperature and nest attendance patterns of incubating Carolina Chickadees (*Poecile carolinensis*). *Wilson. J. Ornithol.* **128**: 719–726.
- Weathers, W. W. & Sullivan, K. A.** 1989. Nest attentiveness and egg temperature in the Yellow-Eyed Junco. *Condor* **91**: 628–633.
- Zanette, L., Doyle, P. & Tremont, S. M.** 2000. Food shortage in small fragments: evidence from an area-sensitive passerine. *Ecology* **81**: 1654–1666.
- Zerba, E. & Morton, M. L.** 1983. The rhythm of incubation from egg laying to hatching in Mountain White-Crowned Sparrows. *Ornis Scand.* **14**: 188–197.
- Zimmerling, J. R. & Ankney, C. D.** 2005. Variation in incubation patterns of Red-Winged Blackbirds nesting at lagoons and ponds in Eastern Ontario. *Wilson Bull.* **117**: 280–290.