

Plasticity in diurnal activity and temporal phenotype during parental care in European starlings, *Sturnus vulgaris*

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We used an automated radiotelemetry system to determine diurnal patterns of activity and temporal phenotype (onset and cessation of activity) in female European starlings during breeding. Parental care is thought to be the most 'costly' part of reproduction, with high rates of intense activity due to foraging and provisioning for chicks, so we predicted that variation in timing of activity should be closely related to breeding success. Diurnal variation in activity varied systematically with breeding stage in a way consistent with specific demands of each phase of parental care: incubating females were more active late in the day (1600–1800 hours), while chick-rearing females were more active early in the morning (0700–1100 hours). There was marked individual variation in timing of onset, and to a lesser extent cessation, of activity, e.g. chick-rearing females first became active 7–127 min after morning civil twilight, with low to moderate repeatability within and among breeding stages (individual explained 2–62% of total variation). On average, females were active later, and ceased being active earlier, during chick rearing compared with incubation. Chick-rearing birds had a longer active day, but only by 2.3% (36% of the seasonal increase in total available daylength). Thus, chick-rearing females were relatively less active ('lazier'), which is consistent with the idea that parents work more efficiently rather than simply working harder. We found little evidence that chick-rearing activity was associated with variation in measures of current reproduction (provisioning rate, number and quality of chicks), future fecundity (initiating a second brood, cumulative 2-year productivity) or survival (local return rate). Our study demonstrates that time-keeping mechanisms show plasticity in response to reproductive state and can be modulated by 'biotic' (e.g. prey availability) or 'social' time (demands of parental care).

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Biological rhythms, cyclical patterns of gene expression, physiology or behaviour are ubiquitous: all living organisms have predictable periodic behaviours that follow a natural rhythm such as the regular alternation of day and night, the seasons, the tides, and the waxing and waning of the moon (Foster, 2010). Chronobiology, the study of biological rhythms, considers sources of variation in, and functional consequences of, biological cycles (Bulla, Oudman, Bijleveld, Piersma, & Kyriacou, 2017; Gwinner, 1986; Naylor, 2010). The most commonly expressed and best-studied biological rhythms are 'circadian rhythms' occurring on a diel timescale (24 h

cycle), typically associated with the light/dark cycle (Foster, 2010). The term 'chronotype' refers to the behavioural output of underlying mechanisms of circadian rhythms (Randler, 2014; Schwartz, Helm, & Gerkema, 2017), e.g. the sleep or wake time of an organism relative to sunset or sunrise (Hoffmann, 1965). Under constant light conditions (in captivity) animals show 'free-running' circadian rhythms with an individually variable period length (tau) that can be shorter or longer than 24 h. Free-living animals are exposed to light–dark cycles and entrain to the 24 h day, so that their period length is 24 h. However, individuals commonly differ in the exact timing of onset of activity, with some being earlier and some later relative to the 24 h light:dark cycle. In the wild 'chronotype' can be determined based on timing of activity onset relative to a salient environmental cue (e.g. sunrise; Dominoni, Helm, Lehmann, Dowse, & Partecke, 2013; Graham, Cook, Needham, Hau, & Greives, 2017). In humans this differential timing can define people as 'morning larks' with an early chronotype and 'night owls' with a late chronotype, and this variation has been correlated with

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several personality traits in humans (Adan et al., 2012; Randler, 2014).

More recent papers have started to extend ideas of circadian rhythms and chronotype to free-living animals, and the terms 'wild clocks' or 'ecological clocks' have been used to describe the integration of chronobiology and ecology with the goal of understanding how behavioural timing might influence individual variation in fitness (Helm et al., 2017). Distinct chronotypes have been demonstrated in other animals (Bulla et al., 2017; Hau et al., 2017) while other studies have confirmed that there is individual variation in diurnal patterns of activity in free-living animals (Aschoff & Wever, 1966; Corinna ; Labyak, Lee, & Goel, 1997; Steinmeyer, Schielzeth, Mueller, & Kempenaers, 2010; Wicht et al., 2014). It is assumed that this variation provides differential fitness advantages by enabling organisms to optimize physiology and behaviour in anticipation of diel changes in the environment (Cuthill & Houston, 1997, pp. 97–120; Pittendrigh, 1993). For example, in birds, Graham et al. (2017) reported a relationship between early chronotype (departing the nest earlier in the morning) and timing of egg laying. Earlier onset of a male's morning singing activity, relative to dawn, was positively correlated with extrapair mating success in blue tits, *Cyanistes caeruleus* (Kempenaers, Borgström, Loës, Schlicht, & Valcu, 2010; Poesel, Kunc, Foerster, Johnsen, & Kempenaers, 2006) and it has long been assumed that males are more active before dawn when their mates are fertile in order to protect paternity (Hinde, 1952; Ward, Alessi, Benson, & Chiavacci, 2014). Helm and Visser (2010) found that male great tits, *Parus major*, sired by an extrapair male have a shorter circadian rhythm compared with their siblings sired by the social father.

Linking individual variation in biological rhythms or chronotype to reproductive success and fitness requires detailed behavioural data, and recent technological developments in biotelemetry or wildlife tracking now allow researchers to monitor large numbers of individual free-living animals 24 h per day, 7 days per week (Wilmers et al., 2015). Here, we used an automated radiotelemetry system (Serota & Williams, 2019) to determine patterns of diurnal variation in activity and temporal phenotype of female European starlings from late incubation through the entire chick-rearing period. Parental care is thought to be the most 'costly' part of reproduction, with high rates of intense activity due to central-place foraging and provisioning of chicks (Clutton-Brock, 1991; Piersma & van Gils, 2011). We include data from a handicapping experiment that manipulated costs of parental care (see Serota & Williams, 2019 for details). Our specific objectives in this paper were (1) to identify patterns of diurnal variation in activity and to test whether these varied in relation to the specific 'demands' of different breeding stages in successful birds; (2) to characterize individual variation in, and repeatability of, 'temporal phenotype' using multiple metrics of daily activity (onset and cessation of daily activity, length of the active day); and (3) to determine whether individual variation in temporal phenotype is related to measures of both current breeding productivity (e.g. number and size of fledglings), future fecundity (e.g. initiating second broods, cumulative 2-year productivity) and survival (local return rate). We predicted that (1) if chronotype in free-living European starlings is consistent with the lark–owl concept, then an 'early' individual should start and end its activity early, and a 'late' individual should start and end its activity late, (2) given that handicapped birds decreased overall activity (Serota & Williams, 2019), they would adjust onset and cessation of activity to compensate, and (3) 'early' birds, or birds with a longer active day, would do better in terms of current productivity due to earlier onset of activity but that this might come at a cost in terms of future fecundity and survival.

METHODS

We collected breeding data on European starlings during March–June 2015 and 2016, from our long-term study population at Davistead Farm, Langley, British Columbia, Canada (49°10'N, 122°50'W). The field site contains about 150 nestboxes mounted on posts around pastures and on farm buildings. Each year, we followed the same basic field protocol: nestboxes were checked daily from late March to determine laying date, egg and clutch size. Nests were monitored until either failure or fledging to quantify productivity. Each nest was checked on day 17 (prior to fledging ~ day 21) to obtain brood size at fledging and chick fledgling mass and tarsus length. Individual breeding females were captured during mid-incubation, measured (mass, tarsus, wing chord) and fitted with colour bands and individually numbered metal bands (Environment Canada permit no. 10646). Similar breeding data were collected for individuals that double-brooded in the same year, as a measure of future fecundity. In the subsequent year we re-located all banded females to obtain data on return rate (local survival) and breeding productivity for first and second broods in the second year. Female provisioning rate was determined as the number of nest visits per 30 min via observations conducted between 0900 and 1400 hours on days 6–8 posthatching (day 0 was defined as the day the majority of chicks in the nest hatched; see Fowler & Williams, 2015 for more details).

In this paper we analyse variation in diurnal activity and temporal phenotype measures for a subset of birds included in a previously published handicapping study (Serota & Williams, 2019). Briefly, adult females were caught during mid-incubation, fitted with a radiotransmitter (see below) and alternately assigned to either a wing-clipping or no-clipping treatment. Wing-clipped birds had every third primary feather (i.e. primaries 2, 5 and 8) from each wing removed near the base with scissors. Here we only use data from successful females rearing at least one chick from their first brood: $N = 17$ females with radiotransmitters and no clipping, and $N = 12$ females with radios and wing clipping. For the larger sample of birds, Serota and Williams (2019) reported that handicapping decreased current breeding success due to higher abandonment and nest failure, but among successful birds (fledging > 1 chick) there was no effect of handicapping on brood size at fledging for the current breeding attempt. Furthermore, comparing among birds with radios, handicapping had no effect on provisioning rate, probability of initiating a second brood, return rate or cumulative 2-year breeding productivity (although, overall, return rate and cumulative productivity were lower in all birds with radiotransmitters compared with nonmanipulated controls; see Discussion).

Activity Data and Automated Radiotelemetry

In 2015 and 2016, females were fitted with a digitally coded Nanotag radiotransmitter (NTQB-4-2, Lotek Wireless Inc., Newmarket, ON, Canada) by means of a leg loop harness (Rappole & Tipton, 1991). Total weight of transmitter and harness was ≤ 2.2 g or 2.4% of body mass for an 85 g female European starling. For the duration of the breeding season, five (2015) or four (2016) Automated Receiving Units (ARUs; Lotek Wireless Inc.) with two to four 5-element Yagi antennas were positioned around the field site. Every 8 s, each antenna at each tower alternately scanned for deployed radiotransmitters (beep rate 2.5 s), allowing continuous monitoring of all tagged females' activity. Preliminary validation confirmed that tags were detected up to distances of approximately 1 km. We calculated 'activity' of females following methods described in Steiger et al. (2013), Ward et al. (2014) and Zúñiga et al. (2016) using data for a single ARU and the antenna closest to the

focal nestbox, i.e. with the strongest average signal for a given individual (preliminary analysis showed that using data from an adjacent antenna, or data from all antennas for the ARU nearest the nestbox gave quantitatively similar results for activity estimates: $r^2 = 0.92$ and 0.73, respectively). Lotek receivers use power as a received signal strength indicator (RSSI) where 1 RSSI value (=power) is approximately 2.2 dBm (Lotek Wireless Inc., personal communication). We applied a minimum power threshold of 50 to control for background noise, which when converted to signal strength is consistent with previous studies that calculate activity (Steiger et al., 2013; Ward et al., 2014; Zúñiga et al., 2016). We used the change in power (Δ) from one detection to the next to determine whether a bird was active or inactive. We determined threshold values for Δ power by observing the change in power of inactive birds during incubation, where a Δ power value <10 indicates an inactive bird. This value is equal to the upper end of the 99% confidence interval of the mean for observed incubating birds. A Δ power threshold of 10 when converted to signal strength (4.5 dBm) is similar to values used in previous studies as thresholds for 'activity' (Adelman, Córdoba-Córdoba, Spoelstra, Wikelski, & Hau, 2010; Steiger et al., 2013; Ward et al., 2014). We restricted analysis of activity to the time between morning and evening civil twilight (National Research Council Canada, <http://www.nrc-cncr.gc.ca/eng/services/sunrise/>). To do this, one of us (C.M.) wrote a script in R (v.3.4.1, The R Foundation for Statistical Computing, Vienna, Austria) that calculated the change in power (Δ) between successive pairs of detections for each individual each day, then scanned these data to identify the first instance after morning civil twilight where this difference was >10 , i.e. the individual bird was 'active'. Similarly, R identified the last 'activity' (Δ power value >10) before evening civil twilight. We analysed activity and temporal phenotype for four breeding stages: incubation (from transmitter deployment to hatch or day 0), brooding (1–5 days posthatching), chick rearing (6–21 days posthatching) and postfledging (>21 days).

Statistical Analysis

Statistical analyses were completed in R Studio (R Studio, Boston, MA, U.S.A.) or SAS v.9.4 (SAS Institute, Cary, NC, U.S.A.). For analysis of diurnal variation in activity patterns, we first calculated each individual's overall mean activity as ($(\text{active detections where } \Delta \text{ power } >10 / \text{total detections} - 1) \times 100$) for each breeding stage. We then calculated the same value for each hour of activity and then used the difference between hourly activity and overall mean percentage of activity, i.e. residual or relative activity, to account for differences among individuals (and treatments). We then used linear mixed-effects models (PROC MIXED) with residual hourly activity as the dependent variable, hour, breeding stage and hour*stage as main effects, and individual (band number), year and treatment as a random factors. We restricted analysis of diurnal variation to 0500–1800 hours to exclude periods with less than one full hour between activity and civil twilight, and also excluded hours with fewer than 10 detections. We also tested models with treatment as a main effect (see Results).

As a measure of 'chronotype', we calculated onset of activity as time in minutes between the start of civil twilight and the first activity in the morning for each day (see above; following Dominoni et al., 2013; Graham et al., 2017). Initially we also calculated the 'midpoint of activity' as a measure of chronotype (following Daan & Aschoff, 1975), but this was highly correlated ($r = 0.82$) with our measure of timing of morning activity, so we did not consider this further. We also calculated cessation of activity as time in minutes between the last activity and evening civil twilight for each day and the length of each bird's active day as the

difference between time of onset and cessation of activity as additional metrics of temporal phenotype. In terms of the 'lark–owl' concept, an 'early' chronotype individual would have a shorter interval between morning civil twilight and first activity and a longer interval between last activity and evening civil twilight. We analysed variation in these three measures of activity among breeding stages using mixed-effects models (PROC MIXED) with activity as the dependent variable, breeding stage as the main effect and individual (band number), year and experimental treatment as random effects. European starlings are highly synchronous in terms of laying date (Williams et al., 2015): laying date varied by ± 2 days in 2015 and ± 4 days in 2016; therefore, we did not include date in our models. When we included treatment and the treatment*stage interaction as main effects, these terms were not significant in any models ($P > 0.16$ in all cases), so we report results with treatment as a random factor. We estimated repeatability of timing of onset and cessation of activity within and between breeding stages for incubation and chick rearing only, in R (package ICC) as the intraclass correlation coefficient using repeated measurements on different days.

For timing metrics and life-history traits, we calculated mean values for timing of onset of activity relative to civil twilight (i.e. 'chronotype') and length of the active day (timing of cessation of activity was less variable, and redundant given the other two measures), for each female and for incubation and chick rearing separately. We then analysed variation in these metrics in relation to variation in (1) current reproduction: provisioning rate, controlling for brood size, brood size at fledging and day 17 chick mass controlling for tarsus, (2) two measures of future fecundity: probability of initiating a second brood and cumulative number of chicks fledged over 2 years and (3) and survival (local return rate), using mixed-effects models (PROC MIXED). For categorical variables we used onset of activity or active day as the dependent variable, initiating second brood (yes/no) or return rate (yes/no) as main effects along with treatment, and the interaction, and year as a random factor. For continuous variables, we used the trait (provisioning rate, chick mass, etc.) as the dependent variable, onset of activity or active day, treatment and the interaction as main effects, and relevant covariates (e.g. brood size, tarsus length) and year as random factors.

Ethical Note

The Canadian Committee on Animal Care (CCAC) approved the research methods described in this paper under Simon Fraser University's Animal Care Committee permit number 1018 B-96. The banding permit to capture and band birds was granted by Environment Canada under permit number 10646 (T.D.W., master permittee) and 10646 N (subpermit to M.W.S.). To reduce the overall stress on the experimental birds, we attempted to reduce the handling time of both radiotagged and wing-clipped birds. Average handling time for both treatment groups was 6.5 min, and there was no statistical difference in the handling time between treatment groups ($P = 0.53$). Transmitters weighed 1.9–2.1 g, or about 2.5% of mean body mass of females at incubation (82.9 g). This is well below the recommended weight of radiotransmitters considering the individual's mass (Barron, Brawn, & Weatherhead, 2010). Most recaptured females did not have their radiotransmitters from the previous year, confirming that transmitters fell off following the breeding period. A few females ($N = 5$) still had their radios from the previous year, but these birds showed no sign of feather wear or skin damage and radios were removed at mid-incubation, so no birds retained a radiotransmitter through their second chick-rearing period.

RESULTS

Effect of Breeding Stage on Diurnal Variation in Activity

The pattern of diurnal variation in activity varied between breeding stages (time*breeding stage interaction: $F_{39,8053} = 5.04$, $P < 0.001$; Fig. 1). Including treatment as a main effect did not change the model output (treatment: $F_{1,8053} = 0.01$, $P > 0.90$). There was significant variation in relative activity with time of day for each breeding stage analysed separately: incubation ($F_{13,1332} = 14.7$, $P < 0.001$), brooding ($F_{13,1324} = 19.1$, $P < 0.001$), chick rearing ($F_{13,4179} = 30.4$, $P < 0.001$) and postfledging ($F_{13,1138} = 2.10$, $P < 0.05$). During incubation, females were significantly more active during 1600–1800 hours ($P < 0.01$ in all cases; Fig. 1a). In contrast, chick-rearing females were significantly more active during 0700–1100 hours ($P < 0.01$ in all cases; Fig. 1c). During brooding, the pattern of diurnal activity was intermediate between that of incubating and chick-rearing birds, with relatively more activity during 0900–1000 hours and 1500–1800 hours (Fig. 1b). Finally, during the postfledging period, diurnal activity was generally less marked than during all other breeding stages (Fig. 1d).

Individual Variation and Repeatability of Temporal Phenotype

Mean (\pm SD) onset of civil twilight in the morning varied from 0439 hours (± 16 min) during incubation to 0352 hours (± 9 min) during the postfledging period. Mean end of civil twilight in the evening varied from 1944 hours (± 15 min) during incubation to 2025 hours (± 9 min) during the postfledging period. The total duration of daylight, including civil twilight, was therefore 15.08 h during incubation and 15.96 h during chick rearing, an increase of 53 min.

There was no difference in timing of onset of activity (i.e. 'chronotype'), timing of cessation of activity, or length of the active day, during chick rearing comparing females with radios only and wing-clipped females ($P > 0.35$ in all cases; Table 1).

Time to onset of activity relative to morning civil twilight varied between breeding stages ($F_{3,724} = 31.3$, $P < 0.001$), being earliest during incubation and latest during the postfledging period (Fig. 2a). Time to onset of activity was not different for incubating and brooding birds (Bonferroni-corrected $P = 0.60$) but chick-rearing birds ($P < 0.001$) and postfledging birds ($P < 0.001$) were both active later compared with incubating birds (Fig. 2a).

Within each breeding stage, time between morning civil twilight and onset of activity was greater than time between cessation of activity and evening civil twilight (paired t test: $P < 0.001$ in all cases), i.e. females remained active for longer into the evening (Fig. 2a). Nevertheless, time between cessation of activity and evening civil twilight also varied between breeding stages ($F_{3,736} = 16.4$, $P < 0.001$). Time from cessation of activity was not different for incubating and brooding birds (Bonferroni-corrected $P = 1.00$), but chick-rearing birds ($P < 0.05$) and postfledging birds ($P < 0.001$) ceased activity earlier compared with incubating birds (Fig. 2a). As a consequence, the length of the active day (from first to last activity) varied between breeding stages ($F_{3,655} = 7.11$, $P < 0.001$; Fig. 2b). However, the increase in the length of the active day between incubation and chick rearing (19 ± 5 min; $P < 0.01$) represented only 36% of the increase in total available daylength (53 min, see above): chick-rearing birds only increased the length of their active day by 2.3%.

Overall, chronotype measured as time to onset of activity was highly variable among individuals: females first became active between 7–122 min (incubation) and 7–127 min (chick rearing) after morning civil twilight. Time to onset of activity was repeatable within breeding stages both during incubation ($ICC = 0.22$, $F_{1,24} = 2.21$, $P < 0.01$; Fig. 3a) and chick rearing ($ICC = 0.36$, $F_{1,26} = 8.11$, $P < 0.001$; Fig. 3b). Individual variation in the cessation of activity was less than in the onset: 1–62 min (incubation) and 4–71 min (chick rearing), and individual explained less of the total variation: cessation of activity was only repeatable during chick rearing ($ICC = 0.18$, $F_{1,26} = 3.72$, $P < 0.001$) and not during

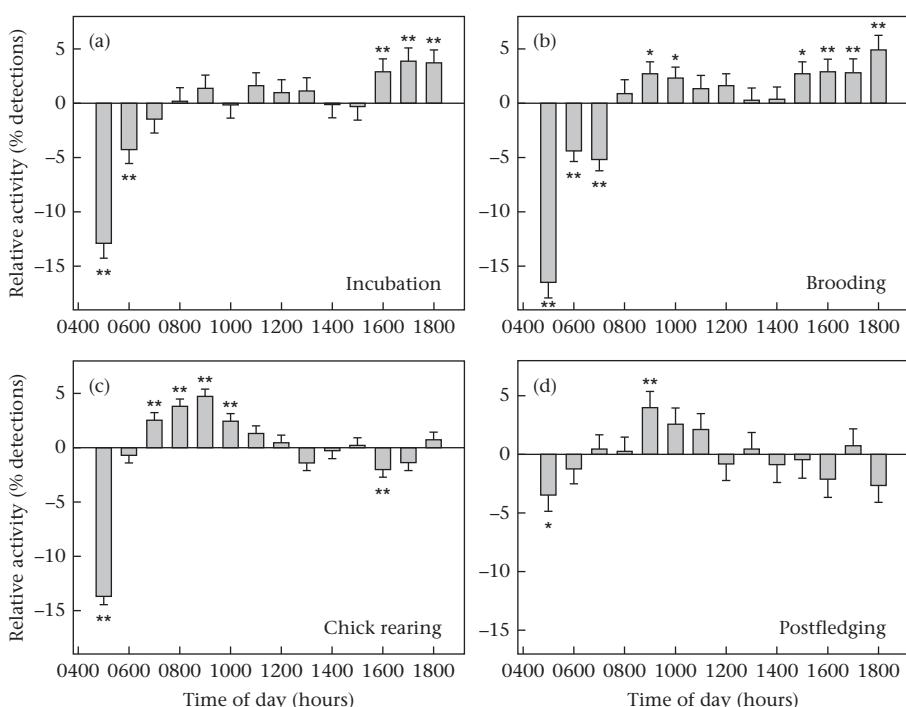


Figure 1. Diurnal variation in activity among successful female European starlings at each breeding stage: (a) incubation (b) brooding (c) chick rearing and (d) postfledging. Data are mean \pm SE residual activity for each hour (P values above bars indicate relative activity significantly different from zero; * $P < 0.05$, ** $P < 0.01$).

Table 1

Timing of onset/cessation of activity (minutes relative to morning/evening civil twilight) and length of active day for handicapped (wing-clipped) females and radio-only females during chick rearing

Activity measure	Wing-clipped, $N = 12$ (range)	Radio-only, $N = 17$ (range)	$F_{1,28}$	P
Onset of activity (min)	73.1 ± 8.7 (14.6–123.4)	72.9 ± 7.3 (7.9–102.3)	0.00	0.98
Cessation of activity (min)	27.3 ± 4.7 (9.4–56.1)	22.5 ± 4.0 (3.5–66.3)	0.60	0.44
Length of active day (h)	14.3 ± 0.2 (13.0–15.6)	14.4 ± 0.2 (13.6–15.6)	0.20	0.66

Values are lsmeans \pm SE, controlling for brood size.

incubation ($ICC = 0.11$, $F_{1,24} = 1.52$, $P = 0.08$). Repeatability of morning onset of activity was marginally significant between incubation and chick rearing ($ICC = 0.30$, $F_{1,26} = 1.83$, $P = 0.065$) and cessation of activity was repeatable between incubation and chick rearing ($ICC = 0.45$, $F_{1,26} = 2.60$, $P < 0.01$).

Among individual females, mean timing of onset and cessation of activity were positively correlated during both incubation (Pearson correlation: $r_{28} = 0.64$, $P < 0.001$; Fig. 4a) and chick rearing ($r_{29} = 0.57$, $P = 0.001$; Fig. 4b), i.e. females that were active later in the morning ceased activity earlier in the evening, resulting in a shorter active day.

Temporal Phenotype and Life-history Traits

Egg-laying date (first egg) and clutch size were independent of any measure of female activity during incubation ($P > 0.07$ in all cases). Female provisioning rate (controlling for brood size; Fig. 5a), brood size at fledging, day 17 chick mass (controlling for tarsus length) and cumulative number of chicks fledged over 2 years (Fig. 5b) were all independent of timing of onset of morning activity

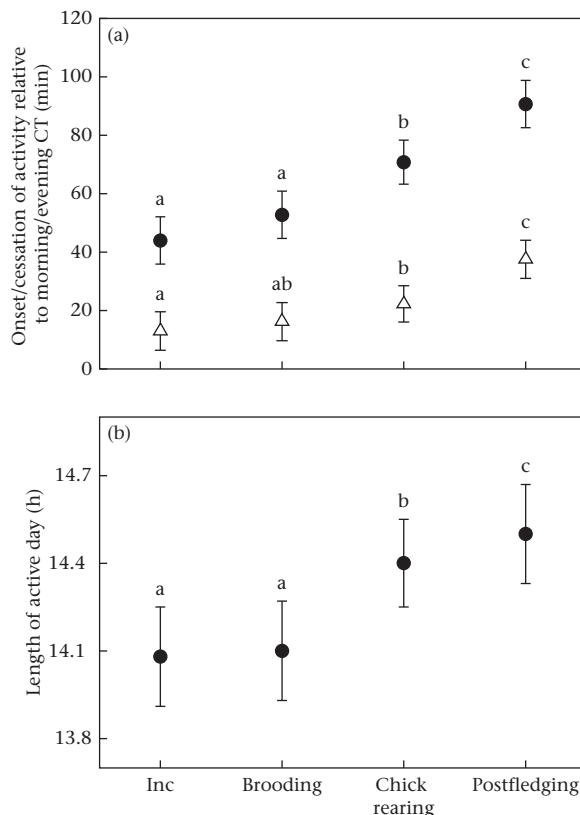


Figure 2. Variation in (a) timing of onset of activity in the morning (closed circles, minutes after morning civil twilight, CT), and timing of cessation of activity in the evening (open triangles, minutes before evening CT), and (b) length of the active day from onset to cessation of activity. Values are lsmeans \pm SE.

relative to civil twilight and to the length of the female's active day (treatment and timing*treatment interaction was not significant in any models: $P > 0.15$ in all cases; Table 2). Similarly, females that returned in year 2 had similar time of onset of activity (73.4 ± 16.0 min) compared with females that did not return (70.0 ± 15.2 min) and similar lengths of the active day (14.4 ± 0.2 h and 14.3 ± 0.17 h, respectively; Table 2). Females that initiated a second brood in year 1 were active earlier in the morning (58.5 ± 14.1 min after civil twilight) during chick rearing compared to females that did not initiate a second brood (82.3 ± 14.1 min), however, there was no difference in length of the active day (14.5 ± 0.17 h versus 14.2 ± 0.17 h, respectively; Table 2).

DISCUSSION

Diurnal variation in patterns of activity of female European starlings were not fixed during the breeding season but varied systematically with breeding stage: incubating females were more

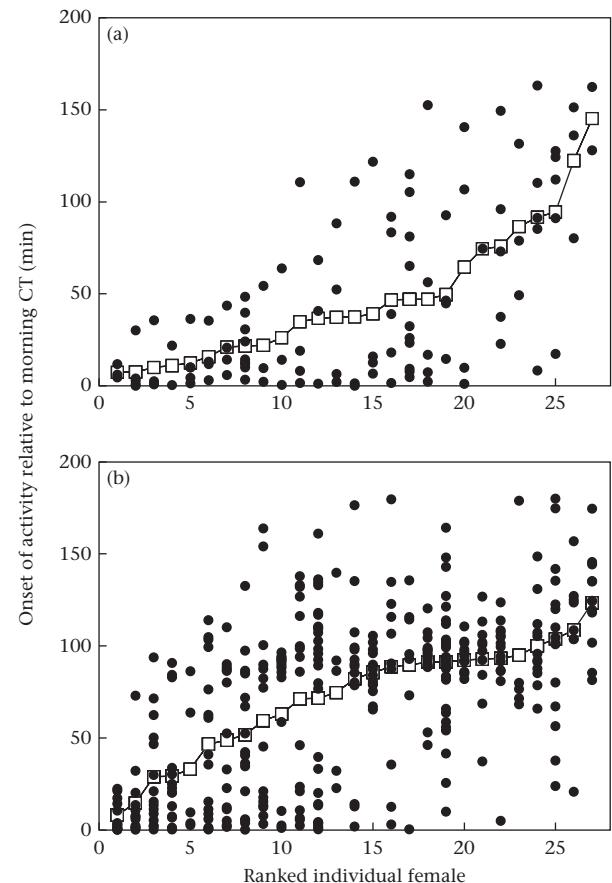


Figure 3. Repeatability of individual variation in female chronotype (onset of activity relative to morning civil twilight, CT) for (a) incubation and (b) chick rearing. Values for different days are plotted as black dots and open squares show mean values for each individual female. Females are ranked from earliest to latest based on mean values.

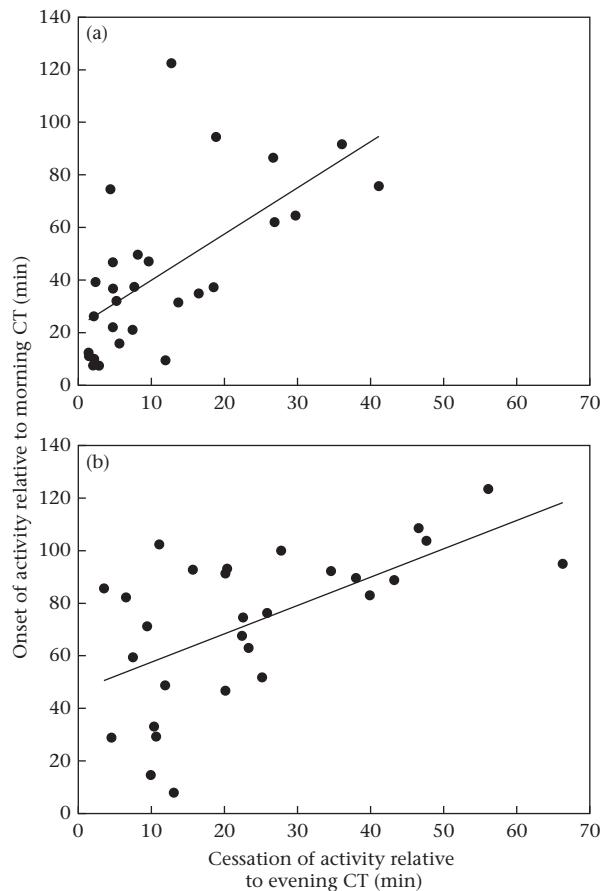


Figure 4. Relationship between onset of morning activity and cessation of evening activity relative to morning/evening civil twilight, CT, in individual females during (a) incubation and (b) chick rearing.

active late in the day, while chick-rearing females were more active early in the morning. In each breeding stage, there was marked individual variation in temporal phenotype, based on first and last activity relative to civil twilight, with low to moderate repeatability within and among breeding stages. Some females were active within minutes of morning civil twilight whereas others were first active up to 2 h after onset of civil twilight. On average, females were active relatively later, and ceased being active earlier, during chick rearing compared with incubation. Females that were active earlier in the morning were also active later in the evening (cf. the prediction based on the concept of the lark–owl chronotype). However, we found relatively little evidence that variation in temporal phenotype was associated with a range of metrics of individual quality, breeding productivity and fitness.

In our analysis, we included data from handicapped (wing-clipped) birds from a study reported by Serota and Williams (2019). Although Serota and Williams (2019) showed that wing-clipped females had 22% lower overall activity compared to radio-only females during chick rearing, we found no evidence that handicapping affected temporal phenotype. There was no difference in the timing of onset or cessation of activity and no difference in the length of the active day during chick rearing between radio-only females and wing-clipped females. Furthermore, 'treatment' was not significant in any models and including treatment as a random factor did not affect model output. This suggests that circadian patterns of activity and chronotype are more robust to

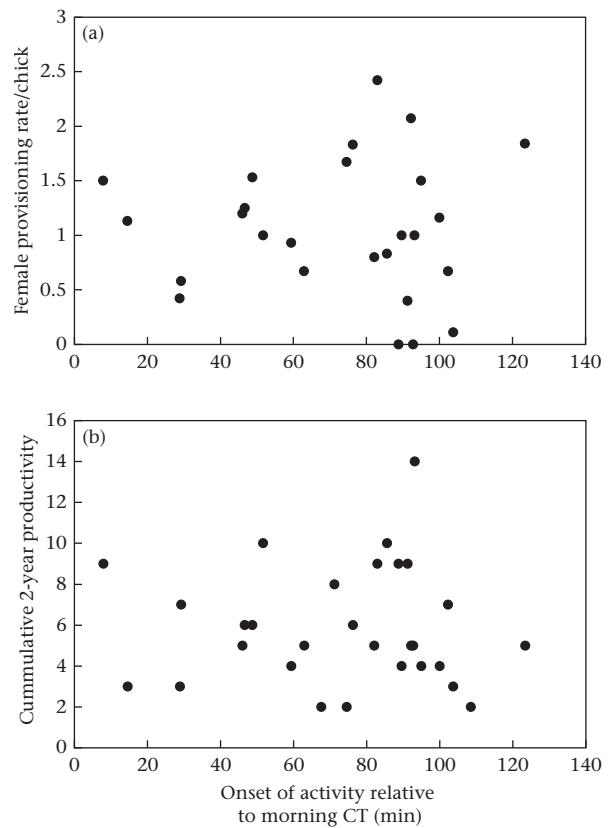


Figure 5. Relationship between timing of onset of activity relative to morning civil twilight, CT, and (a) female provisioning rate per chick per 30 min and (b) cumulative 2-year breeding productivity.

handicapping than overall level of activity and this is consistent with the moderate repeatability we report.

In female starlings, the pattern of diurnal variation in activity varied among breeding stages in a way that is consistent with specific demands of the different phases of parental care. Incubating females were more active later in the day, suggesting that females benefit by self-feeding more, and by being more active, just prior to fasting associated with night-time incubation, which can involve increased energy demand (de Heij, van der Graaf, Hafner, & Tinbergen, 2007). An alternative explanation is that lower overall levels of early morning activity are associated with constraints of incubation, where females delay leaving the nest until ambient temperature has increased so that eggs cool less, decreasing subsequent rewarming effort (Gwinner, Capilla-Lasheras, Cooper, & Helm, 2018). However, this is not consistent with our finding that incubating females first left their nests earlier in the morning than chick-rearing females (see below). During chick rearing the demand of rapidly growing chicks for food, especially after the female and chicks have fasted overnight, would explain why females are relatively more active earlier in the morning. The intermediate pattern of diurnal activity of females at the brooding stage reflects lower food requirements of younger chicks before 5 days of age, and the fact that females still need to brood chicks, especially in cold weather, prior to chicks becoming thermally independent around day 5–6. Finally, during the postfledging period, diurnal activity of female parents was generally less marked than during all other breeding stages. This is likely associated with the fact that (1) chicks are close to somatic maturity at this stage (Cornell & Williams, 2017) and (2) chicks are mobile and can follow parents for feeding, reducing foraging distances and overall activity (Williams, 2018).

Table 2

Model output for relationships between two measures of temporal phenotype (time of onset of activity and length of active day) during chick rearing and various life-history (LH) traits^a

LH trait	Mean \pm SD (range)	Timing metric	F	df	P
Provisioning rate/chick	1.05 \pm 0.63 (0–2.4)	Onset of activity	0.01	1, 21	0.94
		Active day	0.01	1, 21	0.93
First brood size, fledging	3.7 \pm 1.6 (0–6)	Onset of activity	0.43	5, 16	0.82
		Active day	1.92	5, 16	0.15
Day 17 chick mass ^b	74.3 \pm 6.5 (61.8–85.8)	Onset of activity	1.70	1, 22	0.21
		Active day	3.00	1, 22	0.10
Initiating second brood	NA	Onset of activity	6.63	1, 24	0.017
		Active day	1.66	1, 24	0.21
Cumulative 2-year productivity	5.9 \pm 2.9 (2–14)	Onset of activity	0.01	1, 24	0.94
		Active day	0.01	1, 23	0.93
Return rate	NA	Onset of activity	0.10	1, 24	0.76
		Active day	0.04	1, 24	0.84

^a F statistic, df and P values refer to main effect of timing metric; treatment and the treatment*timing interaction were not significant in any models ($P > 0.15$ in all cases).

^b Controlling for chick tarsus length.

Although European starlings are highly synchronous in terms of seasonal timing of breeding and onset of egg laying, with 80% of nests initiated in 4–5 days (see Methods; also see Williams et al., 2015), there was marked individual variation in timing of onset, and to a lesser extent cessation, of diurnal activity. In general, all females had relatively low activity very early in the morning for up to 1–3 h after onset of morning civil twilight (0500–0700 hours). Numerous previous studies had reported earlier onset of morning activity in birds, but for earlier breeding stages; associated with birds seeking extrapair copulation with partners outside of the social pair bond (Hau et al., 2017). For females, extraterritorial forays are most frequent prior to or during egg laying when females are fertile (Chiver, Stutchbury, & Morton, 2008; Double & Cockburn, 2000; Ward et al., 2014). During incubation and chick rearing, female European starlings are not fertile, so early morning activity associated with extrapair copulations would not be expected. In fact, females became active later in the day as breeding progressed over the season. Although chick-rearing birds had a longer active day compared to incubating birds, this only represented a 2.3% increase, and chick-rearing females only used 36% of the seasonal increase in available daylight. Thus, chick-rearing females were effectively relatively less active or more 'lazy'. Dominoni, Carmona-Wagner, Hofmann, Kranstauber, and Partecke (2014) reported a similar seasonal pattern of activity in male European blackbirds, *Turdus merula*, with birds tending to be active earlier in the morning and later in the evening at the incubation stage compared with later breeding stages. This finding, and the only very short increase in the length of the active day, are counterintuitive results given the widely held assumption that parental care is the most demanding stage of an animal's life cycle requiring high-intensity activity at a 'maximal sustained working level' (Drent & Daan, 1980; Piersma & van Gils, 2011; Riechert & Becker, 2017; but see ; Williams, 2018). However, our results would be consistent with the idea that parents might work more efficiently rather than simply working harder (Daunt, Afanasayev, Silk, & Wanless, 2006; Lescroel et al., 2010). For example, female European starlings (and many other species; Swanson, 2010) routinely lose mass between incubation and chick rearing. While this might decrease costs of flight through decreased wing loading (Norberg, 1981), it could also allow for a reduction in overall demands for activity of the female parent. In all breeding stages, time to cessation of activity in the evening was much less than time to onset of activity in the morning. Helm et al. (2017) suggested this pattern would emerge if differences in interindividual variation and in associated payoffs meant that timing of the onset of an activity (e.g. wake-up time) were more relevant for fitness than the timing of its offset (e.g. return to roost). However, this argument has largely been based on costs and

benefits of early season events before laying, e.g. extrapair copulations (Hau et al., 2017) or male singing and display during the dawn chorus (Kacelnik & Krebs, 1982). This highlights the need to identify the benefits of a 'slow start' for chick-rearing females.

The 'lark–owl' concept predicts that individuals with an 'early' chronotype should be active earlier in the morning but also that they should stop being active earlier in the evening, with the reverse being true for late, 'owl' chronotype (e.g. see Figure 3 in Helm et al., 2017). In free-living European starlings we found the opposite pattern, i.e. females that were active earlier in the morning remained active later the evening. Thus, our study suggests that rather than the lark–owl chronotype, we have 'more active' and 'less active' phenotypes. We found low to moderate repeatability of onset and cessation of activity within breeding stages, with individual explaining 2–62% of total variation, but lower repeatability among breeding stages. Previous studies have reported similar, relatively low to moderate repeatability for various activity or sleep–wake metrics especially within breeding stages, but low to no repeatability among breeding stages (Graham et al., 2017; Schlicht, Valcu, Loës, Girg, & Kempenaers, 2014; Stuber, Dingemanse, Kempenaers, & Mueller, 2015). This suggests plasticity in activity traits in response to different selection pressures at different life-history stages (Rattenborg et al., 2004; Steinmeyer et al., 2010).

Despite flexibility in diurnal patterns of activity, marked individual variation in activity and some level of repeatability, we found little evidence that chick-rearing activity was associated with variation in measures of current reproduction (provisioning rate, number and quality of chicks), future fecundity (initiating a second brood, cumulative 2-year productivity) or survival (local return rate). Similarly, variation in activity during incubation was not related to variation in clutch size or laying date (cf. Graham et al., 2017). Females that initiated a second brood were active sooner in the morning, by about 20 min, than females that did not initiate a second brood. However, in our study system, double brooding is not associated with clear costs: females that double-brood have higher return rates. Furthermore, propensity to double-brood is independent of other putative measures of individual quality (clutch size, egg mass, relative female age and nestling provisioning rate; Cornell & Williams, 2016). It is possible that less active female starlings are investing more in self-maintenance and less in reproduction, adopting a 'slow' lifestyle, although it is hard to conceive of 20 min of less activity per day being biologically significant. Most previous studies have focused on activity (or sleep–wake cycles) during the prebreeding period or incubation, not during chick rearing, and provide little unequivocal evidence for a relationship between chronotype, fitness and individual

quality (Graham et al., 2017; Hau et al., 2017; Steinmeyer, Mueller, & Kempenaers, 2013). Based on nest temperature data, Graham et al. (2017) found that incubating female great tits and dark-eyed juncos, *Junco hyemalis*, who first departed from their nest earlier in the morning also initiated nests earlier in the year, but we did not confirm this result. In contrast, Steinmeyer et al. (2013) reported that laying date, clutch size and local survival were independent of any measure of sleep activity in female blue tits, although male blue tits with earlier sleep onset and longer sleep durations were more likely to gain extrapair paternity of offspring.

Internally generated, free running, circadian period lengths (τ) are repeatable and have been demonstrated in a wide range of organisms. Furthermore, some studies have demonstrated fitness consequences of behavioural outputs of circadian rhythms in free-living animals (e.g. Graham et al., 2017; Kempeneers et al., 2010; Lesku et al., 2012), but generally for earlier stages of reproduction. Although we did find evidence for repeatability of measures of activity onset and cessation, activity appeared to be more related to demands of specific stages of parental care, but this was largely independent of a range of reproductive fitness measures. In particular, in our study the lark–owl concept of chronotype developed largely from human studies did not apply to free-living European starlings. Thus, our study confirms that reproductive behaviour is not constrained by ‘fixed’ internal time-keeping mechanisms (Helm et al., 2017) or abiotic cycles (daylength, temperature). Rather activity is plastic and can be modulated by ‘biotic’ (e.g. prey availability) or ‘social’ time (demands of parental care itself; van der Veen, 2017) masking or modulating any true rhythm set by the internal clock. Bulla et al. (2017) found that free-living shorebirds show strong individual differences in tidal and circadian foraging rhythms over the 8–10 months spent as nonbreeders in their tidal environments but rarely maintained such tidal or circadian rhythms during breeding (incubation). Finally, despite the expected increased demands of central-place foraging and chick provisioning, females only increased their active day by 2.3% from incubation to chick rearing, were active later in the morning and ceased being active earlier in the evening. This challenges the conventional view of parents having to work as hard as they can to rear chicks during parental care.

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References

Adan, A., Archer, S. N., Hidalgo, M. P., Di Milia, L., Natale, V., & Randler, C. (2012). Circadian typology: A comprehensive review. *Chronobiology International*, 29(9), 1153–1175. <https://doi.org/10.3109/07420528.2012.719971>.

Adelman, J. S., Córdoba-Córdoba, S., Spoelstra, K., Wikelski, M., & Hau, M. (2010). Radiotelemetry reveals variation in fever and sickness behaviours with latitude in a free-living passerine. *Functional Ecology*, 24, 813–823.

Aschoff, J., & Wever, R. (1966). Circadian period and phase-angle difference in chaffinches (*Fringilla coelebs* L.). *Comparative Biochemistry & Physiology*, 18, 397–404.

Barron, D. G., Brawn, J. D., & Weatherhead, P. J. (2010). Meta-analysis of transmitter effects on avian behaviour and ecology. *Methods in Ecology and Evolution*, 1(2), 180–187. <https://doi.org/10.1111/j.2041-210X.2010.00013.x>.

Bulla, M., Oudman, T., Bijleveld, A. L., Piersma, T., & Kyriacou, C. P. (2017). Marine biorhythms: Bridging chronobiology and ecology. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372, 20160253.

Chiver, I., Stutchbury, B. J. M., & Morton, E. S. (2008). Do male plumage and song characteristics influence female off-territory forays and paternity in the hooded warbler? *Behavioral Ecology and Sociobiology*, 62, 1981–1990.

Clutton-Brock, T. H. (1991). *The evolution of parental care*. Princeton, NJ: Princeton University Press.

Cornell, A., & Williams, T. D. (2016). Individual quality and double-brooding in a highly synchronous songbird population. *Auk*, 133, 251–260.

Cornell, A., & Williams, T. D. (2017). Variation in developmental trajectories of physiological and somatic traits in a common songbird approaching fledging. *Journal of Experimental Biology*, 220, 4060–4067.

Cuthill, I. C., & Houston, A. I. (1997). Managing time and energy. In J. R. Krebs, & N. B. Davies (Eds.), *Behavioural ecology: An evolutionary approach* (4th ed., pp. 97–120). Oxford, UK: Wiley-Blackwell.

Daan, S., & Aschoff, J. (1975). Circadian rhythms of locomotor activity in captive birds and mammals: Their variations with season and latitude. *Oecologia*, 18(4), 269–316. <https://doi.org/10.1007/bf00345851>.

Daunt, F., Afanasyev, V., Silk, J. R. D., & Wanless, S. (2006). Extrinsic and intrinsic determinants of winter foraging and breeding phenology in a temperate seabird. *Behavioral Ecology and Sociobiology*, 59, 381–388.

Dominoni, D. M., Carmona-Wagner, E. O., Hofmann, M., Kranstauber, B., & Partecke, J. (2014). Individual-based measurements of light intensity provide new insights into the effects of artificial light at night on daily rhythms of urban-dwelling songbirds. *Journal of Animal Ecology*, 83(3), 681–692. <https://doi.org/10.1111/1365-2656.12150>.

Dominoni, D. M., Helm, B., Lehmann, M., Dowse, H. B., & Partecke, J. (2013). Clocks for the city: Circadian differences between forest and city songbirds. *Proceedings of the Royal Society B: Biological Sciences*, 280(1763), 20130593. <https://doi.org/10.1098/rspb.2013.0593>.

Double, M., & Cockburn, A. (2000). Pre-dawn infidelity: Females control extra-pair mating in superb fairy-wrens. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 267, 465–470.

Drent, R., & Daan, S. (1980). The prudent parent: Energetic adjustments in avian breeding. *Ardea*, 68, 225–252.

Foster, R. G. (2010). *Seasons of life: The biological rhythms that enable living things to thrive and survive*. New Haven, CT: Yale University Press.

Fowler, M. A., & Williams, T. D. (2015). Individual variation in parental workload and breeding productivity in female European starlings: Is the effort worth it? *Ecology and Evolution*, 5(17), 3585–3599. <https://doi.org/10.1002/ece3.1625>.

Graham, J. L., Cook, N. J., Needham, K. B., Hau, M., & Greives, T. J. (2017). Early to rise, early to breed: A role for daily rhythms in seasonal reproduction. *Behavioral Ecology*, 28(5), 1266–1271. <https://doi.org/10.1093/beheco/arx088>.

Gwinner, E. (1986). *Circannual rhythms*. Berlin, Germany: Springer-Verlag.

Gwinner, H., Capilla-Lasheras, P., Cooper, C., & Helm, B. (2018). ‘Green incubation’: Avian offspring benefit from aromatic nest herbs through improved parental incubation behaviour. *Proceedings of the Royal Society B: Biological Sciences*, 285(1880). <https://doi.org/10.1098/rspb.2018.0376>, 20180376.

Hau, M., Dominoni, D., Casagrande, S., Buck, C. L., Wagner, G., Hazlerigg, D., et al. (2017). Timing as a sexually selected trait: The right mate at the right moment. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372(1734), 20160249. <https://doi.org/10.1098/rstb.2016.0249>.

de Heij, M. E., van der Graaf, A. J., Hafner, D., & Tinbergen, J. M. (2007). Metabolic rate of nocturnal incubation in female great tits, *Parus major*, in relation to clutch size measured in a natural environment. *Journal of Experimental Biology*, 210(11), 2006–2012. <https://doi.org/10.1242/jeb.001420>.

Helm, B., & Visser, M. E. (2010). Heritable circadian period length in a wild bird population. *Proceedings of the Royal Society B: Biological Sciences*, 277(1698), 3335–3342. <https://doi.org/10.1098/rspb.2010.0871>.

Helm, B., Visser, M. E., Schwartz, W., Kronfeld-Schor, N., Gerkema, M., Piersma, T., et al. (2017). Two sides of a coin: Ecological and chronobiological perspectives of timing in the wild. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372(1734), 20160246. <https://doi.org/10.1098/rstb.2016.0246>.

Hinde, R. (1952). The behaviour of the great tit (*Parus major*) and some other related species. *Behaviour*, 2(Suppl.), 1–201.

Hoffmann, K. (1965). Overt circadian frequencies and the circadian rule. In J. Aschoff (Ed.), *Circadian clocks* (pp. 87–94). Amsterdam, The Netherlands: North Holland.

Kacelnik, A., & Krebs, J. R. (1982). The dawn chorus in the great tit (*Parus major*): Proximate and ultimate causes. *Behaviour*, 83, 287–309.

Kempenaers, B., Borgström, P., Loës, P., Schlicht, E., & Valcu, M. (2010). Artificial night lighting affects dawn song, extra-pair siring success, and lay date in songbirds. *Current Biology*, 20, 1735–1739.

Labyak, S. E., Lee, T. M., & Goel, N. (1997). Rhythm chronotypes in a diurnal rodent, *Octodon degus*. *American Journal of Physiology*, 273, 1058–1066.

Lescroel, A., Ballard, G., Toniolo, V., Barton, K. J., Wilson, P. R., Lyver, P. O. B., et al. (2010). Working less to gain more: When breeding quality relates to foraging efficiency. *Ecology*, 91(7), 2044–2055. <https://doi.org/10.1890/09-0766.1>.

Lesku, J. A., Rattenborg, N. C., Valcu, M., Vyssotski, A. L., Kuhn, S., Kuemmeth, F., et al. (2012). Adaptive sleep loss in polygynous pectoral sandpipers. *Science*, 337(6102), 1654–1658. <https://doi.org/10.1126/science.1220939>.

Naylor, E. (2010). *Chronobiology of marine organisms*. Cambridge, UK: Cambridge University Press.

Norberg, R. A. (1981). Temporary Weight decrease in breeding birds may result in more fledged young. *American Naturalist*, 118, 838–850.

Piersma, T., & van Gils, J. A. (2011). *The flexible phenotype. A body-centred integration of ecology, physiology, and behaviour*. Oxford, UK: Oxford University Press.

Pittendrigh, C. S. (1993). Temporal organization: Reflections of a darwinian clock-watcher. *Annual Review of Physiology*, 55, 17–54.

Poesel, A., Kunc, H. P., Foerster, K., Johnsen, A., & Kempenaers, B. (2006). Early birds are sexy: Male age, dawn song and extrapair paternity in blue tits, *Cyanistes* (formerly *Parus*) *caeruleus*. *Animal Behaviour*, 72, 531–538.

Randler, C. (2014). Sleep, sleep timing and chronotype in animal behaviour. *Animal Behaviour*, 94, 161–166.

Rappole, J., & Tipton, A. (1991). New harness design for attachment of radio transmitters to small passerines. *Journal of Field Ornithology*, 62, 335–337.

Rattenborg, N. C., Mandt, B. H., Obermeyer, W. H., Winsauer, P. J., Huber, R., Wikelski, M., et al. (2004). Migratory sleeplessness in the white-crowned sparrow (*Zonotrichia leucophrys gambelii*). *PLoS Biology*, 27, 924–936.

Riechert, J., & Becker, P. H. (2017). What makes a good parent? Sex-specific relationships between nest attendance, hormone levels, and breeding success in a long-lived seabird. *Auk*, 134(3), 644–658. <https://doi.org/10.1642/AUK-17-13.1>.

Schlicht, L., Valcu, M., Loës, P., Girk, A., & Kempenaers, B. (2014). No relationship between female emergence time from the roosting place and extrapair paternity. *Behavioral Ecology*, 25, 650–659.

Schwartz, W. J., Helm, B., & Gerkema, M. P. (2017). Wild clocks: Preface and glossary. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372, 20170211.

Serota, M., & Williams, T. D. (2019). Adjustment of total activity as a response to handicapping during parental care in European starlings (*Sturnus vulgaris*). *Animal Behaviour*, 148, 19–27.

Steiger, S. S., Valcu, M., Spoelstra, K., Helm, B., Wikelski, M., & Kempenaers, B. (2013). When the sun never sets: Diverse activity rhythms under continuous daylight in free-living Arctic-breeding birds. *Proceedings of the Royal Society B: Biological Sciences*, 280, 20131016.

Steinmeyer, C., Mueller, J. C., & Kempenaers, B. (2013). Individual variation in sleep behaviour in blue tits *Cyanistes caeruleus*: Assortative mating and associations with fitness-related traits. *Journal of Avian Biology*, 44, 159–168.

Steinmeyer, C., Schielzeth, H., Mueller, J. C., & Kempenaers, B. (2010). Variation in sleep behaviour in free-living blue tits, *Cyanistes caeruleus*: Effects of sex, age and environment. *Animal Behaviour*, 80(5), 853–864.

Stuber, E. F., Dingemanse, N. J., Kempenaers, B., & Mueller, J. C. (2015). Sources of intraspecific variation in sleep behaviour of wild great tits. *Animal Behaviour*, 106, 201–221. <https://doi.org/10.1016/j.anbehav.2015.05.025>.

Swanson, D. L. (2010). Seasonal metabolic variation in birds: Functional and mechanistic correlates. *Current Ornithology*, 17, 75–129.

van der Veen, D. R., Riede, S. J., Heideman, P. D., Hau, M., van der Vinne, V., & Hut, R. A. (2017). Flexible clock systems: Adjusting the temporal programme. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372, 20160254.

Ward, M. P., Alessi, M., Benson, T. J., & Chiavacci, S. J. (2014). The active nightlife of diurnal birds: Extraterritorial forays and nocturnal activity patterns. *Animal Behaviour*, 88, 175–184.

Wicht, H., Korf, H. W., Ackermann, H., Ekhart, D., Fischer, C., & Pfeffer, M. (2014). Chronotypes and rhythm stability in mice. *Chronobiology International*, 31, 27–36.

Williams, T. D. (2018). Physiology, activity and costs of parental care in birds. *Journal of Experimental Biology*, 221. <https://doi.org/10.1242/jeb.169433>. jeb169433.

Williams, T. D., Bourgeon, S., Cornell, A., Ferguson, L., Fowler, M. A., Fronstin, R. B., et al. (2015). Mid-winter temperatures, not spring temperatures, predict breeding phenology in the European starling *Sturnus vulgaris*. *Royal Society Open Science*, 2(1). <https://doi.org/10.1098/rsos.140301>, 140301.

Wilmers, C. C., Nickel, B., Bryce, C. M., Smith, J. A., Wheat, R. E., & Yovovich, V. (2015). The golden age of bio-logging: How animal-borne sensors are advancing the frontiers of ecology. *Ecology*, 96(7), 1741–1753. <https://doi.org/10.1890/14-1401.1>.

Zúñiga, D., Falconer, J., Fudickar, A. M., Jensen, W., Schmidt, A., Wikelski, M., et al. (2016). Abrupt switch to migratory night flight in a wild migratory songbird. *Scientific Reports*, 6, 34207. <https://doi.org/10.1038/srep34207>.