The effects of season, sex, age and weather on population-level variation in the timing of activity in Eurasian Blue Tits *Cyanistes caeruleus*

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All birds sleep and many do so in a specific location, the roost. Thus, every day each individual needs to decide when to go to (enter) and leave the roosting place. This determines the timing of activity, a trait shaped by both natural and sexual selection. Despite its importance in a variety of contexts, including foraging, predation, mating success and parental care, variation in the timing of activity has rarely been studied. Here, we describe this variation in a population of Eurasian Blue Tits *Cyanistes caeruleus* roosting in nestboxes using data collected over 7 years. We investigate seasonal changes in the start and end of activity and assess to what extent these parameters are sex- and age-specific and affected by weather. We show that the start of activity is relatively constant in relation to sunrise during winter but undergoes drastic changes during the breeding season. The end of activity is markedly later relative to sunset in mid-winter and is also strongly influenced by breeding behaviour. Females generally start their activity later and end it earlier than males. The duration of daily activity is shorter during periods of rain and longer when temperatures are relatively high for the time of year.

**Keywords:** breeding, daily rhythm, diurnal behaviour, long-term dataset, non-breeding, passerine.

All birds, and indeed most animals, sleep (Miyazaki et al. 2017), but the timing of activity and rest may vary dramatically both between and within species (Campbell & Tobler 1984, Randler 2014). Generally, individuals show specific rest-activity cycles, depending on their circadian rhythm (e.g. diurnality, nocturnality) or feeding routines (e.g. crepuscular hunting in owls or tide-dependent feeding in shorebirds; reviewed in Campbell & Tobler 1984). In arctic regions, under periods of constant light or darkness, individuals may also become arrhythmic (e.g. Peiponen 1962, Steiger et al. 2013). At the within-species level, individuals may differ in their level and timing of activity depending on a variety of individual-specific (e.g. condition), environmental (e.g. weather) and social factors (e.g. activity of the partner).

Activity patterns are shaped by both natural and sexual selection. An example of the latter stems from a study on activity in the Pectoral Sandpiper *Calidris melanotos* (Lesku et al. 2012). In this polygynous shorebird that breeds in the high arctic under continuous daylight, males were active on average 90% of the total time during the period when fertile females were present, and the most active males sired the most offspring. A few weeks later, when fertile females were no longer available, activity levels dropped substantially (to about 70%; Lesku et al. 2012). The timing and amount of activity will also be under natural selection, for example to optimize foraging opportunities, to respond to the needs of the offspring (e.g. incubation, Kluijver 1950) or to avoid predation.

Many terrestrial, diurnal birds breed in cavities. They typically also spend the night in a roosting cavity, although some individuals may roost on branches hidden in the foliage (reviewed by Mainwaring 2011). During most of the period they spend inside their roost they sleep, although they may also engage in activities such as resting, preening or nest maintenance (Steinmeyer et al. 2010). The amount of time spent sleeping may especially...
be reduced when individuals are disturbed, for instance by the presence of nestlings or artificial light (Raap et al. 2016, but see Sun et al. 2017). The roost may also serve as a refuge, protecting the individual against predators and adverse weather conditions. Being tied to a roost, however, prohibits other behaviours such as foraging, territory defence, mate guarding and nestling provisioning. It is therefore likely that individuals face fitness-relevant trade-offs about when to enter their roosting place in the evening and when to leave it in the morning (Mainwaring 2011). Despite the importance of the timing and amount of activity, studies that describe the start and end of activity in detail, span a larger period and monitor more than a few individuals remain rare.

The few existing studies are mostly about solitarily roosting, cavity-nesting songbirds, specifically Eurasian Blue Tits Cyanistes careuleus (hereafter, ‘Blue Tit’) and Great Tits Parus major (Kluijver 1950, Hinde 1952, Steinmeyer et al. 2010, Schlicht et al. 2014, Stuber et al. 2015). The first two studies present data on only one (Hinde 1952) or a few (Kluijver 1950) individuals during breeding, with many data points per individual (>50), whereas the last three investigated many individuals, but with relatively few data points per individual across the year. Several other studies have investigated the start and/or end of activity, but instead of providing detailed information on timing, they focus on the relationship with other variables (see below). Furthermore, many studies do not investigate the start and end of activity itself, but rather related behaviour, usually the start of dawn song (e.g. Cuthill & McDonald 1990, Poesel et al. 2004, Da Silva & Kempenaers 2017).

Several predictors of the timing of activity have been investigated. First, the main determinant of the start and end of daily activity is day length (Kluijver 1950, Hinde 1952, Amlaner & Ball 1983). Songbirds are generally day-active and vision-dependent, so a link with ambient light levels is inevitable. Nonetheless, small-scale variation in light levels at the roost did not influence an individual’s timing of entering or leaving the roost in one study of Blue Tits (Steinmeyer et al. 2010). In accordance with the importance of light levels, rainfall or cloudiness delayed the start of morning activity and hastened the time when individuals retired in the evening across several species (Kluijver 1950, Hinde 1952, Bruni et al. 2014, Da Silva et al. 2016). However, the effect of rain may also be driven by reduced foraging success, reduced predator recognition and hampering of flight. Finally, several studies showed that exposure to artificial night lighting influences activity patterns and sleep (e.g. Kempenaers et al. 2010, Dominoni et al. 2013, 2014, Russ et al. 2015, Raap et al. 2016, Da Silva et al. 2017, Sun et al. 2017; but see Raap et al. 2018).

Second, the timing of activity seems to be temperature-dependent, although findings vary. For example, Bruni et al. (2014) found that individuals of several songbird species started to sing earlier when it was warmer, but Da Silva et al. (2016) found no such effect for several other songbird species. In further contrast, Hinde (1952) reported that Great Tits emerged later when temperatures were higher. Lower temperatures may be linked to reduced foraging success or increased need for energy saving (explaining later emergence and earlier start of roosting), but the higher need for energy and reduced foraging efficiency may also force individuals to be active for longer. It is therefore likely that the effects of relative temperature vary, for example with the season, with latitude and with individual traits such as body size or dominance.

Third, the start and end of daily activity are known to change abruptly during the breeding season (Kluijver 1950, Hinde 1952, Amlaner & Ball 1983, Steinmeyer et al. 2010). For example, male Blue Tits became active earlier relative to females at the start of the breeding season (Steinmeyer et al. 2010), and Great Tit females showed a much shorter active period during incubation (Kluijver 1950). Similarly, female Blue Tits emerged earliest around the time when they lay their first egg (Schlicht et al. 2014), and the same pattern has been reported in several species for the start of male dawn singing (e.g. Cuthill & McDonald 1990, Halfwerk et al. 2011). In females, an advance in emergence times could be driven by energetic needs prior to laying, allowing increased foraging time. Alternatively, hormonal changes may influence activity patterns. For instance, the daily and seasonal timing of female reproduction may be linked to differences in the timing of the photosensitive period (Graham et al. 2017). Males may also advance their emergence times as a result of energetic demands or changes in hormone levels, or they may follow female emergence patterns to ensure paternity. Testosterone levels peak with
singing activity in temperate-zone songbirds, and testosterone may therefore have an impact on the start or end of activity. However, a study of Blue Tits did not find a relationship between experimentally elevated testosterone levels and the timing of the dawn chorus (Kunc et al. 2006).

Fourth, several individual-specific traits are known to influence the timing of activity. For example, females typically enter their roosting place earlier in the evening and leave later in the morning than males (e.g. Kluijver 1950, Hinde 1952, Steinmeyer et al. 2010, Stuber et al. 2015), and younger birds may be less active than older ones (e.g. roosting in fledgling Great Tits compared with adults, Kluijver 1950; start of dawn singing in yearling vs. adult male Blue Tits; Poesel et al. 2004). The timing of activity also varies with hormone levels (Greives et al. 2015) and food availability (Kluijver 1950, Cuthill & McDonald 1990; but see Saggese et al. 2011), suggesting a potential influence of condition.

Fifth, the start and the end of activity may be individual-specific. Although a study of Great Tits reported no repeatability of both start and end of activity (Stuber et al. 2015), these traits were moderately and significantly repeatable in Blue Tits (r ≃ 0.3–0.4, Steinmeyer et al. 2010, Schlicht et al. 2014) and in Common Blackbirds Turdus merula (r ≃ 0.5, Dominoni et al. 2013). Similarly, Mace (1986) and Kluijver (1950) reported that two individual Great Tits (of fewer than 10 studied) emerged from their respective roosts more than 1 h apart on the same date and during nesting provisioning, when activity (foraging) should be under strong selection. Interestingly, the start of morning activity appears to be less variable than the time an individual retires to roost (Hinde 1952, Amlaner & Ball 1983, Slagsvold 1996, see also Da Silva et al. 2017). This could indicate that selection on the timing of morning behaviour is stronger than selection on evening behaviour. Such an effect could be linked to a strongly pronounced dawn chorus compared with the dusk chorus (Catchpole & Slater 2008). Alternatively, waking-up times, which correlate closely with emergence times (Steinmeyer et al. 2010), may be genetically or physiologically determined (Steinmeyer et al. 2012, Stuber et al. 2016), for example via light and melatonin levels (Greives et al. 2015).

Other variables that may influence patterns of activity are latitude (Amlaner & Ball 1983, Da Silva & Kempenaers 2017), predation risk (Amlaner & Ball 1983, Santema et al. 2019), noise (Arroyo-Solís et al. 2013; but see Da Silva et al. 2017), the lunar phase (York et al. 2018) and the risk of territorial intrusions (Foote et al. 2011; but see Amrhein & Erne 2006).

Here, we report on a comprehensive, 7-year study of the start and end of activity in a population of Blue Tits. The aim of this study is three-fold:

- To describe within-population variation in year-round activity patterns (separately for the non-breeding and the breeding period)
- To assess how activity patterns vary with sex and age
- To test the effects of season (which includes variation in day length), temperature and rainfall as important mediators of the timing of activity.

We discuss the general implications of our findings in relation to previous work and with respect to the ecological and behavioural causes and consequences of variation in activity. We provide the full dataset to allow other researchers to verify our results and to extract data as a basis for experiments, own data collection or power analyses.

**METHODS**

**Study species**

Blue Tits are small (9–11 g), diurnal, hole-nesting passerines that are non-migratory in central Europe (Cramp & Perrins 1993). They readily accept nestboxes for breeding and roosting. Blue Tits are typically social unisexual monogamous, but social polygyny regularly occurs (Kempenaers 2019). During the breeding season, Blue Tits build nests made of moss with a feather and hair lining. The female lays on average 10 eggs, usually one each morning. She then incubates the clutch alone, while her mate often provides her with food (Bambini et al. 2018). The eggs hatch about 2 weeks after the start of incubation and the nestlings are fed by both parents for about 20 days. Blue Tits are generally single-brooded; we never observed a second clutch in our study population, although replacement breeding attempts after failure of the first regularly occur.

In winter, nestboxes are used for roosting, especially by males. Blue Tits often use the same
nestbox on consecutive nights but may switch to a new roost or to a previous one after disturbance or for no apparent reason. Towards the breeding season, males reduce their use of nestboxes for roosting, whereas females start to use them more frequently, often roosting in the future nesting box. In the days before and during egg-laying, females usually spend the night in the nesting box and continue to roost there until a few days before the young fledge (Schlicht et al. 2014). After the breeding season, individuals rarely sleep in nestboxes and we have no record of a Blue Tit roosting inside a nestbox during summer (between 27 June and 1 October; present authors’ unpublished data).

Study area and breeding data

We studied a Blue Tit population in a mixed-deciduous oak forest (Westerholz, 48°08′26″N, 10°53′29″E) close to Landsberg am Lech, Germany. Since 2007, the 40-ha forest patch has contained 277 small-holed nestboxes. During breeding, we visited each nestbox weekly and close to the start of egg-laying and hatching, daily, to determine the date of the first egg (lay date), clutch size and hatch date. We caught Blue Tits in winter, either inside a nestbox or in a mist-net at feeding stations. We also caught individuals at their nestbox during nestling provisioning. Up to the summer of 2014, individuals were generally caught during provisioning and only a few individuals were caught in winter. Later, we set up mist-nets almost daily during each winter and caught most individuals soon after they arrived. As a result, we have more data on the timing of entering and leaving the nestbox in winter from the autumn of 2014 onwards.

After capture, we banded each individual with a metal ring and one to three colour rings, measured tarsus and wing (3rd primary) length and body mass, and visually determined age (yearling or older; Cramp & Perrins 1993). A 5- to 15-μL blood sample was taken from the brachial vein for paternity analysis and sex determination. A PIT-tag was inserted under the skin on the back (2010–12: EM4102 ISO animal tag 134.2 kHz ISO, 8.5 × 2.12 mm, 0.067 g; 2013–16: BIO-MARK HPT8 animal tag 134.2 kHz FDXB, 8.4 × 1.4 mm, 0.03 g, Biomark, ID; 2016–17: SMARTTRAC Glass tag 134 kHz, EM4305, 1.41 × 8.3 mm, 0.03 g). Sex was determined by genotyping with the marker P2P8 (Griffiths et al. 1998). For further details on the study area and the field procedures see Schlicht et al. (2012).

Data on activity patterns

Whenever a PIT-tagged Blue Tit entered or left a nestbox, a radiofrequency identification (RFID) reader located around the entrance of the box recorded the individual’s identity and the date and time, and two light barriers, one inside and one outside the box, recorded the direction of the bird’s movement (for details see Loës et al. 2019). All RFID readers were active year-round. Because sometimes individuals entering or exiting the nestbox were not registered or the direction may have been mis-assigned, we conservatively used data only if an individual carrying a transponder was recorded both when entering the box in the evening and when leaving it the next morning, and when the direction of both movements was certain.

In 2012 and 2013, we used morning sound recordings from inside 33 nestboxes to test the reliability of the RFID data (given that a bird’s movements inside the nestbox and when it leaves are audible). In 214 of 336 recordings, the RFID data suggested that the bird spent the night inside the nestbox, and this was confirmed by the sound recordings. The remaining 122 RFID recordings suggested that the bird spent the night outside the nestbox, but this was confirmed in only 12 cases (10%) by the sound recordings. This implies that our criteria to use the RFID data are conservative and that valid data are excluded from the analysis. In most cases this is because the evening entry could not unequivocally be confirmed. Erroneously excluding data only results in a loss of data, whereas including doubtful cases may result in erroneous data. We therefore accepted a loss of data quantity to ensure high data quality. We then assessed how the timing of the start of activity differed between RFID and sound recording data in cases where overnight roosting in the nestbox was recorded by both (n = 214). We excluded four data points where the exact time of emergence could not be assessed in the sound data because females emerged after the end of the recording. On average, estimates of exit times based on the sound recordings were 100 s later than estimates based on the RFID readers (n = 210, range = -71 to 35 min); 90% of all estimates from both methods lay within 12 min of each other.
For further analyses, we discarded two types of data. We excluded all data from replacement clutches and from clutches where the start of activity was experimentally manipulated (some clutches in 2012–13, Schlicht et al. (2014) and some in 2017, Sanema et al. (2019)). Second, we visually inspected whether fitted models fulfilled the assumptions of homoscedasticity and normal distribution of residuals. Because these model assumptions were strongly violated when using the entire dataset, we removed outliers (26 data points, 7%) using the definition of a boxplot (Tukey 1977). This yielded a sufficient fit of the model assumptions. Note that models that included these outliers gave qualitatively similar results. Overall, our dataset included 34 824 roosting events (evening entry plus morning exit) of 769 individuals across 7 years (2011: n = 809, \( n_{\text{ind}} = 81 \); 2012: \( n = 2491 \), \( n_{\text{ind}} = 159 \); 2013: \( n = 2669 \), \( n_{\text{ind}} = 134 \); 2014: \( n = 4008 \), \( n_{\text{ind}} = 136 \); 2015: \( n = 7594 \), \( n_{\text{ind}} = 206 \); 2016: \( n = 8964 \), \( n_{\text{ind}} = 252 \); 2017: \( n = 8289 \), \( n_{\text{ind}} = 266 \)). Thus, we obtained an average of 45 data points per individual (range: 1–405), and 36% (\( n = 282 \)) of individuals were recorded in more than one breeding season (two seasons: 78 males, 97 females; three seasons: 34 males, 37 females; four seasons: eight males, 14 females; five seasons: five males, six females; six seasons: one male, two females).

We defined ‘Start of activity’ as the time in minutes to sunrise when an individual emerged from the nestbox in which it roosted. Similarly, we defined ‘End of activity’ as the time in minutes to sunset when an individual entered the nestbox in the evening. Because an individual was only scored as ‘roosting in the box’ if it was recorded both in the evening and the next morning, the number of recorded evening entry and morning exit times is identical.

### Weather data

We obtained hourly meteorological data from a nearby weather station (http://www.am.rlp.de, station 61: Landsberg, \( \approx 10 \) km from the study site). Temperatures (°C) were measured 2 m above ground, and rainfall was measured in mm/h. Temperatures recorded during the time of this study ranged between −15.8 and 26.1 °C. Rainfall ranged between 0.0 and 8.2 mm/h (see Fig. S1 for seasonal distribution).

Decisions about entering or leaving the roost may depend on weather conditions around dusk and dawn, but they may also be influenced by the conditions during the day or night. Thus, for rainfall, we used both average daily values and hourly values closest to time of nestbox exit or entry in separate models. Because daily averages resulted in qualitatively similar, but overall smaller effects, we present the results using hourly rainfall data. For temperature, we used daily averages because these values correlated strongly with the hourly values around dawn and dusk (\( r = 0.91–0.98 \)).

### Statistical analyses

All statistical analyses were performed using generalized additive mixed models (GAMMs) calculated with the package ‘gamm4’ (Wood & Scheipl 2017) in R 3.6.1 (R Core Team 2019). A GAMM applies a smooth function to an explanatory variable of choice (here Julian date or days to the first egg) and uses this ‘smoothed’ variable in a (generalized) mixed model (package ‘lme4’, Bates et al. 2015). For smoothing we used a thin-plate regression spline (‘tp’) as a basis with the dimension \( k = 40 \) (for details on the choice of \( k \), see Appendix S1). Smoothing was performed either within each sex and age class (for models on age) or within each sex (for all other models).

We performed all analyses for two time periods: (1) the non-breeding season (1 October–31 March) and (2) the breeding season (3 weeks before the start of egg-laying until 31 July). Note that the two periods overlap and that their definitions are somewhat arbitrary. We chose to end the non-breeding period on 31 March because during the years that are part of this study, egg-laying started after this date. We chose the start of the breeding season as 3 weeks before the first egg was laid because 95% of nests are completed within 2 weeks and we assumed that territory establishment, pair formation and nest-site choice take at least 1 week. In each year, non-breeding individuals (30% of all individuals) were included only in analyses for the non-breeding season.

We calculated models using three different response variables: start of activity (minutes to sunrise), end of activity (minutes to sunset) and total time spent active (hours). First, we modelled each of these three response variables separately for males and females, and for the non-breeding and the breeding period (12 models, results in Figs 1–3, where each panel presents two separate
Seasonal changes in the start of activity (emergence from the roost) for male (blue) and female (red) Blue Tits. The left set of panels shows data between October and 31 March (‘non-breeding’, months indicated by letters); the right set shows the data from 21 days before the focal female’s first egg (day 0) until July (‘breeding’). The approximate breeding stage is shown in between the right set of panels (Nest building, Egg-laying, Incubation, Nestling period, Post-breeding). The upper two panels show the raw data using modified boxplots, where the filled dots represent the medians, the white space between the whiskers represents the interquartile range (‘boxes’), the whiskers are 1.5 times the interquartile range, and the open dots are any values outside of the whisker range. The bottom panel displays the smoothed values of the start of activity as calculated by the GAMM (solid line; see Methods) and the 95% confidence intervals (dashed lines). The corresponding sample sizes are given in Figures S2 and S3. A repeatability estimate ($R$) is given in each panel.
Figure 2. Seasonal changes in the cessation of activity (roost entry) for male (blue) and female (red) Blue Tits. The left set of panels shows data between October and 31 March ('non-breeding', months indicated by letters); the right set shows the data from 21 days before the focal female's first egg (day 0) until July ('breeding'). The approximate breeding stage is shown in between the right set of panels (Nest building, Egg-laying, Incubation, Nestling period, Post-breeding). The upper two panels show the raw data using modified boxplots, where the filled dots represent the medians, the white space between the whiskers represents the interquartile range ('boxes'), the whiskers are 1.5 times the interquartile range and the open dots are any values outside of the whisker range. The bottom panel displays the smoothed values of the start of activity as calculated by the GAMM (solid line; see Methods) and the 95% confidence intervals (dashed lines). The corresponding sample sizes are given in Figures S2 and S3. A repeatability estimate ($R$) is given in each panel.
The explanatory variables in these models are ‘smoothed’ day of the year (non-breeding period) or ‘smoothed’ days to the female’s first egg (breeding period). Time spent active is a composite variable: it is completely defined by the daily start and end of activity. Hence, in all further models, we focus exclusively on the start and end of activity. Second, we tested whether the start and end of activity differed between males and females, and between yearling and adult individuals. We ran GAMMs for the non-breeding and the breeding period separately, with start and end of activity as the response variable (smoothed, as explained above, separately for each age–sex-class), and age (yearling or adult) and sex (male or female) and their interaction as explanatory variables (four models; results are presented in Fig. 4 and Table S1). Finally, we investigated whether weather variables (rainfall and temperature) explained activity patterns. We used the same GAMMs as described above, but added either rainfall or temperature as an explanatory variable, including a three-way interaction with sex and age. We did not include rainfall and temperature together in the same model because these two variables are strongly correlated, making the interpretation of the effects in a joint model difficult. Results of the four models are described in Figure 5 and Table S2. Interactions between age and rainfall or temperature were not significant, except in one model (age × rainfall during the breeding season). The main effects of age have already been presented in the previous analyses. We therefore also ran the models excluding age. This yielded qualitatively similar results. Thus, to simplify the description of the results, we present the models without age as an explanatory variable and discuss the statistically significant interaction separately.

We modelled both scaled (standardized and centred) variables to allow assessment of the relative importance of the effect sizes (Figs 4 and 5), and unscaled variables to allow biologically meaningful interpretation in terms of units (Tables S1 and S2).

Finally, to calculate individual repeatabilities, we fitted GAMMs similarly to those described above. As the response variable we used the timing of either the start or the end of activity. We calculated repeatability separately for each sex and each period (non-breeding and breeding season). Thus, we ran eight different models and present the respective repeatability estimates in the panels of Figures 1 and 2. As explanatory variables, we included the smoothed day of year or the number of days to the first egg (for the non-breeding and breeding season, respectively), average daily temperature and rainfall at dawn (for the start of activity) or dusk (for the end of activity). We then extracted the adjusted repeatabilities from the LME-part of the GAMM by dividing the variance
Figure 4. Effects of sex and age on the start and cessation of activity in Blue Tits. Shown are estimates based on a GAMM (see Methods) and the 95% confidence intervals (CI). For this figure, age class and sex were included in the model as a four-level factor instead of an interaction (Table S1). (a, b) Start of activity, i.e. timing of emergence from the nestbox; (c, d) cessation of activity, i.e. timing of entering the nestbox to roost. (a, c) Winter and early breeding season (October–31 March); (b, d) breeding season (period from 21 days before the first egg until July).

explained by the random intercept ‘individual ID’ by the sum of the variance explained by ‘ID’ and the residual variance. We do not present confidence intervals for these repeatability estimates here, because these are not straightforward to compute in a GAMM. Note that the estimate
of repeatability we use here will capture both short-term temporal autocorrelation and individual-specific preferences.

**RESULTS**

**Seasonal variation in activity patterns**

**Start of activity**
Start of activity is shown in Figure 1. Overall, both males and females usually left their roost before sunrise, with no distinct seasonal changes outside the breeding season. Males on average became active somewhat earlier as the season progressed, whereas females emerged later. About 2 weeks before the female laid her first egg, both pair members emerged progressively earlier until shortly before laying. Females then suddenly changed their behaviour. On the day before and on the day of laying, they emerged approximately 10 min later than previously. During laying and incubation, females progressively delayed emergence until the young hatched, when the pattern reversed and females emerged earlier again. In contrast, males emerged progressively later from the end of the laying period onwards. The repeatability of the start of activity was high (0.39–0.67) in both sexes and both outside and during the breeding season.

**End of activity**
End of activity is shown in Figure 2. Overall, in both sexes, individuals usually entered the roost before sunset, except during mid-winter when the days are shortest. In winter, individuals were therefore active for a much shorter period than in summer (Fig. 3). During the breeding season, individuals changed their timing around the start of laying: both sexes entered the nestbox progressively earlier in the evening, but the pattern was most pronounced in females during the incubation period.

![Figure 5](image-url)
period. Individuals returned to pre-breeding times of roost entry during the nestling period. The repeatability of the end of activity was moderate to high (0.29–0.79) in both sexes and both outside and during the breeding season.

**Effects of sex and age on activity patterns**
Across most of the year, and particularly during the early breeding season, males emerged significantly earlier and entered the roost significantly later than females (Figs 1, 2 and 4; Table S1). In the non-breeding season, males emerged on average > 5 min earlier and entered the roost > 5 min later than females (Fig. 4a,c). During the breeding season, males emerged > 15 min earlier and went to roost ≈ 5 min later (Fig. 4b,d). The difference between males and females was especially pronounced during the egg-laying and incubation period.

Activity patterns are also age-dependent, but these effects are much smaller than the effects of sex (Fig. 4; Table S1). In winter, adult males started and stopped activity earlier than yearlings, whereas during breeding they started to be active earlier and stopped activity later than yearling males. Adult and yearling females were more similar in the timing of their behaviour, except that during the breeding season adult females entered their roost about 2 min later compared with yearling females.

**Effects of rainfall and temperature on activity patterns**
Overall, an additional 1 mm of rainfall delayed the start 4–6 min and advanced the end of activity by ≈ 4 min for both sexes across all periods (Fig. 5; Table S2). The start, but not the end, of activity was more delayed for males than for females. At dawn, during the breeding period, older individuals responded more strongly to increased rainfall than yearlings (slope of rainfall on the start of activity for yearlings: 0.10 ± 0.01, interaction with male age: 0.01 ± 0.01, \( t = 2.03, \ P = 0.04 \); estimated after removal of the non-significant three-way interaction between rainfall, age and sex).

An increase in temperature (given the time of year) by 1 °C was associated with an advance in the start by ≈ 6 s and a delay in the end of activity by 41–55 s for both sexes across all periods (Fig. 5; Table S2). The start of activity was influenced similarly for males and females. However, when temperatures were higher, females delayed going to the roost more than males in winter and early breeding, but not during the breeding season.

**DISCUSSION**
This study shows that Blue Tit activity patterns are strongly shaped by seasonal changes in day length and by breeding activities. During the non-breeding season, the start of activity changes little relative to sunrise, but the birds go to roost later relative to sunset in mid-winter. Blue Tits had slightly shorter active days during periods of rainfall and longer days when temperatures were higher.

**Seasonal patterns**
Confirming previous studies (Hinde 1952, Amlaner & Ball 1983, Slagsvold 1996), we found that the start of activity in the morning closely follows sunrise and thus overall light levels (Fig. 1). Indeed, despite extreme changes in the environment from warm and long summer days with abundant food to cold and short winter days with little food, individuals varied surprisingly little in their start of activity in relation to sunrise. This means that the period during which individuals were active ranged from about 9 h in winter to about 14 h in summer. However, individuals used a higher proportion of the available daylight when days were short by ending their activity later in the evening (Figs 2 and 3). This suggests that they may be constrained in winter by the time required to find sufficient food. In line with previous findings, our results suggest that the start of activity is relatively fixed, whereas the end of activity is more flexible (Hinde 1952, Amlaner & Ball 1983, Slagsvold 1996, Da Silva et al. 2017). When foraging success is unpredictable, individuals may face strong selection to start their activity as early in the day as possible to ensure that they have enough time to acquire resources to survive the coming night. In contrast, in the evening, when some individuals have fed well but others have not, selection may favour flexibility, with individuals adjusting their behaviour to their current state.

Our results clearly show sex differences in activity patterns (Figs 1–4; Table S1). Across the year, females emerged from roost later in the morning and entered it earlier in the evening compared with males (see also Kluijver 1950, Hinde 1952, Steinmeyer et al. 2010, Stuber et al. 2015). Outside the breeding season, sex differences cannot be attributed to different tasks the sexes have to perform. Males are generally somewhat larger than...
females and dominate over them (e.g. Hegner 1985, Hogstad 1989). Because subdominant individuals seem to have limited access to the preferred food sources (see Hogstad 1989 and references therein), females may have reduced access to food and hence may need more time for foraging or use alternative foraging strategies. If this is the case, females might have to use a larger proportion of the day for foraging, but our results do not show this. The difference in activity seems more pronounced later in winter and during early spring, when males start to defend territories, and may thus be linked to sexual selection.

During the breeding season, activity patterns show drastic changes. Towards the start of egg-laying, both males and females advanced their emergence times substantially, whereas the end of activity remained relatively constant. The former may be related to the energetic demands the breeding season makes on the individuals, as it allows more time for foraging. Alternatively, the daily and seasonal timing could be correlated. Many animals possess a photosensitive period during which light exposure triggers reproductive behaviour. In Japanese Quail Coturnix japonica, this photosensitive period occurs 10–16 h after the lights turn on (i.e. sunrise, Nicholls et al. 1983). Graham et al. (2017) propose that females that emerge earlier in the morning may be sensitive to photic stimulation earlier in the evening. As days grow longer, these females would be the first to experience sunlight in their photosensitive period. They would therefore be early in developing reproductive behaviour and would start to lay relatively early. The advance in emergence time before egg-laying may therefore be a by-product of the effect that early emergence triggers egg-laying. The delay in emergence times as well as the gradual advance of the end of activity once egg-laying starts (Figs 1 and 2) could then simply result from the time it takes to lay the egg and later to incubate the clutch. Why females had already emerged substantially later one day before they started laying remains unclear. Males generally followed similar patterns and were overall active longer than females. This suggests a role of sexual selection. For example, males may benefit from being active to defend their territory or to guard their fertile partner. Males that started singing earlier also sired more extra-pair offspring (Poeseel et al. 2004, Kempenaers et al. 2010). Later during the breeding season, differences in activity levels between males and females seem related to sex-specific roles (e.g. only females lay eggs and incube them). Interestingly, the male activity pattern partially follows that of females (Figs 1–3). This is expected during the fertile period (e.g. because of mate guarding), but also occurs during incubation. Despite other (extra-pair) females being available, males generally did not continue to emerge early, suggesting that extra-pair mating opportunities do not strongly influence male activity patterns at that time. It has been reported that males accompany their mate to the roost in the evening and from it in the morning (Hinde 1952, Poeseel et al. 2004). Although these are anecdotes, such behaviour may be important for the social pair bond and may explain the match between male and female timing.

Adult males (but not females) emerged on average 2.6–2.8 min earlier than yearling males both during the non-breeding and during the breeding season (Fig. 4; Table S1). A previous study investigating Blue Tit sleep in the same study area reported that yearlings (across sexes) emerged on average 4 min later than older individuals (Steinmayr et al. 2010). Similarly, Poeseel et al. (2004) reported that yearling males started to sing later than older males. In contrast to Steinmayr et al. (2010), we found that older males also entered the roost later in the evening during breeding, but it remains unknown whether this also influences reproductive success. During the non-breeding season, however, older males entered the roost earlier than younger males. Several studies reported that older males have an advantage over younger males in terms of food acquisition because of experience and social dominance (Hogstad 1989 and references therein, Lahti et al. 1996, Edler & Friedl 2010), but other studies did not find an age effect (Hegner 1985, Kivula et al. 1993, Zanette & Ratcliffe 1994). If older males are dominant, they may be able to obtain resources faster in winter, whereas subdominant, yearling individuals may need to stay active for longer to feed. Interestingly, we again found that the start of activity is less flexible than the end of activity. The age-related differences in males are unlikely to be driven by testosterone levels because these are age-independent in male Blue Tits (Peters et al. 2006). Melatonin levels appear to decrease with increasing age in birds, but only later in life (senescence; Tarlow et al. 2003 and references therein). It seems unlikely that our classification of ‘yearlings’ and ‘older’ individuals captures this process.
Effects of rainfall and temperature on activity patterns

As in previous studies (e.g. Kluijver 1950, Hinde 1952, Bruni et al. 2014, Da Silva et al. 2016), we found that rainfall caused Blue Tits to leave their roost later in the morning, and enter it earlier in the evening, independent of time of year (Fig. 5, Figs S8 and S9). Rainfall implies cloud cover and lower light levels, which in turn may affect activity. However, a previous study of Blue Tits in the same study area found no relationship between local light levels and activity patterns (Steinmeyer et al. 2010). Thus, the effect of rain on activity may also be related to the reduced benefits of being active, for example because of reduced foraging efficiency or because the noise associated with rain impedes acoustic communication. During the breeding season, older individuals delayed their emergence times more compared with yearlings during periods of rain. Older individuals generally emerged earlier than yearlings during the breeding season (Table S1) and may have a greater potential to delay their emergence.

In accordance with Bruni et al. (2014, but see Hinde 1952, Da Silva et al. 2016) we found that higher temperatures – given the time of the year – were linked to earlier morning emergence and later evening entry in both sexes (Fig. 5; Table S2); that is, on a relatively warm day, individuals were active longer than on a cold day. Higher temperatures may increase foraging success and reduce the need for individuals to save energy. We investigated how the relationship between temperature and activity changes across the year based on monthly estimates (Figs S6 and S7). The relationship between temperature and the start and end of activity was weak or absent in the winter months, especially around the time when days are shortest (November–January; winter solstice: 21 December). Effect sizes increased towards the breeding season. In winter, individuals may be less flexible and responsive to variation in temperature because they may need all available time during the short days.

CONCLUSIONS

The timing of the start and end of activity is likely to be shaped by two mechanisms: (1) a ‘fixed’ genetic predisposition, modulated for example by hormonal changes in response to increased daylength (Graham et al. 2017) or hormonal differences between the sexes (Dawson et al. 2001, see also Yu et al. 2018), and (2) a ‘flexible’ trade-off between costs and benefits of being inside or outside the roost (reviewed by Mainwaring 2011). Benefits of being inside the roost may be avoidance of avian predators (e.g. Eurasian Sparrowhawks Accipiter nisus), energy conservation, sleep and essential behaviour related to breeding such as egg-laying, incubation and nest maintenance. Benefits of being outside the roost are the ability to feed, to avoid parasites and predators that enter cavities (e.g. mustelids or snakes), and to engage in breeding behaviours such as territory establishment and defence, mate acquisition, mate guarding and (extra-pair) copulation.

The close match of the start and end of activity to sunrise and sunset, respectively, shows that overall patterns are primarily determined by light levels, presumably through the light-regulated hormone melatonin (e.g. El Halawani et al. 2009, Greives et al. 2015). Our results show that individuals can fine-tune their behaviour in response to environmental factors (rain and temperature) and in relation to breeding activities.

Blue Tits show the greatest flexibility in emergence times during the breeding season: both sexes advance their start of activity before laying and delay it afterwards. The advance in the start of activity before laying may be related to nest-building and acquiring resources for egg production (for females) and to mate-guarding and advertising for extra-pair copulations (for males). The delay in emergence times during laying and afterwards seems to be driven mostly by the constraints of egg-laying and incubation.

In winter, when survival during short and cold days is key, individuals need to budget their energy income and expenditure. In small songbirds, energy reserves are limited. For example, in Eurasian Tree Sparrows Passer montanus, energy reserves are sufficient for at most 24 h (Pinowski et al. 2006). In winter it may therefore be key to be active for as long as possible. Indeed, Blue Tits went to their roost later in the evening in winter (in relation to sunset) and were thereby active for a longer proportion of the total day (period when light was available). Also, individuals adjusted the timing of their activity to temperatures only outside of the winter months (Figs S6 and S7). Potentially, the flexibility in the timing of activity in winter is limited.

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In winter, when the need to save energy is high, an alternative strategy to adjusting activity patterns could be to use nestboxes more frequently (reviewed by Mainwaring 2011). Indeed, Vel’ky (2006) reports that Great Tits roosted most frequently in nestboxes when temperatures were lowest. Our data do not support this, as sample sizes (equivalent to occupancy rates) are – if anything – lower in mid-winter (Fig. S1).

Although we present population-wide patterns, individuals may vary substantially in their activity patterns on a day-to-day basis (examples in Figs S4 and S5). Despite this variation, we found high or moderately high repeatabilities in both the start and the end of activity for both males and females, and both outside and during the breeding season (all repeatability estimates between 0.29 and 0.79, Figs 1 and 2). However, it is likely that much of this repeatability can be explained by temporal autocorrelation in data recorded within a relatively short period (e.g. within a few days or weeks). It remains unclear how much can be attributed to the individual per se, in other words its ‘chronotype’. Note that this is also the case for repeatability estimates reported previously (Steinmeyer et al. 2010, Dominoni et al. 2013, Schlicht et al. 2014, Stuber et al. 2015). A more refined analysis controlling for temporal autocorrelation is beyond the scope of this paper. Some individuals emerged unusually late, more than 1 h after sunrise. Although we cannot exclude that some of these cases are RFID data errors, we confirmed four of these cases during early breeding by sound recordings inside the nestbox. This also confirms anecdotes described by Kluijver (1950), who studied breeding Great Tits and mentioned ‘two inexplicable cases in which she (the Great Tit female) became active very late’. Why some individuals sometimes leave their nestbox so late remains unexplained but might be associated with the presence of a predator nearby (Sanetma et al. 2019).

We could only assess activity patterns of a subset of all Blue Tits present in the population, namely those that roost in a nestbox. Decisions to roost in a box may depend on the local availability of natural cavities or other roosting sites, weather conditions, and the presence of parasites and predators (Vel’ky et al. 2010, Mainwaring 2011). All nestboxes in our study area are cleaned once a year after the young have fledged, which presumably reduces parasite infestation. Thus, as with other studies using nestboxes, results may differ for populations without nestboxes or where nests are not removed.

This study presents detailed information about the start and end of daily activity in Blue Tits. We show clear seasonal patterns, with drastic behavioural changes towards the breeding season. We also show that rain consistently shortens the overall time spent active, but the effects of variation in temperature are less clear. The general patterns described here can be used as the foundation for other (experimental) studies of activity patterns in Blue Tits and similar species. Our results lead to several questions that need to be addressed at the between- and within-individual level. For example, how far does the start and end of activity in males during the breeding season track that of their mate? Do individuals change their activity patterns through life (e.g. from yearling to adult)? We also need to understand the fitness consequences of individual variation in activity patterns. For example, do females that emerge earlier in the early breeding season or that are active for longer (relative to day length) also lay eggs earlier (Graham et al. 2017)? Does variation in the timing of emergence or in overall male activity affect reproductive success? Which components of reproductive success are affected (e.g. paternity gain or loss)? Finally, we do not yet understand why most females seem to emerge earliest 2 days before they lay their first egg.

We thank all members of the Blue Tit group and two anonymous reviewers for constructive feedback. We are especially grateful to everyone who collected data in the field, in particular Agnes Türk, Andrea Wittenzellner and Carol Gilsenan, to Peter Loës and Peter Skripsky for designing and maintaining the automated nestbox system, and to Mihai Valcu for establishing and maintaining the database.

**DATA AVAILABILITY STATEMENT**

All code and data (.RData and .csv) are supplied in the R package ‘BTemergence’ (Schlicht 2019).

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Received 16 August 2019; revision accepted 15 January 2020.
Associate Editor: Stuart Sharp

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. The choice of K in the GAMMs. Figure S1. (A) Temperature and (B) rainfall at dawn and (C) at dusk across the year.
Figure S2. Sample sizes in relation to date.
Figure S3. Sample sizes in relation to progress of the breeding season.
Figure S4. Examples of the start of activity of a yearling and adult male and female Blue Tit.
Figure S5. Examples of the cessation of activity of a yearling and adult male and female Blue Tit.

Figure S6. Estimates of the effect of average daily temperature on the start of activity.

Figure S7. Estimates of the effect of average daily temperature on the cessation of activity.

Figure S8. Estimates of the effect of average rainfall at dawn on the start of activity.

Figure S9. Estimates of the effect of average rainfall at dusk on the cessation of activity.

Table S1. Start and cessation of activity for male and female and for yearling and adult Blue Tits.

Table S2. Effects of rainfall and temperature on the start and the cessation of activity.