



Temperature affects frequency but not rhythmicity of nocturnal awakenings in free-living great tits, *Parus major*



E. F. Stuber^{a,*}, N. J. Dingemans^{b,c}, J. C. Mueller^a

^a Max Planck Institute for Ornithology, Department of Behavioural Ecology and Evolutionary Genetics, Seewiesen, Germany

^b Max Planck Institute for Ornithology, Research Group Evolutionary Ecology of Variation, Seewiesen, Germany

^c Ludwig-Maximilians University of Munich, Department of Biology, Behavioural Ecology, Munich, Germany

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Several bird species display periodic nocturnal sleep–wake patterns, resembling the ultradian rhythms expressed by mammals. Although relatively little is known about the underlying molecular properties of ultradian biological clocks, field observations demonstrate that the frequency of nocturnal awakenings (which may relate to rhythmicity) increases with ambient environmental temperature. To understand how ambient environmental temperature conditions affect the nocturnal sleep–wake pattern of birds, we experimentally heated nestboxes during the night and monitored the frequency and rhythmicity of awakening behaviour of roosting great tits. More than 80% of great tits displayed ultradian rhythmicity in major nocturnal awakenings, with awakenings occurring every 50–170 min. Experimental increases in temperature, on average, 5 °C, caused birds to wake up approximately 30% more frequently over the course of the night, with the strongest temperature effect occurring during the first part of the night. However, the period length of the predominant nocturnal awakening rhythm was unaffected by increased temperature, likely because most additional awakenings were arrhythmic and clustered during the beginning of the night. We suggest that short-duration awakenings elicited primarily during the first part of the night may not be regulated by an ultradian biological clock, and may respond directly to current environmental conditions, such as the risk environment. Longer-duration awakening bouts, which were not affected by experimental heating, may instead be endogenously regulated by an ultradian clock to optimize clock-controlled sleep patterns and sleep homeostasis.

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Organisms have evolved complex biological time-keeping systems to govern changes in behaviour and physiology corresponding to the daily rhythms of light and dark. Although the sleep–wake cycle is partly regulated via homeostatic mechanisms, it is also regulated by an endogenous circadian (cycling with a period of approximately 24 h) clock (Lavie, 2001), which strongly responds to natural and manipulated light regimes (Raap, Pinxten, & Eens, 2015, 2016). Sleep is further characterized by ultradian (cycling with a period less than 24 h) fluctuations between rapid-eye-movement (REM) and non-REM sleep stages with a period length ranging from approximately 90 min (humans, *Homo sapiens*; Globus, 1970; Hirshkowitz, 2004), or behavioural awakening cycles of 50 and 110 min (great tits; Stuber, Dingemans, Kempnaers, & Mueller, 2015), or >120 min (blue tits, *Cyanistes caeruleus*; Mueller, Steinmeyer, & Kempnaers, 2012). As few studies of sleep

are performed under free-living conditions, it is unknown how closely the rhythms observed in sleep patterns are linked to a biological clock versus other factors unrelated to internal clocks. For example, some awakening patterns in sleep may not be generated by an ultradian clock, including the short awakening bouts occurring predominantly during the beginning of the night (Mueller et al., 2012). Instead, such irregular patterns may arise through homeostatic mechanisms (Phillips, Robinson, & Klerman, 2013) or be directly influenced by local environmental conditions such as predation risk (Stuber et al., 2014).

Biological rhythms strongly respond to ambient temperature as an entraining cue in ectotherms. Although less work has been performed in endotherms, it appears as though temperature constitutes a relatively weak entraining agent for circadian rhythms (Refinetti, 2010, 2015). The difference in entrainment characteristics of ectotherms and endotherms may be attributed to differences in their thermoregulatory strategies, whereby endotherms use internal body temperature as a resetting cue for biological clocks (Buhr, Yoo, & Takahashi, 2010) and are insensitive to fluctuations in ambient

* Correspondence and present address: E. F. Stuber, Nebraska Cooperative Fish and Wildlife Research Unit, School of Natural Resources, 508 Hardin Hall, University of Nebraska-Lincoln, Lincoln, NE 68583, U.S.A.

E-mail address: efstuber@gmail.com (E. F. Stuber).

temperature. However, correlational and experimental work has revealed a relationship between ambient temperature and behavioural rhythms, including hibernation, timing of egg laying, torpor bouts and daily activity, downstream of the biological clock in birds and mammals (Lehmann, Spoelstra, Visser, & Helm, 2012; Meijer, Nienaber, Langer, & Trillmich, 1999; Nemeth, Nyitrai, & Altbacker, 2009; Pongelley & Fisher, 1963; Salvante, Vezina, & Williams, 2010; Schaper et al., 2012; Visser, Holleman, & Caro, 2009).

Recent work in birds has revealed a relationship between ambient temperature and circadian period length (Lehmann et al., 2012), rhythmicity, or frequency of nocturnal awakenings in free-living individuals (Mueller et al., 2012; Steinmeyer, Schielzeth, Mueller, & Kempenaers, 2010; Stuber et al., 2015). Birds in warmer locations awaken more often and are more likely to display ultradian rhythmicity in these awakenings. Based on these findings, we aimed to experimentally test whether there is a causal relationship between ambient temperature and rhythmicity in nocturnal awakenings in birds. A relationship between ambient temperature and periodic awakenings during the sleep phase would indicate that the clock regulating this behaviour responds to ambient temperature. A relationship between temperature and frequency of awakenings, but not between temperature and period length of the awakening rhythm, would suggest different regulation of the nonrhythmic and rhythmic components of awakening behaviour.

METHODS

Data for this study were collected from roosting great tits during 14–23 February 2013 from three nestbox plots, consisting of forested areas of 9–12 ha with 50 nestboxes each, that were established in 2009 in southern Germany (Stuber et al., 2013). All birds had previously been implanted with a subcutaneous passive integrated transponder (PIT) tag for identification (Destron Fearing™, Eagan, MN, U.S.A.).

We performed night checks of each plot sequentially, the night prior to the beginning of the experiment to identify the locations of all birds individually roosting in the nestboxes by scanning the outer walls of each nestbox with a hand-held PIT tag reader. This allowed us to record the roosting location of all previously identified birds without disturbance (Stuber et al., 2015). During the daytime of the following day, when birds do not occupy the nestboxes, we installed small infrared cameras in the lid of every nestbox where a bird had been recorded sleeping. Collectively, we randomly selected 21 of these birds that were assigned to either the control ($N = 7$) or the treatment ($N = 14$) group. We expected little variation in sleep behaviours between subsequent nights in unmanipulated individuals and therefore recorded fewer individuals in this group. Previous work demonstrated that great tits exhibit short-term roost site fidelity (estimated 100% over consecutive days; Stuber et al., 2013); we assumed the same individual occupied the same nestbox throughout the experiment. We placed HOBO® data loggers (Onset Computer Corp., Bourne, MA, U.S.A.) on top of and inside each of these 21 nestboxes to record ambient external temperature and light intensity (lx), as well as internal nestbox temperature at 1 min intervals. We attached a small insulated wooden chamber to the underside of each nestbox (control and treatment groups; same dimensions as the nestbox, height: approximately 5 cm), which contained a custom battery-powered heating element (29.4×21.0 mm, resistance 13.7–13.9 Ω , heating power 10.5 W; treatment group only).

Experimental Heating Validity

A mixed-effects model of heat treatment (yes/no) on internal nestbox temperature demonstrated that our experimental heating

significantly increased the interior temperature of nestboxes on experimental heating days by approximately 5 °C (95% CI: 1.9, 8.6) throughout the course of the night regardless of changes in ambient temperature. On average, in the evening (from 30 min before sunset to 30 min after sunset) heat-treated nestboxes were 2.7 °C (95% CI: 0.4, 4.8) while the interiors of unheated nestboxes were on average –1.6 °C (95% CI: –4.6, 1.5). At midnight (recorded ± 30 min around midnight), heat-treated nestboxes were 1.5 °C (95% CI: –0.2, 3.2) while control nestboxes were on average –3.2 °C (95% CI: –6.9, 0.6). In the morning (recorded ± 30 min around sunrise), heat-treated nestboxes were 1.9 °C (95% CI: 0.4, 3.3) while control nestboxes were on average –4.5 °C (95% CI: –7.4, –1.5).

All individuals in the experiment, except two individuals recorded on nonsubsequent days due to equipment issues, were recorded for 2 successive nights during the study period. Individuals in the control group were recorded both nights without any heat manipulation; individuals in the treatment group were exposed to increased heat from the heating elements during one of the two recording nights, in random order by plot. Heating elements were powered from at least 1 h before sunset (i.e. before birds begin to roost) and were removed the following day after birds had left the nestbox. Video cameras were programmed to record from 1 h before sunset to 1 h after sunrise to capture individuals' time of entry, exit, and entire sleep duration overnight. From these videos we quantified the frequency (number of awakenings per hour) and timing of nocturnal awakenings using a motion detection software program modified from the AForgeVision image processing library (aforget.net.com; Surhone, Tennoe, & Henssonow, 2010) following Stuber et al. (2014, 2015). A bird was considered asleep when it assumed a classical sleeping posture with its feathers fluffed and beak tucked back into the scapular feathers (Amlaner & Ball, 1983). This sleep posture was consistent throughout recordings made during the winter (E. F. Stuber, personal observation). The bird was considered awake if its beak was out and facing forward, or if it was actively moving within the nestbox; awakening bouts had to last at least 2 s and consecutive awake bouts had to be separated by at least 10 s to be considered separate bouts.

We obtained both of the two planned recordings from 13 individuals, but collected one recording each from eight individuals due to technical failures of the recording equipment ($N = 34$ observations from 21 individuals in total).

Additionally, we reanalysed a large set ($N = 225$ observations from 120 individuals during winter) of observational data collected in a previous study (see Stuber et al., 2015, for details) using similar collection methods as those described here and models following the previous study. Here, we used a more conservative acceptance criterion for period length estimates, which did not allow for period estimates at the limits of our considered range (50–180 min) to be selected if the estimate did not lie fully within the 50–180 min range (this affected 12 recordings; see Data Analysis for details regarding maximum entropy spectral analysis). Furthermore, we explored potential sources of variation in the likelihood of sleep–wake cycles to be rhythmic using a binomial mixed model with sex, age, month, light intensity and temperature as predictors of whether or not an individual's night of sleep was classified as rhythmic.

Data Analysis

For each video recording (34 experimental, 225 observational), behavioural data (binary: sleep/awake per 2 s) were aggregated into 1 min bins of proportion time spent awake (see Fig. 1 for a sample time series plot); the first and last 15 min of the time series were removed because these could represent falling asleep and

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