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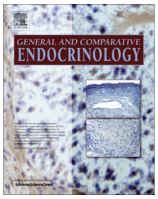

Is microevolution the only emergency exit in a warming world? Temperature influences egg laying but not its underlying mechanisms in great tits

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ABSTRACT

Many bird species have advanced their seasonal timing in response to global warming, but we still know little about the causal effect of temperature. We carried out experiments in climate-controlled aviaries to investigate how temperature affects luteinizing hormone, prolactin, gonadal development, timing of egg laying and onset of moult in male and female great tits. We used both natural and artificial temperature patterns to identify the temperature characteristics that matter for birds. Our results show that temperature has a direct, causal effect on onset of egg-laying, and in particular, that it is the pattern of increase rather than the absolute temperature that birds use. Surprisingly, the pre-breeding increases in plasma LH, prolactin and in gonadal size are not affected by increasing temperature, nor do they correlate with the onset of laying. This suggests that the decision to start breeding and its regulatory mechanisms are fine-tuned by different factors. We also found similarities between siblings in the timing of both the onset of reproduction and associated changes in plasma LH, prolactin and gonadal development. In conclusion, while temperature affects the timing of egg laying, the neuroendocrine system does not seem to be regulated by moderate temperature changes. This lack of responsiveness may restrain the advance in the timing of breeding in response to climate change. But as there is heritable genetic variation on which natural selection can act, microevolution can take place, and may represent the only way to adapt to a warming world.

1. Introduction

Matching the timing of breeding with the local peak of food abundance is of critical importance for many animals such as insectivorous birds that rely on external food sources for feeding their nestlings (Baker, 1938; Lack, 1968; Visser et al., 2006). Any deviation from this favorable period has dramatic consequences in terms of energy expenditure, reproductive success and for the survival of both the parents and the offspring (Thomas et al., 2001; van Noordwijk et al., 1995; Visser et al., 1998). Because the time at which the local food peak occurs varies from year to year, and because the decision to start breeding is taken weeks in advance of the period of maximal food demand from the offspring, birds must use predictive environmental cues to try to match the annual optimal breeding period. These cues include photoperiod, temperature, vegetation development and/or social interactions (e.g. opposite-sex behaviors have been shown to enhance gonadal development and/or advance laying in a variety of species (Bentley et al., 2000; Lehrman, 1964; Morton et al., 1985; Wingfield and Kenagy, 1991)). While photoperiod plays an important role in seasonal timing (Dawson et al., 2001; Farner, 1964), it cannot account for the year to year variation in optimal timing. As a consequence, in most geographic zones of the world, birds have to use additional cues that allow fine-tuning the best moment to start breeding within the broad time-window opened by the stimulatory effect of increasing photoperiod on the reproductive system. In the temperate zone ambient temperature is the environmental variable that generally best correlates with this variation in seasonal timing: many observational field studies have shown robust correlations between mean population timing of reproduction and ambient temperature (Crick et al., 1997; Dunn, 2004).

In recent years, the observation that the world's climate is changing at an unprecedented rate has induced a clear upsurge of interest in the influence of temperature on ecological mechanisms. One of the best-documented impacts of global warming on living organisms is on phenology (i.e. seasonal timing). Clear phenological shifts have been observed in all taxonomic groups in terrestrial, aquatic

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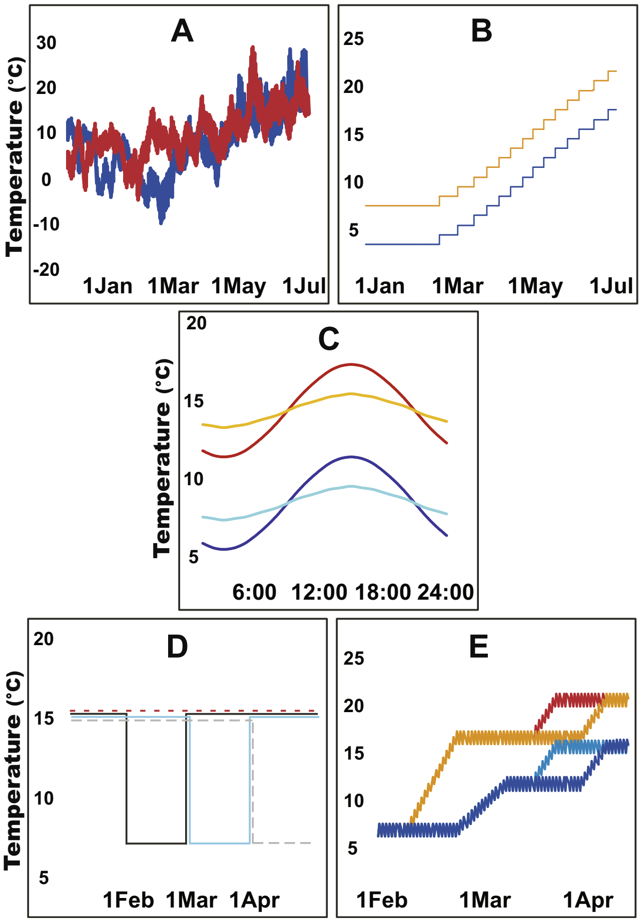

Fig. 1. Temperature profiles used during experiments conducted in climate-controlled aviaries. (A) Temperature fluctuations mimicking actual patterns of a “warm” (red line) and a “cold” spring (blue line) during which wild great tits respectively bred exceptionally early (1998) and late (1986). On average the two treatments differed by 4 °C. (B–E) Artificial patterns of temperature variation. (B) Stepwise increase of temperature throughout spring (increase of 0.65 °C per week) with a constant 4 °C difference between the two treatments. (C) Variation in the daily amplitude of temperature. Birds were exposed to one of four temperature treatments, each composed of a high or low mean temperature (14 *vs.* 8 °C) with either a high or low day-night amplitude (6 *vs.* 2 °C). Note that the x-axis only ranges over 24 h, i.e. there was no seasonal variation. (D) Variation in the onset and termination of a cold period. Birds were kept at 15 °C from December onwards. One group remained at 15 °C for the whole spring (dashed red), while the other three groups were temporarily exposed to a lower temperature (7 °C) in February (black), March (light blue) or April (dashed grey). This latter group remained at 7 °C until laying. (E) Variation in the onset and the rate of increase of temperature. Four groups of birds were exposed to two consecutive temperature increases. A first increase occurred either in early (orange and red), or late (light and dark blue) February. A second increase occurred either in early (red and light blue) or late (orange and dark blue) March. Temperatures increased at different rates in February, but not in March. A day-night fluctuation of 2 °C was superimposed to each of the four temperature profiles. Adapted from Schaper et al. (2012), Schaper et al. (2011), Visser et al. (2009) and Visser et al. (2011).

and marine environments over time (Cleland et al., 2007; Parmesan and Yohe, 2003; Root et al., 2003; Thackeray et al., 2010). However, the rate at which different species change their phenology is highly variable, causing phenological mismatches in food chains (Post and Forchhammer, 2008; Visser and Both, 2005; Visser and Holleman, 2001). These mismatches can influence population viability and can lead to natural selection on the mechanisms underlying timing, especially on the intensity with which ambient temperature affects timing. Establishing the causal effect of temperature on phenology is thus critical if we want to predict the maximum rate of temperature increase organisms can cope with, or adapt to in the coming decades (IPCC, 2007). At present, this causal effect of temperature on seasonal timing and the underlying physiological basis of temperature integration in birds and mammals is still poorly understood (Caro et al., 2013).

The first experiments investigating the effect of temperature on birds’ reproduction date back to 1937 (Suomalainen, 1937) and since then many more studies have addressed this question (Dawson, 2005; El Halawani et al., 1984; Engels and Jenner, 1956; Maney et al., 1999; Perfito et al., 2005; Silverin and Viebke, 1994; Silverin et al., 2008; Wada, 1993; Wada et al., 1990; Wingfield et al., 1996, 1997, 2003). Very few studies have looked at the effect of temperature on timing of reproduction directly, by obtaining laying dates under controlled conditions (Meijer et al., 1999; Salvante et al., 2010). Most experiments used temporal patterns of hormone concentration or gonadal growth, generally in males (Caro, 2012), as proxies for timing of reproduction. No clear pattern emerges from these studies: there is variation both among species and between populations of the same species on how temperatures affect the timing of reproductive development. There are moreover potential problems with using proxies for timing of breeding as their relationship with laying dates is not always straightforward (see below and Schaper et al., 2012).

Temperature can affect seasonal timing of reproduction in two ways. Particularly low or high ambient temperatures can lead to an unfavorable energy balance and thus no energy can be allocated to breeding. In these cases temperature may constrain reproduction (Perrins, 1970; Stevenson and Bryant, 2000; Vézina and Williams, 2002). Alternatively, temperature may be a source of information. In that case, the effect of temperature on timing is that temperature acts as a cue predicting future environmental conditions, i.e. the optimal period for breeding to take place, and by using this predictive value of temperature, animals increase their fitness (Wingfield and Kenagy, 1991). It should be noted that this predictive character of temperature may sometimes only be indirect, via a third variable such as vegetation phenology or food abundance. If temperature acts as a constraint or as an indirect predictive cue, birds would not need to directly sense and interpret temperature information to adapt to a changing climate. In addition, we would not only need to incorporate the relationship between temperature and timing in the models predicting the future consequences of global warming, but we would also need to take the effects of temperature on the third variable into account. As a consequence, one critical question for understanding and predicting the consequences of climate change is whether temperature has a direct signaling effect on seasonal timing of reproduction in birds.

2. Temperature has a direct effect on timing of breeding in great tits

Demonstrating a direct effect of ambient temperature on timing requires experiments under controlled conditions in the laboratory (Seebacher and Franklin, 2012). In 1999 we started a research program that aims at deciphering the possible causal relationships between temperature and breeding phenology in great tits (*Parus major*). This research program makes use of 36 climate-controlled aviaries, in which single pairs of great tits are housed. During the first 6 years, birds were exposed to a slowly increasing photoperiod and to temperature patterns mimicking the actual temperature variation of a year when great tits bred respectively very early (1998, the “warm” treatment) and very late (1986, the “cold” treatment) in the wild (Visser et al., 2009) (Fig. 1A). In this set-up, the two temperature profiles to which birds were exposed varied in many different aspects, but the average temperature difference between the treatments was only 4 °C. Although there was large