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Black-capped chickadees (*Poecile atricapillus*) use temperature as a cue for reproductive timing

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ABSTRACT

Reliable environmental cues, such as photoperiod, act as initial predictive cues that allow birds to time reproduction to match peak food abundance for their offspring. More variable local cues, like temperature, may, however, provide more precise information about the timing of food abundance. Non-migratory birds, in particular, should be sensitive to temperature cues and use them to modulate their reproductive timing. We conducted two experiments to examine the effect of temperature on reproductive condition (gonad size and circulating androgen levels) in non-migratory black-capped chickadees (*Poecile atricapillus*). First, we exposed groups of birds in outdoor aviaries to three different over-winter temperature treatments and assessed gonad size in the spring. Second, we manipulated temperature in environmental chambers under photostimulatory and non-photostimulatory photoperiodic conditions and assessed gonad size and circulating testosterone levels. Temperature had no independent effect on gonad size or testosterone levels, but when photostimulated birds exposed to warmer conditions became reproductively ready earlier than birds experiencing cooler conditions. We conclude that temperature acts as a supplementary cue that modulates the photoperiod-driven timing of reproduction.

1. Introduction

The seasonal regulation of reproductive behaviour and physiology is important for animals living at high latitudes. For resident passerine birds in northern temperate or arctic climates, the breeding season is short, the onset of insect abundance is rapid, and the timing of reproductive events must be precise. It is important for birds to time their seasonal reproduction correctly to ensure adequate resources for both themselves, and their offspring (Martin, 1987). By timing reproduction to coincide with peak food abundance, birds are able to ensure that food for the young is plentiful (Dawson et al., 2001, Visser et al., 1998). Birds use external environmental cues to achieve this proper timing.

Photoperiod is the main environmental cue that drives the transition between reproductive states in birds (Dawson et al., 2001; Sharp, 2005). It is the most significant environmental factor for seasonal reproduction because it is reliable and unaffected by year to year variation in weather. Photostimulation, the response by photosensitive birds to lengthening days in the spring, leads to gonadal maturation in preparation for reproduction (Dawson et al., 2001). Photostimulation also triggers physiological changes such as gonadotropin release (Hahn et al., 2004), and behavioural changes such as increased song production (Phillmore et al., 2006). Because photoperiod acts as a proximate factor (Baker, 1938) to prepare animals for reproduction in advance of the breeding season it is often referred to as an initial predictive cue (Wingfield, 1980; Ball, 1993). More variable localized factors, such as temperature, could potentially serve as supplementary cues to fine-tune the timing of reproduction (Wingfield, 1980; Ball, 1993; Dixit et al., 2018). Temperature, for example, is known to drive timing of insect emergence, and can thus be an accurate predictor of peak food abundance (Visser et al., 2006; Perrins, 2008). Resident birds may be sensitive to these more variable cues. Using them in combination with reliable cues like photoperiod could allow individuals to time reproduction more accurately.

There is evidence that warmer spring temperatures are correlated with earlier reproduction in birds (Visser et al., 1998). It has been suggested that birds are able to track temperature changes and

Abbreviations: 6H, 6 h of additional heat; 24H, 24 h of additional heat

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subsequently adjust their breeding timing (Hinsley et al., 2016; Phillimore et al., 2016). Glądalski et al. (2016) found that populations of great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*) in Poland changed their lay date in response to changes in temperature. Källander et al. (2017) found similar trends in marsh tits (*Poecile palustris*). These correlations suggest that temperature may act as a predictive cue, either along with photoperiod or independently.

Visser and colleagues (2009) provided evidence that temperature can have casual effects on reproductive timing. Non-migratory great tits experiencing natural photoperiods altered their lay dates as a direct result of temperature. Conversely, in a study by Singh et al. (2012), migratory blackheaded buntings (*Emberiza melanocephala*) held under photostimulatory thresholds failed to develop reproductively ready gonads, regardless of temperature condition. While these studies provide evidence that photoperiod and temperature interact to modulate reproductive timing, little is known about how non-migratory species might respond to temperature cues in the absence of photoperiodic cues, and what effect, if any, these temperature cues have on reproductive development.

We performed two experiments that examined both the combined and independent effects of temperature and photoperiod on reproductive condition (measured as gonad size and circulating androgen levels) in black-capped chickadees. Black-capped chickadees are a non-migratory resident songbird in Canada and the northern United States (Smith, 1991), and use photoperiod cues to time annual events (MacDougall-Shackleton et al., 2003a,b). As residents, black-capped chickadees may also be sensitive to temperature cues because they can be an accurate predictor of spring green-up and thus, food abundance (Cleland et al., 2007).

We hypothesised that individuals would be sensitive to ambient temperature, and that birds would use temperature to modulate their reproductive timing. We predicted that birds experiencing warming would have the greatest gonadal development and highest androgen levels. Because chickadees become absolutely photorefractory (Phillmore et al. 2005) we predicted that temperature effects would occur only in birds that were photostimulated. In the first experiment, we exposed groups of birds to three different over-winter temperature treatments (no heat supplement, 24 h heat supplement, or night-time heat supplement) under semi-natural conditions (outdoor aviaries) and assessed gonadal development in the spring. In the second experiment, we used a 2 X 2 factorial design to determine the effect of warm vs. cool temperatures and photostimulatory vs. non-photostimulatory day-lengths on gonadal development and circulating testosterone levels in birds held in environmental chambers.

2. General methods

We captured a total of 47 black-capped chickadees (38 male, 9 female) using Potter traps near London, Ontario, Canada over two years (2017–2018) and housed them at the Advanced Facility for Avian Research at the University of Western Ontario. In both experiments, birds had *ad libitum* access to a maintenance diet of ground Mazuri Small Bird Diet (PMI Nutrition International, Brentwood, MO, U.S.A.) and powdered sunflower chips, as well as whole black-oil sunflower seeds and water. Birds were group housed in large aviaries (2.5 × 3.0 × 2.5 m) from the time of capture until the start of their respective treatments. During treatments birds were individually housed in cages (0.46 × 0.46 × 0.46 m) but not visually or acoustically isolated. At the end of each experiment birds were sacrificed to obtain neural tissue for a separate study and gonadal measurements were performed at the time of sacrifice. All work was completed under Canadian Wildlife Permit CA 0236 and University of Western Ontario Animal Use Protocol 2015–019.

3. Experiment one

In this experiment birds were housed in outdoor aviaries under semi-natural conditions. Birds were exposed to natural photoperiod, and a transparent roof shielded birds from direct precipitation. We exposed birds to one of three manipulated temperature treatments: no heat supplementation, heat supplement at night, or heat supplementation 24 h per day. We assessed gonadal development in both males and females.

3.1. Methods

Twenty-one birds (12 male, 9 female) were used to assess the influence of winter temperature on reproductive condition. As part of a parallel study (Martin and Sherry, 2019), individuals were housed in outdoor aviaries exposed to natural temperature (range −25 °C to 16 °C) and photoperiod (from 10.25L:13.75D to 9L:15D) and provided with access to a roosting box (7.6 × 7.6 × 7.6 cm) from the time of capture until the beginning of treatment (maximum 76 days for birds caught November 1). Beginning on 15 January 2017, individuals were randomly assigned to one of three temperature treatments and moved to individual outdoor cages. The treatments were; 1) no artificial heat (Control, n = 4 M:3F), 2) 6 h of artificial heat at night (6H, n = 5:2), 3) 24 h of artificial heat (24H, n = 3 M:4F). Birds in the Control group experienced natural temperature conditions throughout the experiment, while both the 6H and 24H groups experienced additional heat. Individuals in the 6H condition received additional heat between 10 pm and 4am daily, the overnight period that typically imposes the greatest thermoregulatory challenge. Individuals in the 24H group received additional heat for the entire duration of the experiment, simulating overall winter warming. Individuals were sacrificed over two days (5/6 April 2017), and the gonads of each individual were measured post-mortem. All artificial heat was provided by PrimeGLO Telescopic Electric Heaters (AZ Patio Heaters, Peoria, AZ). Temperature was measured at randomly selected roosting boxes (two each for Control and 6H, three for 24H) in all treatments (see Supp. material) using HOBO® Pendant® Data Loggers (Onset Computer Corporation, Bourne, MA).

3.1.1. Reproductive condition

Reproductive condition of males was scored by calculating the volume of the testes at the time of sacrifice. Digital calipers were used to obtain a maximum length and width of the left testis of each individual. Volumes were calculated using the formula for the volume of an ellipsoid. Male testes were compared to a breeding condition threshold of 20 mm^3 (Phillmore et al., 2006) to assign males to breeding or non-breeding condition.

Reproductive condition of females was assessed by visual examination of the ovaries at the time of sacrifice and weighing the ovaries. Ovaries were visually scored using the following 5-point scale, adapted from MacDougall-Shackleton et al. (2001): 1) smooth with no visible follicular development; 2) granular appearance; 3) small, uniform follicles apparent; 4) follicles apparent with evident hierarchy; 5) large yolky follicles. Once visually scored, the ovaries were removed, and their mass was recorded (± 0.1 mg).

All gonadal scoring was done by individuals blind to treatment group.

3.1.2. Statistical analysis

Reproductive condition was compared among temperature conditions for each sex independently. For males, a one-way ANOVA was used to compare testis volume among temperature treatments. Tukey's post-hoc tests tested pair-wise differences between treatments. Reproductive condition (breeding vs non-breeding) was analysed using a Pearson's chi-square test. For females, ovary development scores were analysed using a Kruskal-Wallis analysis of variance due to the ordinal

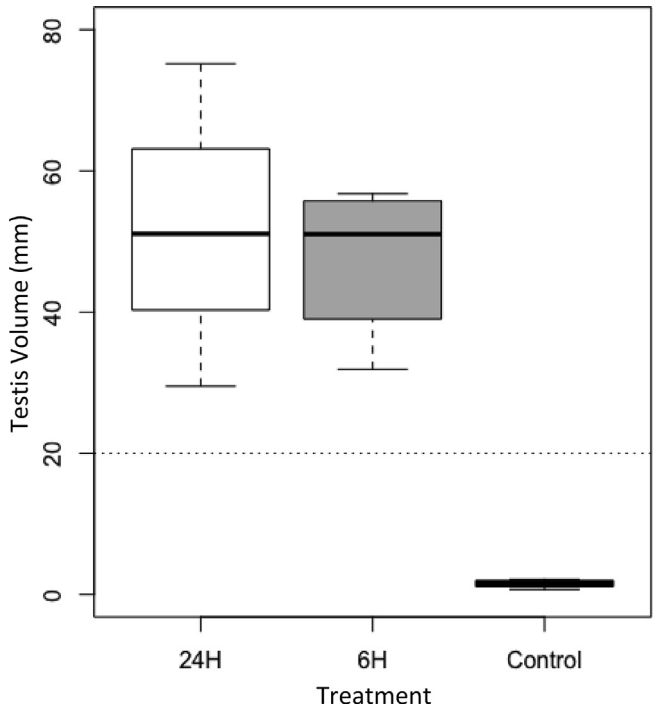

Fig. 1. Testis volumes of males in the three temperature groups in Experiment One with the breeding condition threshold (Phillmore et al., 2006) indicated by the dotted line (24H n = 4, 6H n = 5, Control n = 3). Boxes encompass 50% of the data, while the tails encompass the additional 50%. The dark bar shows the mean value. Birds in the 6H and 24H groups did not differ significantly, but both had significantly larger testis volumes than birds in the Control group. All birds in the 6H and 24H groups were in breeding condition, while none of the Control birds were in breeding condition.

nature of the data, and differences between groups were examined using Dunn's Test post-hoc and a Bonferroni correction was applied. In addition, a one-way ANOVA was used to compare ovary mass among temperature treatments. All statistical tests were done using R (R Core Team, 2017).

3.2. Results

3.2.1. Male reproductive condition

Temperature treatment had a significant effect on testis volume in males with larger testis volume observed in males receiving additional heat ($F_{2,9}$ = 17.7, p = 0.0008; Fig. 1). The Control group differed from both the 24H group (Tukey's: p = 0.0017) and the 6H group (p = 0.0014). There was no difference between the 6H group and the 24H group (p = 0.86).

Temperature had a significant effect on reproductive condition of males (χ^2 = 12, df = 2, p = 0.002). None of the Control birds were in breeding condition, whereas all the birds that received additional heat were in breeding condition, regardless of whether they were in the 6H or 24H group.

3.2.2. Female reproductive condition

Temperature did not have a significant effect on ovary mass in females ($F_{2,6}$ = 2.287, p = 0.18), but did have a significant effect on ovary development score (χ^2 = 6.5, df = 2, p = 0.039; Fig. 2). Birds in the 24H treatment were more reproductively advanced than birds in the Control condition (Dunn Test: Z = 2.54, p_{adj} = 0.034), while the birds in the 6H group were not significantly different from either the 24H (Z = 0.85, p_{adj} = 1.00) or the Control (Z = 1.58, p_{adj} = 0.34) groups.

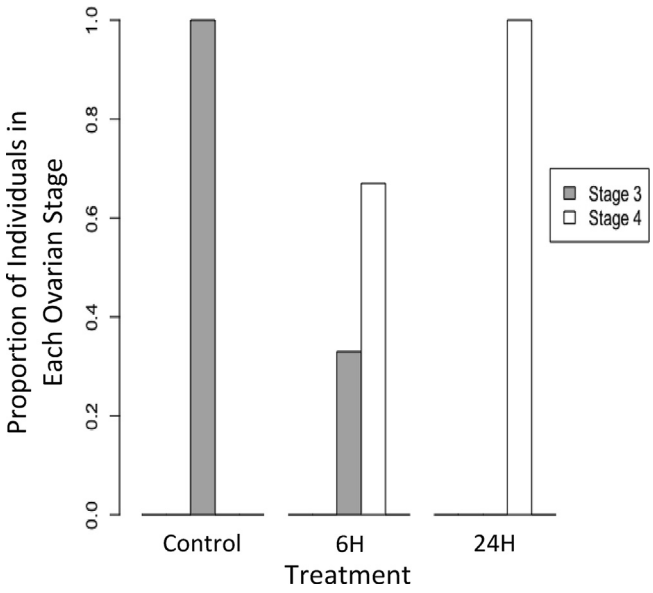

Fig. 2. Proportion of females in Experiment One at each ovarian developmental stage at the time of sacrifice (Control n = 3, 6H n = 3, 24H n = 4). 24H birds were significantly more reproductively advanced. All Control birds were scored at stage 3, while all the 24H birds were scored at stage 4.

3.3. Discussion

Gonadal development was accelerated in both male and female black-capped chickadees that experienced a warmer winter, but males and females were not affected equally. Males that received additional heat, either 6H or 24H, had larger testes than males that received no additional heat. In addition, all the males that received additional heat were in breeding condition by the end of the study, while males that experienced natural conditions were not. Although there was no difference in ovary mass, females that received 24H of additional heat were in a more advanced breeding state - as indicated by a hierarchy of follicle sizes in the ovary - than those that experienced natural temperature conditions. Unlike the males however, none of the females were in full breeding condition. These results indicate that birds responded to temperature in addition to photoperiodic cues, though the sexes did not respond equally. These findings alone, however, are not sufficient to confirm a causal relationship between temperature and reproductive condition. The heaters we used emit low light levels and it is possible that the photoperiod of heated birds was unintentionally altered. The treatment groups were not visually isolated, however, and so all groups, including the Control group, would be expected to have received some additional light. In addition, birds were observed to roost overnight in dark nest boxes, reducing the possible effect of additional light. Nevertheless, additional light is a potential confounding variable in Experiment One. Furthermore, because we included both males and females in the three treatment groups, sample size is small for some sex by treatment combinations. We therefore performed a second experiment in which we could precisely control temperature and photoperiod independently in environmental chambers. Because males appeared to show a greater response to warming in Experiment One, we included only males in Experiment Two.

4. Experiment two

In this experiment we assessed the roles of photoperiod and temperature on reproductive timing independently. We used environmental chambers to precisely control both photoperiod and temperature (± 0.1 °C). We used only male black-capped chickadees and assessed both gonadal development and circulating testosterone levels.

4.1. Methods

Twenty-six male black-capped chickadees were used to assess the interaction between temperature and photoperiod using a 2x2 factorial design. Birds were randomly assigned to either long days (14 h L:10 h D) or short days (10 h L: 14 h D) and either warm (14 °C) or cold (6 °C) spring temperatures. These manipulations resulted in four treatment groups: Long-Days-Warm (n = 6), Long-Days-Cold (n = 7), Short-Days-Warm (n = 7) and Short-Days-Cold (n = 6). Birds were run in two cohorts, with both long-day exposure groups beginning on 30 November 2018, and both short-day exposure groups beginning 11 January 2019. Birds were exposed to treatments for a total of 29 days.

4.1.1. Gonadal development

Gonadal development was measured at two time points. On treatment days 12 and 13 left testis length was measured by laparotomy. During laparotomies, each bird was anesthetized with isoflurane, was restrained on a surgical board, and a small incision was made in the flank. The testis was then inspected visually measured to the nearest 0.1 mm by locking the tips of forceps on either side of the testis and then measuring the distance between the forcep tips with dial callipers. The length of testes too small to measure (< 1.0 mm) were estimated visually. Birds were treated with analgesia (meloxicam) for 2 days following surgery. On treatment day 28, birds were sacrificed, and left testis length was measured directly using dial calipers.

4.1.2. Plasma testosterone

Plasma testosterone was measured at four time points for each individual. Blood samples were taken on treatment days −3, 7, 17, and 28 (trial start was Day 0). Blood was collected by puncturing the alar vein with a 26 g needle and collecting up to 300 μL of whole blood into heparinized microhematocrit tubes. Samples were then centrifuged and the supernatant plasma collected and stored at −80 °C until assayed.

Testosterone concentration was determined by enzyme immunoassay (EIA) using a kit that has been validated for a variety of bird species (Cat. #1–2402, Salimetrics Corporation; Washburn et al., 2007). Samples were run at a 1:5 dilution and were replicated across three plates (intra-plate CV: 1.52%, 5.33%, and 0.37%, interplate CV: 34.5%). We excluded all values (n = 3) below the detection limit of the assay (6.1 pg/ml).

4.1.3. Statistical analysis

We used linear mixed models for both gonadal development and testosterone concentrations. For gonadal development, photoperiod and temperature were included as fixed factors. For plasma testosterone, photoperiod, temperature and time were included as fixed factors. For both models, Bird ID was included as a random factor. All statistical analyses were performed using SPSS (IBM Corp, v. 25, 2017).

4.2. Results

4.2.1. Gonadal development

There were no differences in testes length at the time of the laparotomies on treatment days 12 and 13 ($F_{1,24}$ = 0.001, p = 0.97). Testis length was small at this time in every group: Long-Days-Warm group (mean ± SE: 1.03 ± 0.08 mm), Long-Days-Cold group (1.28 ± 0.27 mm), Short-Days-Warm (1.10 ± 0.10 mm), Short-Days-Cold (1.10 ± 0.12 mm) groups. By the end of treatment, however, birds experiencing the long-day photoperiod had significantly larger testes than birds experiencing the short-day photoperiod ($F_{1,48}$ = 12.09, p = 0.001; Fig. 3). There was no significant effect of temperature ($F_{1,48}$ = 0.48, p = 0.49), and no significant interaction between photoperiod and temperature ($F_{1,48}$ = 0.17, p = 0.68). Testis length was greatest in the Long-Days-Warm group, followed by the Long-Days-Cold group. Testis length remained small in both the Short-Days-Warm and Short-Days-Cold groups.

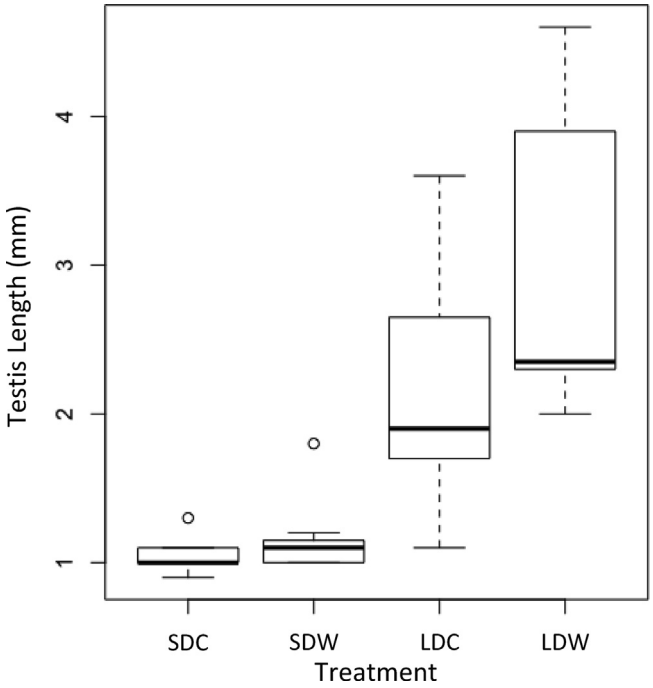

Fig. 3. Male testis length at the end of Experiment Two (post-mortem measurements). Birds experiencing long days had significantly greater testis length than birds experiencing short days regardless of the temperature condition (Short-Days-Cold (SDC); n = 6, Short-Days-Warm (SDW); n = 7, Long-Days-Cold (LDC); n = 7, Long-Days-Warm (LDW); n = 6). Boxes encompass 50% of the data, while the tails encompass the additional 50%. Open circles are outliers in the data set. The dark bar shows the mean value.

4.2.2. Plasma testosterone

Birds experiencing long photoperiods had higher testosterone levels than birds experiencing short photoperiods ($F_{1,97}$ = 4.84, p = 0.03). Neither temperature ($F_{1,97}$ = 0.96, p = 0.33), nor time ($F_{3,97}$ = 0.70, p = 0.56) had a significant main effect on testosterone levels. There was a significant interaction, however, between photoperiod and temperature treatment ($F_{1,97}$ = 4.63, p = 0.03; Fig. 4). Birds in the Long-Days-Warm treatment had higher testosterone levels by day 20 than birds in the Long-Days-Cold treatment, while temperature had no effect on testosterone levels in the short-day groups.

4.3. Discussion

The higher testosterone levels in photostimulated birds experiencing warm conditions indicate that while photoperiod is a primary initial predictive cue, reproductive timing is modulated by temperature as a supplementary cue. Although a significant interaction between temperature and photoperiod was not detected for testis length in Experiment Two, we suggest that the rank ordering of testis length observed between long day warm and long day cold groups may indicate that more sensitive measures might detect further differences in reproductive condition resulting from exposure to warm temperatures. Our results also indicate that temperature had no effect on reproductive timing in the absence of a simulatory long-day photoperiod.

5. General discussion

For many seasonally breeding birds, photoperiod is the primary cue that stimulates the hypothalamic-pituitary–gonadal (HPG) axis. The endocrine changes that are associated with reproductive development, such as testosterone secretion, occur rapidly (Perfito et al., 2005; DeVries et al., 2011; Henare et al., 2011; reviewed in Dawson, 2015). Many researchers have demonstrated a link between temperature and

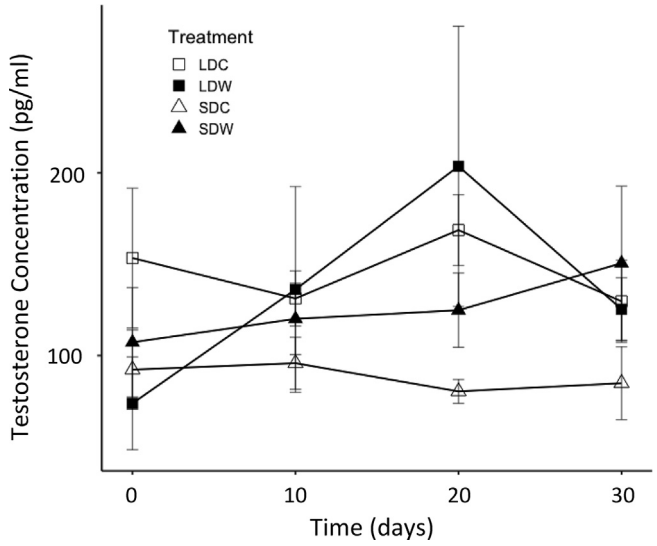

Fig. 4. Male testosterone levels in Experiment Two. Mean (± SE) plasma testosterone levels for all treatments are shown at four time points. Birds experiencing long days had elevated plasma testosterone levels compared to birds experiencing short days. There were no main effects of time or temperature. There was a significant interaction, however, between photoperiod and temperature treatment. Birds in the Long-Days-Warm group had higher peak plasma testosterone levels than birds in the Long-Days-Cold group by day 20, indicating that temperature had an effect on testosterone levels in photostimulated birds.

reproductive phenology (e.g. Visser et al., 2009; Watts et al., 2018), and others have investigated temperature in relation to changes in hormone cycles (e.g. Caro et al., 2013; Zhang et al., 2017). Here we have investigated the roles of both these cues and their interaction. Our results show that temperature can act as a supplementary cue that modulates reproductive condition through the upregulation of androgens, but only in the presence of stimulatory photoperiod cues.

In Experiment One, males that experienced continuous additional heat (24H), and birds that experienced heat only overnight (6H), were in the same reproductive state, as assessed by gonad size. This suggests that overnight temperature is an important regulator of reproductive readiness, regardless of daytime temperature. This is of particular interest because black-capped chickadees are known to employ facultative hypothermia, a strategy used by some animals to combat low temperatures to survive cold winter nights (McKechnie and Lovegrove, 2002; Grossman and West, 1977). While Chaplin (1974) found that facultative hypothermia decreased metabolic costs in black-capped chickadees, our results potentially suggest that this survival strategy comes with the associated cost of delayed gonadal development. We suggest that birds exposed to warmer night-time temperatures might be able to avoid the use of facultative hypothermia, allowing them to allocate more resources to reproductive processes such as androgen circulation and gonadal development.

Black-capped chickadees rely on insect prey to feed their young in spring (Smith, 1991), and therefore benefit from matching their reproductive timing, particularly egg hatching, with peak abundance of insect prey. Recent evidence suggests that black-capped chickadees do not flexibly alter their foraging behaviours in response to temperature cues (Martin and Sherry, 2019), making this precise timing even more important. While great tits in northern Europe have not demonstrated the ability to flexibly alter reproductive timing to synchronize egg laying with peak caterpillar abundance (Visser et al., 1998), there is correlational evidence that a shift in lay date is occurring (Visser et al., 2005). Our results from Experiment Two suggest that black-capped chickadees are able to flexibly modulate their reproductive timing to correspond to current temperature. This suggests that unlike the great tits, chickadees may be better able to actively synchronize their laying date with peak food abundance, at least under long day photoperiods.

Our results also provide some evidence to suggest that using temperature to modulate reproductive condition could create an intersexual reproductive mismatch in breeding pairs. In Experiment One, although both sexes appeared to respond to warmer winter conditions with advanced reproductive readiness, males and females did not respond in the same way. Males that experienced warmer winter conditions (either 6H or 24H) were in full breeding condition, while no females, regardless of temperature condition, were in full breeding condition, although most were progressing toward egg production. Increased environmental temperature may, therefore, affect the reproductive synchrony of male and female black-capped chickadees, though it is important to view these results within the relative limitations of the small sample size of Experiment One.

6. Conclusions

We found evidence for a causal relationship between temperature and reproductive timing but only in the presence of a photoperiodic cue. In both experiments, birds exposed to warmer temperatures experienced accelerated reproductive readiness. When the roles of photoperiod and temperature where considered independently, however, temperature was only a factor in the presence of a photoperiodic cue. We suggest that once photostimulated, birds use temperature to modulate their reproductive timing on a finer time scale than is possible with a photoperiodic cue alone.

CRediT authorship contribution statement

R. Jeffrey Martin: Conceptualization, Methodology, Formal analysis, Investigation, Writing - original draft, Visualization. **M. Charlotte Kruger:** Conceptualization, Methodology, Formal analysis, Investigation, Writing - original draft, Visualization. **Scott A. MacDougall-Shackleton:** Conceptualization, Methodology, Investigation, Resources, Writing - review & editing. **David F. Sherry:** Conceptualization, Methodology, Resources, Writing - review & editing, Supervision.

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Author contributions

All authors participated in conceptualizing the research question and contributed to study design. RJM and MCK conducted experimental trials, data collection, and data analysis, and drafted the manuscript. SAM performed all surgical procedures and aided in data analysis. RJM and MCK drafted the manuscript. DFS and SAM provided consultation throughout the project, and helped edit and refine the manuscript. All authors gave approval for publication.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ygcen.2019.113348.

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