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The effects of temperature on photoperiodic responses: implications for climate change

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Birds aim to time their breeding so that the time that their young are growing most rapidly coincides with peak food availability. The physiological changes associated with sexual maturation begin a considerable time before breeding. Food itself is therefore of little value as a proximate cue. Birds use the annual cycle in photoperiod as the major predictive cue to time gonadal maturation and regression such that the eggs are laid at the optimum time (the breeding season) and not at any other time. However, for most species the increase in biomass of their food resource will be temperature dependent. Consequently, climate change is likely to advance the time of peak food availability. If birds rely entirely on photoperiod to time breeding, the peak in food availability may have already passed by the time young require it. There is evidence that this is happening (Visser *et al.* 2004).

Can temperature modulate photoperiodic responses to allow a degree of flexibility in the timing of sexual maturation? Controlled environment facilities were used to test this. Captive Starlings *Sturnus vulgaris* were held as free-flying groups in indoor aviaries. Photoperiod was changed daily to simulate the natural annual cycle in photoperiod at 52°N. Two groups were held at very different temperatures (20 and 5 °C). Changes in testis size and the progression of moult were recorded. Despite the large temperature difference, temperature had no apparent effect on the timing or rate of testicular maturation. However, unexpectedly, higher temperatures advanced the time of regression and the start of moult (Dawson 2005). The 20 °C group showed significant testicular regression between 3 April and 24 April ($P < 0.001$). The 5 °C group underwent regression 3 weeks later, between 24 April and 14 May ($P < 0.001$). Testicular volume was significantly less in the 5 °C group than in the 20 °C group on 24 April ($P < 0.001$). Consequently, the duration of full testicular function (volume > 125 mm³ when active sperm are present) was 1.5 times greater in the 5 °C group (58 days vs. 37 days; $P < 0.001$). The postnuptial moult, which is closely associated with gonadal regression, started 27 days later in the 5 °C group (9 June vs. 13 May; $P < 0.0001$). It then proceeded more rapidly in the 5 °C group (duration 82 days vs. 99 days; $P < 0.0001$). The effect on moult rate was a consequence of the start date for moult rather than a direct effect of temperature. In a separate study, Starlings that had just started to moult were divided into two groups at different temperatures; there was no effect on subsequent moult duration. To test how robust this temperature effect was, the experiment was repeated during the following year, with the groups reversed, i.e. those that had been at the higher temperature were then held at the lower temperature. The result was the same (Dawson 2005).

A similar study was done on Greenfinches *Carduelis chloris*, which have a longer breeding season than Starlings. Two groups of birds were held at 18 or 8 °C. Again, there was no significant effect on the time or rate of testicular maturation (Figure 1). The duration of full maturation was greater than in Starlings, reflecting the longer breeding season. As in Starlings, at the higher temperature regression and moult were advanced, although the effect was not as dramatic as in Starlings.

A study by Silverin *et al.* (2008) on Great Tits *Parus major* resulted in a similar conclusion; temperature had little effect on testicular maturation but low temperatures delayed regression.

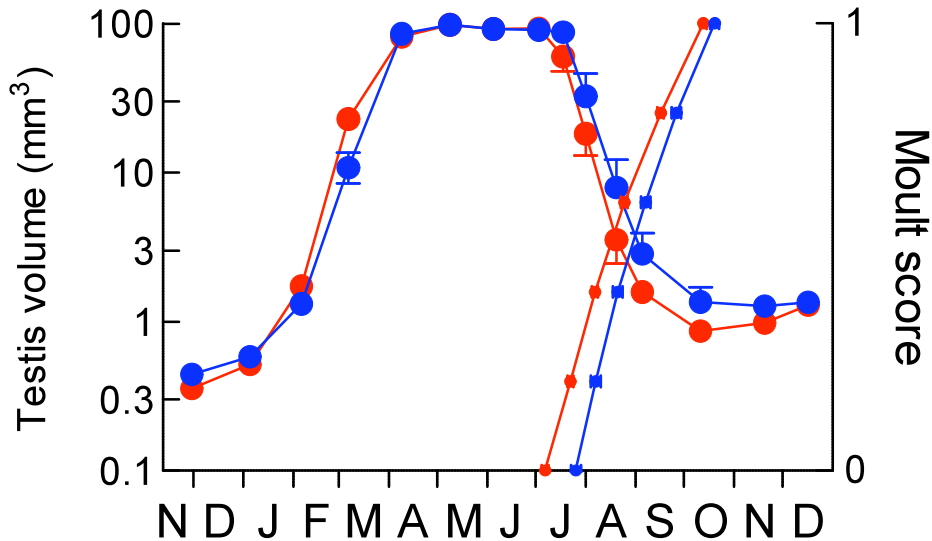


Figure 1. Changes in testicular volume (large circles) and the progress of moult (small circles) in Greenfinches held under a simulated natural annual cycle in photoperiod at 52°N at two different temperatures: 18 °C (red) or 8 °C (blue). There was a significant interaction between time and temperature ($P < 0.001$). There was no significant difference in testis size during maturation, but regression occurred sooner in the 18 °C group. Moulting started 19 days earlier in the 18 °C group ($P < 0.0001$) and took 12 days longer.

One limitation of these experiments was that birds were held as groups with no opportunity to breed. The effect of temperature on the timing of egg-laying could not be assessed. In a later study, Great Tits were kept in pairs in a set of 36 climate-controlled aviaries in which egg-laying could be monitored as well as other reproductive parameters. All birds were exposed to a simulated natural annual cycle in photoperiod and gradually increasing temperatures to simulate spring, but for 18 pairs, temperature was always 4 °C higher than for the other pairs. Again, temperature did not affect the timing or rate of testicular maturation, nor ovarian maturation. The timing of first egg-laying was unaffected by temperature. However, under the lower temperatures birds terminated egg-laying later, their testes regressed later and they started their moult later.

Temperature can, in some way, affect the timing of laying (Visser *et al.* 2009) but the nature of the temperature cue and the mechanism underlying this is unclear. The experiments described in this paper show that higher temperature does not advance the timing of gonadal maturation. This suggests that in the face of climate change, birds may be constrained in the degree to which they can advance breeding to compensate for the advanced phenology in food abundance. Furthermore, because higher temperatures advanced the time of gonadal regression, it is possible the climate change may decrease the number of breeding attempts in multi-brooded species. There is evidence that this may be happening (Husby *et al.* 2009).

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