Erschienen in: Behavioral Ecology ; 28 (2017), 5. - S. 1266-1271
https://dx.doi.org/10.1093/beheco/arx088

Early to rise, early to breed: a role for daily rhythms in seasonal reproduction

Jessica L. Graham,[a] Natalie J. Cook,[b] Katie B. Needham,[a] Michaela Hau,[c] and Timothy J. Greives[a]
[a]Department of Biological Sciences, North Dakota State University, Fargo, ND, USA, [b]Department of Biology, Benedictine College, Atchison, KS, USA, and [c]Evolutionary Physiology Group, Max Planck Institute for Ornithology, Seewiesen, Germany, University of Konstanz, Konstanz, Germany

Vertebrates use environmental cues to time reproduction to optimal breeding conditions. Numerous laboratory studies have revealed that light experienced during a critical window of the circadian (daily) rhythm can influence reproductive physiology. However, whether these relationships observed in captivity hold true under natural conditions and how they relate to observed variation in timing of reproductive output remains largely unexplored. Here we test the hypothesis that individual variation in daily timing recorded in nature (i.e. chronotype) is linked with variation in timing of breeding. To address this hypothesis and its generality across species, we recorded incubation behavior data to identify individual patterns in daily onset of activity for 2 temperate-breeding songbird species, the dark-eyed junco (*Junco hyemalis aikeni*) and the great tit (*Parus major*). We found that females who first departed from their nest earlier in the morning (earlier chronotype) also initiated nests earlier in the year. Date of data collection and ambient temperature had no effect, but stage of incubation influenced daily onset of activity in great tits. Our findings suggest a role for daily rhythms as one mechanism underlying the observed variation in seasonal timing of breeding.

Key words: **chronotype, daily rhythms, seasonal timing.**

INTRODUCTION

Seasonal bouts of reproduction have been observed in many vertebrate species and have long thought to have been shaped by selection (Baker 1938; Hau 2001; Bronson 2009). The physiological and behavioral changes that animals must undergo to prepare for seasonal breeding are predominantly timed by photoperiod (Dawson *et al.* 2001; Dawson 2003). Photic control of endogenous daily (i.e. circadian) rhythms has been linked to seasonal photoperiodic responses through a variety of laboratory-based studies. Specifically, animals possess a photo-inducible phase of the circadian rhythm, whereby light experienced during this phase induces reproductive responses appropriate for long days, whereas the absence of light during this critical phase of the circadian rhythm leads to short-day reproductive responses (Hamner 1963; Follett and Sharp 1969; Milette and Turek 1986; Hazlerigg and Wagner 2006; Paul *et al.* 2008). In vertebrates breeding during long days, exposure to light during this photo-inducible phase of the circadian rhythm will be encoded as a reproductively stimulatory day length (Hazlerigg and Wagner 2006). In Japanese quail (*Cortunix japonica*), this photo-inducible phase ranges between 10 and 16 h after the lights come on, the laboratory equivalent of dawn (Nicholls *et al.* 1983), suggesting that timing of the photo-inducible phase is variable between individuals of the same species.

Variation among individuals in behavioral and physiological outputs of circadian rhythms is commonly observed in animals held under constant laboratory conditions (Aschoff and Wever 1966; Horne and Ostberg 1977; Duffy *et al.* 2001) and recent work in wild caught individuals has suggested there is a heritable component to these rhythms (Helm and Visser 2010). Whether individual variation in endogenous daily rhythms may influence variation in the time of day an individual is sensitive to photo-induction, and thus responses to light exposure at the end of an early spring day, remains unknown. For example, an individual with a shorter free-running circadian rhythm may have a slightly advanced photo-inducible phase compared to an individual with a longer free-running rhythm, leading to earlier reproductive responses under the same photoperiod (Figure 1). Thus, individual variation in circadian rhythms may underlie individual variation in seasonal timing of breeding as suggested by Helm and Visser (2010) by shifting the timing of the photo-inducible phase. This hypothesis has not yet been tested in the

Address correspondence to J.L. Graham, 201 Stevens Hall, Department of Biological Sciences 1340 Bolley Drive, Fargo, ND 58102, USA. E-mail: jessica.l.graham@ndsu.edu

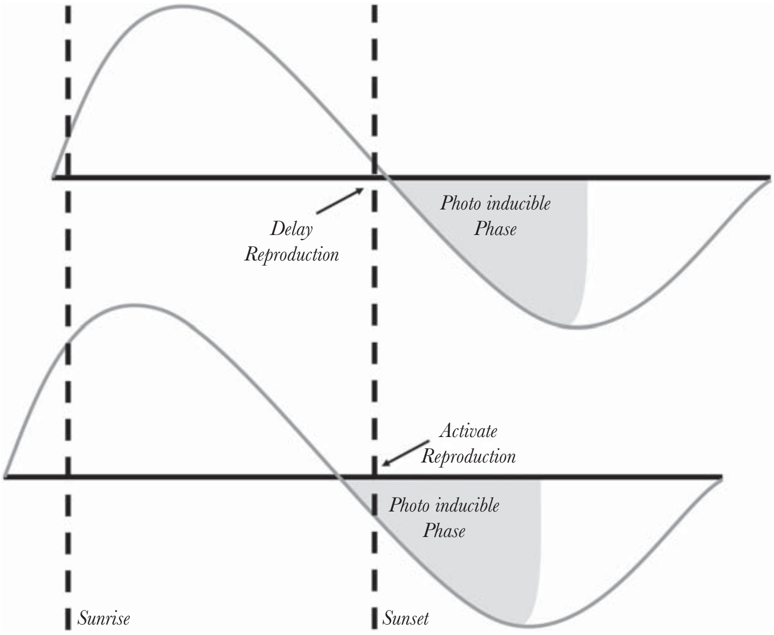

Figure 1

Two individuals entrained to a 24-h day; however, differing chronotypes (i.e. earlier onset of activity with respect to sunrise in the bottom individual) change the phase of the endogenous rhythm at which light is experienced. Hence, timing of the photo-inducible phase varies the reproductive response within an individual.

wild, where natural selection pressures are acting and these traits are being expressed.

Measuring the period length of an individual's circadian rhythm in the wild, however, presents many challenges. The daily light-dark cycle, social interactions and other environmental cues entrain the circadian system to a period of 24 h (Crowley and Bovet 1980; Johnson *et al.* 2003; Dunlap *et al.* 2004), thus making it impossible to measure the endogenous free-running circadian period of an individual in the wild. Alternatively, we can measure the phenotypic output of circadian rhythms by measuring the chronotype, or the timing exhibited by an individual relative to a salient environmental cue (e.g. sunrise) and other population members (Lehmann *et al.* 2012; Dominoni *et al.* 2013b). Evidence in humans and birds has uncovered clear links between endogenous rhythms and chronotype; individuals with a shorter free-running circadian period exhibit an earlier chronotype and become active earlier in the day (Aschoff and Wever 1966; Duffy *et al.* 2001; Dominoni *et al.* 2013b; c.f. Majoy and Heideman 2000; Helm and Visser 2010). As selection acts upon phenotypes expressed in nature, we would expect it to act upon chronotype in free-living organisms.

Here we test the hypothesis that variation in daily rhythms, expressed as chronotype, is an underlying mechanism driving individual variation in seasonal timing of breeding. Specifically, we predicted that female songbirds who show an earlier seasonal activation of reproductive function and thus initiate egg laying earlier, would also be active earlier in the morning (i.e. a chronotype related to a shorter circadian period) compared to females with later chronotypes that departed from their nest later in the morning. We assessed the chronotype of females repeatedly during incubation to quantify the repeatability of this trait and collected data from females of 2 free-living species of songbird on 2 continents, dark-eyed juncos (*Junco hyemalis*) and great tits (*Parus major*) to determine the generality of this pattern across species.

METHODS

Ethics

All animal use was conducted with approval from the NDSU Institutional Animal Care and Use Committee (Protocol #A13063) and the animal ethics committee of the state of Baden-Württemberg, Germany.

Study system

We studied a population of dark-eyed juncos (*Junco hyemalis aikeni*) near Lead, SD, USA (44°14'38"N, 103° 51'55"W), from 28 May 2015 to 5 July 2015 and 15 May 2016 to 26 June 2016. This subspecies of dark-eyed junco is a small, ground nesting passerine that resides primarily in pine forests in the central United States and typically begins laying eggs around mid to late May with an incubation period of approximately 12 days (Nolan *et al.* 2002).

In addition, data collected from a free-living population of great tits (*Parus major*) near Radolfzell, Germany (47° 44'24"N, 8° 58'48"E) from 20 April 2010 to 28 April 2010 were utilized. Great tits are small, secondary cavity nesting songbirds that readily breed in nest boxes (Drent 1987; Cramp and Perrins 1993). Egg laying at this study site begins in early April and incubation lasts approximately 12 days (Cramp and Perrins 1993).

Daily timing

Thermochron iButtons (Model DS1921G-F5# with iButton Connectivity Kit Model SK-IB-R) were placed in the nest of incubating great tits and dark-eyed juncos. The iButtons were programmed to record nest temperature to the nearest 0.5 °C every 2–3 min. At least 2–8 mornings worth of data were collected for every individual. iButtons were also placed near the nest of dark-eyed juncos to collect ambient temperature every 30 min in 2015, while Onset HOBO data loggers (Model UA-002-08) were used to collect ambient temperature and light intensity every 5 min in

2016. Ambient temperature and light intensity was not collected for great tits.

Determining onset of activity

Observer (JLG) was kept blind to nest initiation date while determining activity onset times for all individuals. Daily onset of activity was calculated by subtracting onset of activity time from sunrise times derived for each study site from the United States Naval Observatory data base (www.usno.navy.mil/USNO) and determined by graphing incubation bouts from 03:00 to 08:00 and finding the first major dip in temperature indicating nest departure (Supplementary Figure S1). This method has previously been shown to correlate strongly with video recorded nest departure times (Joyce *et al.* 2001). The dip was generally greater than 2°C below the average nest temperature from 03:00 to 08:00, however, this was not true in all cases. Eight dark-eyed juncos (10 mornings in total) and 2 great tits (4 mornings in total) had 1 or 3 mornings of data where nest temperature did not drop more than 2 °C. Removing those mornings did not change the results, so all measures were included in analysis.

Statistical analyses

All statistical analyses were performed using the free software R 3.2.2 (R Core Team 2015) with the package "lme4" (Bates *et al.* 2015) for mixed-effect modeling. To calculate repeatability of activity onset, a linear mixed-effects model was run with day of incubation included as a fixed effect and nest ID as a random effect. The resulting variance of the intercept was then divided by the sum of the variance of the intercept and variance of error (Dingemanse and Dochtermann 2013). To calculate 95% confidence intervals, "confint" was used. Lower and upper values were squared to get standard deviations for the variance of intercept and variance of error. Standard deviation for variance of the intercept was divided by the sum of standard deviations for variance of the intercept and variance of error for upper and lower values. This provided confidence intervals of repeatability.

Separate linear mixed-effects models were used to determine if activity onset was related to first egg of the season for individual dark-eyed juncos and great tits (hereafter referred to as egg 1 date), the day of incubation squared (Cooper and Voss 2013), and date of data collection (included as fixed effects). Year (for dark-eyed juncos) and nest ID were included as random effects. Ambient temperature data were not collected for great tits and ambient temperature did not influence onset of activity for the dark-eyed junco; thus temperature was not included in the final models. In year 2 for the dark-eyed juncos, we additionally collected light intensity at the nest. A third linear mixed-effects model was used to determine if light intensity at sunrise was related to onset of activity in this reduced data set. Significance level was set at $\alpha = 0.05$.

RESULTS

Dark-eyed junco activity onset ranged from 04:25 to 07:13 MDT. When calculated with respect to sunrise, times varied from 41 min pre-sunrise to 117 min post-sunrise. Repeatability of activity onset was 0.73 (*CI*: 0.67, 0.76) when controlling for day of incubation ($n = 36$). Onset of activity in female great tits ranged from 06:15 to 07:04 CEST. When calculated with respect to sunrise activity onset varied from 8 min pre-sunrise to 43 min post-sunrise. Repeatability of onset of activity was 0.27 (*CI*: 0.02, 0.42) when controlling for day of incubation ($n = 13$).

We found that the date a female laid her first egg of the season was positively related to daily onset of activity in both dark-eyed juncos ($F = 5.300$, $df = 1$, 19.45, $P = 0.03$, Figure 2a) and great tits ($F = 8.621$, $df = 1$, 9.64, $P = 0.01$, Figure 2b): individuals that laid their first egg earlier in the year had earlier daily activity onset. We also found the closer a female's eggs were to hatching, the onset of activity became later in great tits ($F = 6.996$, $df = 1$, 11.47, $P = 0.02$), but not in dark-eyed juncos ($F = 2.295$, $df = 1$, 85.80, $P = 0.13$). There was no relationship of activity onset with calendar date of data collection in either species (dark-eyed juncos: $F = 0.454$, $df = 1$, 33.35, $P = 0.50$; great tits: $F = 0.003$, $df = 1$, 16.54, $P = 0.95$).

When we restricted our data to only include dark-eyed juncos with data for light intensity at sunrise ($n = 24$), light intensity was significantly related to onset of activity ($F = 7.838$, $df = 1$, 84.80,

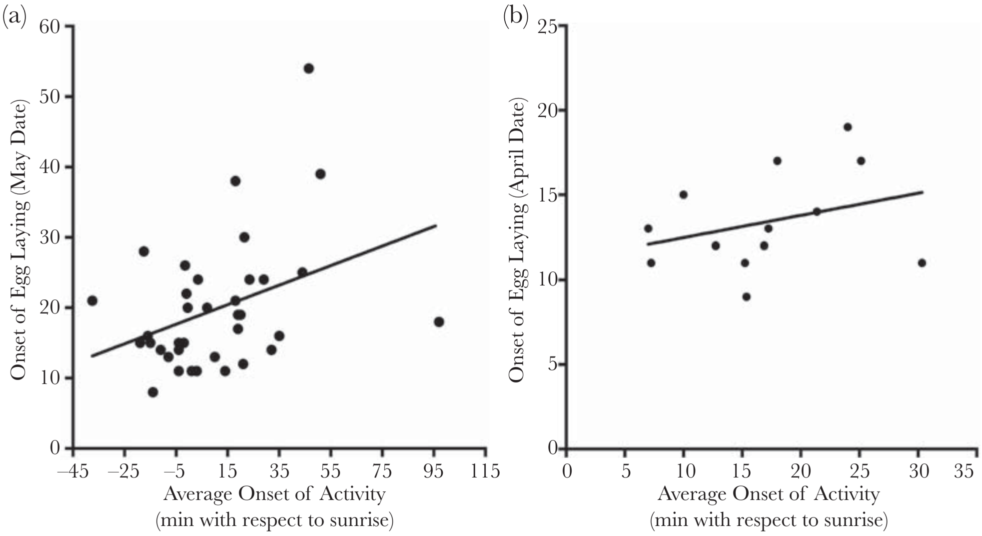

Figure 2
Individual averages of raw data for onset of activity graphed against first egg of the season shows as nest initiation dates shifts later in the season, females become active later in the day. Both dark-eyed juncos (a) and great tits (b) show this pattern.

$P < 0.01$). We still saw a trend for individuals that laid eggs earlier in the year to also have earlier onset of activity ($F = 3.349$, $df = 1$, 21.97, $P = 0.08$). Calendar date of data collection and day of incubation showed no relationship with onset of activity (date of data collection: $F = 0.003$, $df = 1$, 23.65, $P = 0.96$; day of incubation: $F = 1.483$, $df = 1$, 75.15, $P = 0.23$).

DISCUSSION

Our data support the hypothesis that individual variation in daily rhythm phenotype influences individual variation in seasonal onset of breeding. Females of both dark-eyed juncos and great tits that became active earlier in the morning (i.e. earlier chronotype) had earlier nest initiation dates than females that became active later in the morning. As previous findings have demonstrated that earlier chronotypes are manifestations of shorter circadian period lengths (Aschoff and Wever 1966; Duffy *et al.* 2001; Dominoni *et al.* 2013b), our findings of a relationship between early onset of activity and clutch initiation provide evidence that variation in endogenous circadian rhythms may act as a mechanism influencing individual variation in seasonal timing of breeding in wild populations.

We observed consistent individual differences in daily onset of activity during the breeding season. While our study necessarily collected timing data after the decision to lay eggs had been made, we believe that our findings are indicative of an individual's chronotype prior to nest initiation. Other studies, including in our study species, have also observed within year consistency in individual female awakening and nest departure times both during and outside the breeding season (Steinmeyer *et al.* 2010; Schlicht *et al.* 2014; Stuber *et al.* 2015). In addition, onset of activity for 6 dark-eyed junco females in our study was collected during a known second nesting attempt. Nest initiation date for the first nesting attempt of these individuals was known and was included in the model with activity onset recorded during the second attempt. Females that laid eggs early during the first nesting attempt still fit the observed pattern of becoming active earlier, even on a second nesting attempt, compared to late breeding females. This provides some support that females with early chronotypes consistently exhibit early chronotypes compared to those with late chronotypes, regardless of time of season. Interestingly, timing of reproductive characteristics like egg laying date in females and onset of dawn song in males, are repeatable (Noordwijk *et al.* 1980; Sydeman and Eddy 1995; Nussey *et al.* 2005; Murphy *et al.* 2008; Naguib *et al.* 2010). Males that sing earlier also pair with early breeding females (Murphy *et al.* 2008), suggesting males who awaken earlier (i.e. have shorter endogenous rhythms) are pairing with females that breed earlier and also have shorter endogenous rhythms. These combined observations suggest that an individual's onset of daily activity is consistent with respect to other individuals in the population, and likely reflects individual variation in endogenous rhythms, though future work is needed to confirm this result.

A recent study found no relationship between chronotype and timing of breeding in captive-housed great tits (Helm and Visser 2010). One reason for this deviation may have been due to using artificial lighting in aviaries while organisms are better able to respond more precisely to natural external cues (Fleissner and Fleissner 2002; Helm and Visser 2010). Captive great tits do show altered timing of sleep behaviors, including earlier awakening and nest departure times and shortened sleep duration, even when kept under naturalistic conditions compared to their free-living counterparts (Stuber *et al.* 2015). A study in European blackbirds (*Turdus merula*) did find that chronotype measured during the breeding season under free-living conditions was related to the length of an individual's free-running rhythm measured in captivity later on in the same breeding season (Dominoni *et al.* 2013b). While the study by Helm and Visser (2010) contained important findings, our study utilized measurements of rhythmic daily and seasonal behaviors in a natural environment. This may indicate the importance of measuring these traits and their relationship with seasonal timing decisions in the wild.

It has been generally observed that early breeding individuals in temperate zone habitats are few in number compared to the rest of the population, but have higher reproductive success compared to individuals that breed later (Perrins 1970; Bourdon and Brinks 1983; Olsson and Shine 1997; Dawson and Clark 2000). This observed pattern is consistent with patterns observed in the length of endogenous rhythms; that shorter rhythms are rare compared to longer rhythms while an intermediate rhythm length is most common (Helm and Visser 2010). Flexibility in timing of breeding is important for adapting to year to year variation in the environment, but variation in the length of endogenous rhythms may be one mechanism regulating individual reproductive timing relative to other individuals within a given year. The relationship between individual variation in behavioral rhythms and clutch initiation suggests the possibility that individual variation in the timing of the photo-inducible phase in the early spring may directly influence seasonal reproductive onset.

Light intensity at the nest at sunrise appears to play an important role in onset of activity as well. Though we only collected a single year of data for dark-eyed juncos, our findings agree with other studies showing that higher light intensity leads to an advanced onset of daily activity (Aschoff 1979; Newberry *et al.* 1988; Dominoni *et al.* 2014; Stuber *et al.* 2015). Urban dwelling birds are exposed to higher light intensities at night and will also advance their timing of reproduction compared to forest dwelling birds (D. Dominoni *et al.* 2013a). With nighttime and sunrise light intensity affecting onset of activity (Dominoni *et al.* 2014), roosting behavior prior to the breeding season could be an important factor in determining onset of reproduction by influencing intensity of light experienced by an individual during this crucial time.

Additional non-photic cues that interact with endogenous daily rhythms may also play a role in onset of activity and observed timing of reproduction. For example, a high fat diet is capable of lengthening activity rhythms in mice (Kohsaka *et al.* 2007). The ability to obtain a high-quality diet under pre-breeding conditions could then advance the onset of reproduction. A common phenomenon observed in songbirds is the tendency for older females to initiate reproduction earlier in the season than younger females (Perrins 1970; Mills 1973; Nol and Smith 1987). The age of the individuals in the current investigation was unknown, but it may be likely that age-related changes in endogenous rhythms influence age-related changes in clutch initiation in birds. Age related shifts in the endogenous rhythms and chronotypes of humans have been extensively studied, showing a significant increase in early rising behavior in advanced age (Tankova *et al.* 1994; Hur and Bouchard 1997; Roenneberg *et al.* 2004; Roenneberg *et al.* 2007). Studies in *Drosophila* and birds have obtained similar results, with older individuals spending less time sleeping and awakening earlier in the day, though many of these studies are cross-sectional (Shaw *et al.* 2000; Steinmeyer *et al.* 2010; Stuber *et al.* 2015). To our knowledge, connections between age-related shifts in chronotype and reproductive timing have not been tested. The findings from our study suggest that changes in chronotype with age may at least in part underlie the observed pattern of older individuals initiating seasonal reproduction earlier than first year individuals in temperate-breeding species (Mills 1973; Nol and Smith 1987). However, future work is needed to address the potential relationship between advances in chronotype and timing of breeding from year to year.

CONCLUSION

We found female songbirds that became active earlier, exhibiting an early chronotype, initiated clutches earlier in the season compared to females with a late chronotype that became active later. This supports our hypothesis that variation in daily rhythms are a likely underlying mechanism driving individual variation in seasonal onset of timing of breeding, though further experiments directly measuring length of free-running endogenous rhythms would strengthen these findings. Endogenous daily rhythms may also underlie other commonly observed patterns related with variation in timing of breeding (e.g. age), as well as other seasonal phenomena like migration. The fact that similar results were obtained in 2 unrelated species from 2 continents attests to the generality of our findings. Further research should aim at addressing the detailed mechanistic underpinnings of the observed relationships, test the hypothesis that similar patterns are also found in males, and examine possible seasonal and ecological variations in the connections between daily and seasonal rhythms.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

FUNDING

This work was supported by a National Science Foundation International Research Fellowship (grant number IRFP-0852986 to T.J.G.) and the Division of Integrative Organismal Systems (grant number IOS-1257527 to T.J.G.); North Dakota EPSCoR to T.J.G.; and Max Planck Institute for Ornithology to M.H. and T.J.G.

The authors would like to thank G. Beltrami, S. Kingma, J. Lodde Greives, E. Bertucci, A. Pearson, and A. Rutherford for field assistance. The authors also thank C. Bauer, N. Dochtermann, B. Heidinger, A. Kucera, R. Royauté, J. Schmidt, A. Sirman, and E. Stewart for feedback on data analysis and during the writing process.

Data accessibility: Analyses reported in this article can be reproduced using the data provided by Graham *et al.* (2017).

Handling editor: Naomi Langmore

REFERENCES

Aschoff J. 1979. Circadian rhythms: influences of internal and external factors on the period measured in constant conditions. Z Tierpsychol. 49:225–249.

Aschoff J, Wever R. 1966. Circadian period and phase-angle difference in chaffinches (Fringilla coelebs L.). Comp Biochem Physiol. 18:397–404.

Baker JR. 1938. The evolution of breeding seasons. In: de Beer GR, editor. ‘Evolution: Essays on Aspects of Evolutionary Biology’. Oxford: Clarendon Press. p. 161–177.

Bates D, Maechler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using lme4. J Stat Softw. 67:1–48.

Bourdon RM, Brinks JS. 1983. Calving date versus calving interval as a reproductive measure in beef cattle. J Anim Sci. 57:1412–1417.

Bronson FH. 2009. Climate change and seasonal reproduction in mammals. Philos Trans R Soc Lond B Biol Sci. 364:3331–3340.

Cooper CB, Voss MA. 2013. Avian Incubation Patterns Reflect Temporal Changes in Developing Clutches. PLoS One. 8:e65521.

Cramp S, Perrins CM. 1993. Handbook of the birds of Europe, the Middle East, and North Africa: The birds of the Western Palearctic. Vol. 7: flycatchers to shrikes. Oxford: Oxford University Press.

Crowley M, Bovet J. 1980. Social Synchronization of Circadian Rhythms in Deer Mice (*Peromyscus maniculatus*). Behav Ecol Sociobiol. 7:99–105.

Dawson A. 2003. Photoperiodic control of the annual cycle in birds and comparison with mammals. Ardea. 90:355–367.

Dawson A, King VM, Bentley GE, Ball GF. 2001. Photoperiodic control of seasonality in birds. J Biol Rhythms. 16:365–380.

Dawson RD, Clark RG. 2000. Effects of hatching date and egg size on growth, recruitment, and adult size of lesser scaup. Condor 102:930–935.

Dingemanse NJ, Dochtermann NA. 2013. Quantifying individual variation in behaviour: mixed-effect modelling approaches. J Anim Ecol. 82:39–54.

Dominoni D, Quetting M, Partecke J. 2013a. Artificial light at night advances avian reproductive physiology. Proc R Soc Lon B Biol Sci. 280:20123017.

Dominoni DM, Carmona-Wagner EO, 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. J Anim Ecol. 83:681–692.

Dominoni DM, Helm B, Lehmann M, Dowse HB, Partecke J. 2013b. Clocks for the city: circadian differences between forest and city songbirds. Proc Biol Sci. 280:20130593.

Drent PJ. 1987. The importance of nestboxes for territory settlement, survival and density of the great tit. Ardea 75 [cited 2015 Nov 10]. Available from: http://depot.knaw.nl/14273/1/Drent_Ardea_87.pdf.

Duffy JF, Rimmer DW, Czeisler CA. 2001. Association of intrinsic circadian period with morningness-eveningness, usual wake time, and circadian phase. Behav Neurosci. 115:895–899.

Dunlap JC, Loros JJ, DeCoursey PJ. 2004. Chronobiology: biological timekeeping. Sinauer Associates [cited 2017 Feb 8]. Available form: http://psycnet.apa.org/psycinfo/2003-06316-000.

Fleissner G, Fleissner G. 2002. Perception of Natural Zeitgeber Signals. In: Kumar V, editor. Biological Rhythms. Berlin-Heidelberg: Springer. p. 83–93. [cited 2017 Apr 4]. Available from: http://link.springer.com/chapter/10.1007/978-3-662-06085-8_8.

Follett BK, Sharp PJ. 1969. Circadian rhythmicity in photoperiodically induced gonadotrophin release and gonadal growth in the quail. Nature. 223:968–971.

Graham JL, Cook NJ, Needham KB, Hau M, Greives TJ. 2017. Data from: early to Rise, Early to Breed: A Role for Daily Rhythms in Seasonal Reproduction. Dryad Digital Repository. http://dx.doi.org/10.5061/dryad.h297n.

Hamner WM. 1963. Diurnal Rhythm and Photoperiodism in Testicular Recrudescence of the House Finch. Science. 142:1294–1295.

Hau M. 2001. Timing of breeding in variable environments: tropical birds as model systems. Horm Behav. 40:281–290.

Hazlerigg DG, Wagner GC. 2006. Seasonal photoperiodism in vertebrates: from coincidence to amplitude. Trends Endocrinol Metab. 17:83–91.

Helm B, Visser ME. 2010. Heritable circadian period length in a wild bird population. Proc R Soc Lon B Biol Sci. 277:3335–3342.

Horne JA, Ostberg O. 1977. Individual differences in human circadian rhythms. Biol Psychol. 5:179–190.

Hur Y-M, Bouchard TJ. 1997. Genetic and environmental influence on morningness-eveningness. In: Behavior genetics. Vol. 27. New York (NY): Plenum Publishing Corp, p. 594–594. [cited 2016 Aug 10]. Available from: https://www.researchgate.net/profile/Thomas_Bouchard2/publication/222794446_Genetic_and_environmental_influence_on_morningness-eveningness/links/54fdc6110cf270426d12ccd2.pdf.

Johnson CH, Elliott JA, Foster R. 2003. Entrainment of circadian programs. Chronobiol Int. 20:741–774.

Joyce EM, Sillett TS, Holmes RT. 2001. An inexpensive method for quantifying incubation patterns of open-cup nesting birds, with data for black-throated blue warblers. J Field Ornithol 72:369–379.

Kohsaka A, Laposky AD, Ramsey KM, Estrada C, Joshu C, Kobayashi Y, Turek FW, Bass J. 2007. High-fat diet disrupts behavioral and molecular circadian rhythms in mice. Cell Metab. 6:414–421.

Lehmann M, Spoelstra K, Visser ME, Helm B. 2012. Effects of temperature on circadian clock and chronotype: an experimental study on a passerine bird. Chronobiol Int. 29:1062–1071.

Majoy SB, Heideman PD. 2000. Tau differences between short-day responsive and short-day nonresponsive white-footed mice (Peromyscus leucopus) do not affect reproductive photoresponsiveness. J Biol Rhythms. 15:501–513.

Milette JJ, Turek FW. 1986. Circadian and photoperiodic effects of brief light pulses in male Djungarian hamsters. Biol Reprod. 35:327–335.

Mills JA. 1973. The Influence of Age and Pair-Bond on the Breeding Biology of the Red-Billed Gull Larus novaehollandiae scopulinus. J Anim Ecol 42:147–162.

Murphy MT, Sexton K, Dolan AC, Redmond LJ. 2008. Dawn song of the eastern kingbird: an honest signal of male quality? Anim Behav 75:1075–1084.

Naguib M, Kazek A, Schaper SV, Van Oers K, Visser ME. 2010. Singing Activity Reveals Personality Traits in Great Tits. Ethol 116:763–769.

Newberry RC, Hunt JR, Gardiner EE. 1988. Influence of light intensity on behavior and performance of broiler chickens. Poult Sci. 67:1020–1025.

Nicholls TJ, Follett BK, Robinson JE. 1983. A photoperiodic response in gonadectomized Japanese quail exposed to a single long day. J Endocrinol. 97:121–126.

Nol E, Smith JNM. 1987. Effects of Age and Breeding Experience on Seasonal Reproductive Success in the Song Sparrow. J Anim Ecol 56:301–313.

Nolan V, Ketterson ED, Cristol DA, Rogers CM, Clotfelter ED, Titus RC, Schoech SJ, Snajdr E. 2002. Dark-eyed junco (*Junco hyemalis*). In: Poole A, Gill F, editors. BNAO. [cited 2014 Jul 23]. Available from: http://bna.birds.cornell.edu/bna/species/716/articles/introduction.

Noordwijk A van, Van Balen J van, Scharloo W. 1980. Heritability of ecologically important traits in the Great Tit. Ardea. 68:193–203.

Nussey DH, Postma E, Gienapp P, Visser ME. 2005. Selection on heritable phenotypic plasticity in a wild bird population. Science. 310:304–306.

Olsson M, Shine R. 1997. The seasonal timing of oviposition in sand lizards (*Lacerta agilis*): why early clutches are better. J. Evol. Biol. 10:369–381.

Paul MJ, Zucker I, Schwartz WJ. 2008. Tracking the seasons: the internal calendars of vertebrates. Philos Trans R Soc Lond B Biol Sci. 363:341–361.

Perrins CM. 1970. The timing of birds' breeding seasons. Ibis 112:242–255.

R Core Team. 2015. R: A language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing. Available from: https://www.R-project.org. Accessed October 13, 2015.

Roenneberg T, Kuehnle T, Juda M, Kantermann T, Allebrandt K, Gordijn M, Merrow M. 2007. Epidemiology of the human circadian clock. Sleep Med Rev. 11:429–438.

Roenneberg T, Kuehnle T, Pramstaller PP, Ricken J, Havel M, Guth A, Merrow M. 2004. A marker for the end of adolescence. Curr Biol. 14:R1038–R1039.

Schlicht L, Valcu M, Loës P, Girg A, Kempenaers B. 2014. No relationship between female emergence time from the roosting place and extrapair paternity. Behav Ecol 25:650–659.

Shaw PJ, Cirelli C, Greenspan RJ, Tononi G. 2000. Correlates of sleep and waking in Drosophila melanogaster. Science. 287:1834–1837.

Steinmeyer C, Schielzeth H, Mueller JC, Kempenaers B. 2010. Variation in sleep behaviour in free-living blue tits, Cyanistes caeruleus: effects of sex, age and environment. Anim Behav. 80:853–864.

Stuber EF, Dingemanse NJ, Kempenaers B, Mueller JC. 2015. Sources of intraspecific variation in sleep behaviour of wild great tits. Anim Behav. 106:201–221.

Sydeman WJ, Eddy JO. 1995. Repeatability in Laying Date and Its Relationship to Individual Quality for Common Murres. Condor. 97:1048–1052.

Tankova I, Adan A, Buela-Casal G. 1994. Circadian typology and individual differences. A review. Pers Indiv Differ. 16:671–684.