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

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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.
showing higher levels of male incubation feeding (Matysioková & Remes 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, Chalfont & 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 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 S1).

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-μL 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, Matysiková & Reměš 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 ± 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

![Graphs](image-url)

**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.

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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 ± 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, Campbell & 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: \( \text{on1} \rightarrow \text{off1} \rightarrow \text{on2} \rightarrow \text{off2} \). 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 (\( \Delta \text{exit duration} = \text{off2-duration} - \text{off1-duration} \)). 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 ± 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 ± sd = 4 ± 3), lasted 8–14 days
(mean ± sd = 12 ± 1 days) and there were 12–24 days (mean ± sd = 16 ± 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 38–218 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 ± 0.4 h/day (range 12–14 h/day), of which they spent on average 7.2 ± 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 ± 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 ± 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 ± 0.6 times per hour and median exit duration was 7 min (mean = 15 ± 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

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**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.
Female ID = tP
male ID = sired offspring in the male
sired extra-pair offspring.

Paternity loss: whether an extra-pair
qualitatively similar results. Paternity gain: whether a male
explained by random effects: pair ID
and each nest represents one data point (n = 171). Shown are
model, removal of the non-significant square-root term gave
results from linear mixed models with male, female and pair
identity as well as year as random factors. In the second

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 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
callizations.

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

**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

| Fixed effect | Estimate  | 95% CI | t      | P       |
|--------------|-----------|--------|--------|---------|
| Intercept    | 1.1       | 0.3–1.7| 0.1    | 0.93    |
| Clutch size  | 0.002     | −0.05–0.06| 0.1 | 0.93    |
| Male age     | −0.14     | −0.33–0.08| −1.5 | 0.13    |
| Female age   | 0.08      | −0.08–0.3 | 0.9  | 0.38    |
| Paternity gain (yes/no) | −0.15 | −0.3–0.03 | −1.7 | 0.09    |
| Paternity loss (yes/no) | 0.007 | −0.2–0.2 | 0.1  | 0.95    |
| Intercept    | 0.60      | 0.46–0.72| 0.2   | 0.84    |
| Clutch size  | −0.001    | −0.01–0.01| −0.2 | 0.84    |
| Male age     | 0.003     | −0.03–0.04| 0.2  | 0.81    |
| Female age   | −0.004    | −0.03–0.03| −0.3 | 0.80    |
| Male feeding visit rate | 0.02 | −0.15–0.21 | 1.1  | 0.25    |
| √(male feeding visit rate) | 0.11 | −0.08–0.30 | 0.3  | 0.79    |

*Variance explained by random effects: pair ID = 21%; male ID = 27%; female ID = 13%; year = 13%.

**Table 2.** Predictors 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
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| Fixed effect | Estimate  | 95% CI | t      | P       |
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| Male age     | −0.14     | −0.33–0.08| −1.5 | 0.13    |
| Female age   | 0.08      | −0.08–0.3 | 0.9  | 0.38    |
| Paternity gain (yes/no) | −0.15 | −0.3–0.03 | −1.7 | 0.09    |
| Paternity loss (yes/no) | 0.007 | −0.2–0.2 | 0.1  | 0.95    |
| Intercept    | 0.60      | 0.46–0.72| 0.2   | 0.84    |
| Clutch size  | −0.001    | −0.01–0.01| −0.2 | 0.84    |
| Male age     | 0.003     | −0.03–0.04| 0.2  | 0.81    |
| Female age   | −0.004    | −0.03–0.03| −0.3 | 0.80    |
| Male feeding visit rate | 0.02 | −0.15–0.21 | 1.1  | 0.25    |
| √(male feeding visit rate) | 0.11 | −0.08–0.30 | 0.3  | 0.79    |

*Variance explained by random effects: pair ID = 0.01%; male ID = 0.01%; female ID = 0.01%; year = 0.01%.

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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
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 & Novák 1990 for a similar result). This decline was not present when considering male visit rate relative to female time spent in the nestbox (Table S7). Thus, males did not decrease feeding intensity over the day, but followed the pattern of female presence in the nestbox.

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 nestbox). 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   | t      | P     |
|---------------------------------------|----------|----------|--------|-------|
| Response: Male feeding visit ratea     |          |          |        |       |
| Intercept                             | 1.1      | 0.7–1.4  | −3.4   | < 0.001|
| Total daily rain (mL)                 | −0.02    | −0.03 to −0.01 | −3.4 | < 0.001|
| Temperature (T) 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 attendanceb     |          |          |        |       |
| Intercept                             | 0.49     | 0.45–0.53 | 0.3   | 0.75   |
| Total daily rain (mL)                 | 0.0002   | −0.002 to 0.001 | −0.3 | 0.75   |
| Temperature (T) 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|

| aVariance explained by random effects: nest ID = 21%, year = 31%. | bVariance explained by random effects: nest ID = 14%, year = 32%. |

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.

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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 & Remes 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, Lifsjeld & 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 & Remes 2010, Amininasab et al. 2017, but see Martin & Wiebe 2000, Kotél 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 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 vary 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 & Reměš 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.

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**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 Δ 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.