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Seasonal timing in a warming world

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Climate change has a number of well-documented effects on avian reproduction such as shifts in seasonal timing, or phenology, where birds over recent decades have initiated reproduction earlier in spring. However, these seasonal shifts are often not sufficient to maintain synchrony with the, also shifting, seasonal peak in food abundance. Climate change may thus lead to a phenological mismatch, a widespread phenomenon (Visser and Both 2005). Such mismatch will lead to selection on seasonal timing: early-laying birds will have a higher fitness than late-laying birds and hence natural selection will favour early laying (Visser *et al.* 1998). Seasonal timing is also known to be heritable and in combination with the increased selection for earlier laying this will lead to a genetic change, or micro-evolution, in seasonal timing which could restore the phenological match. However, whether this will happen will depend strongly on the rate of micro-evolution relative to the rate of climate change (Visser 2008). If the rate of micro-evolution is too low, the mismatch will persist with negative effects on population viability (Both *et al.* 2006).

To forecast the rate of micro-evolution it is important to understand the genetic variation among individuals; i.e. we need to understand the genetic variation in the mechanisms underlying seasonal timing (Visser *et al.* 2010). Where in the physiological mechanism is the genetic variation that selection can act on? How do birds that differ in their laying date differ in their physiological mechanism? We are currently exploring two mechanisms: variation in seasonal timing due to variation in cue sensitivity and variation in the energetics associated with reproduction (such as the costs of egg production; Visser *et al.* 1998, Visser 2008).

Great Tits *Parus major*, like many other birds, are phenotypically plastic in their seasonal timing. The same individual will lay at different times when the annual conditions differ. The birds use cues, such as photoperiod and temperature, to time their reproduction but birds may differ in their cue sensitivity. If differences in cue sensitivity are genetic, they could account for the genetic variation in laying date (the *cues hypothesis*). We use our set of 36 climate aviaries to test this hypothesis. We use genetically related individuals and keep these under different temperatures (with a difference of 4 °C). We monitor hormone levels and the onset and the termination of egg-laying. Although in earlier aviary experiments there was an effect of temperature on laying date (Visser *et al.* 2009) this was not the case in this experiment (M. E. Visser *et al.* unpubl. data). There was, however, a clear effect of temperature on the termination of reproduction, with pairs kept under warmer conditions terminating reproduction and starting moult earlier (see Dawson & Visser, 2010) as well as a family effect, indicating genetic variation in cue

sensitivity (M. E. Visser *et al.* unpubl. data). This demonstrates that the genetic variation in laying dates in the field can at least partly be explained by genetic variation in cue sensitivity and hence that natural selection can act on this sensitivity.

Egg production is costly, in terms of both energy and fitness. Individuals may differ in how costly egg production is and in that case some individuals are able to produce eggs already earlier in spring, under harsher conditions (*constraint hypothesis*; Visser *et al.* 1998, Visser 2008). To test this hypothesis we obtained energetic measurements on wild Great Tits using doubly labelled water to calculate the daily energy expenditure of early- and late-laying birds during the egg-laying period. These energetic measurements showed that early and late individuals do not differ in the costs of egg production (L. te Marvelde *et al.* unpubl. data). This would indicate that variation in the costs of producing eggs does not explain the genetic variation in laying dates in the field.

The constraint and the cues hypothesis differ in the way natural selection will act on seasonal timing. Under the cues hypothesis, there is genetic variation in cue sensitivity and genetic change will lead to better timed reproduction. However, under the constraint hypothesis, birds are mismatched with their food but advancing their laying date will imply reproduction under harsher conditions and thus increased costs of egg-laying and a decline in fitness. Only when selection will reduce the cost of egg production, for instance via selection for smaller eggs, can laying date advance (for further discussion see Visser *et al.* 1998, Visser 2008).

To distinguish between the cues and the constraint hypothesis we need to manipulate laying date in the wild. This is not a trivial task but if we can experimentally shift the birds to an earlier laying date and then measure fitness, the prediction of the cues hypothesis is that the experimental birds will have the highest fitness while the constraint hypothesis predicts that the controls will have the highest fitness (see Fig. 1).

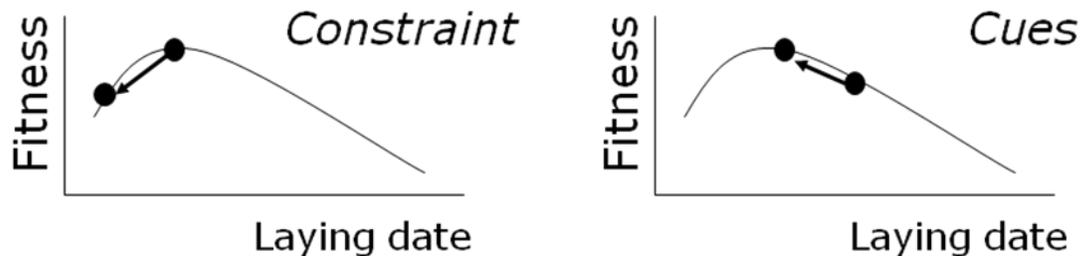


Figure 1. Predictions of the effect of experimentally shifting laying date forward (indicated by the arrow) on fitness (the number of surviving offspring and the female's own survival combined). Under the constraint hypothesis the fitness of the experimental animals will be lower than the control while under the cues hypothesis the fitness of the experimental animals will be higher.

Finally, we need to estimate the heritability and the selection on the mechanism underlying seasonal timing (Visser *et al.* 2010) and from that estimate the rate of micro-evolution in reproductive traits. At present, our estimates are that the rate of micro-evolution will not be sufficient to keep up with the rate of climate change. Phenological mismatches will then persist with possible severe consequences for avian population viability.

References

- Both, C., Bouwhuis, S., Lessells, C. M. & Visser, M.E. 2006. Climate change and population declines in a long-distance migratory bird. *Nature* 441: 81–83.
- Dawson, A. & Visser, M.E. 2010. The effects of temperature on photoperiodic responses: implications for climate change. *BOU Proceedings – Climate Change and Birds*. <http://www.bou.org.uk/bouproc-net/ccb/dawson&visser.pdf>
- Visser, M.E. 2008. Keeping up with a warming world; assessing the rate of adaptation to climate change. *Proc. R. Soc. Lond. B* 275: 649–659.
- Visser, M.E. & Both, C. 2005. Shifts in phenology due to global climate change: the need for a yardstick. *Proc. R. Soc. Lond. B* 272: 2561–2569.
- Visser, M.E., van Noordwijk, A.J., Tinbergen, J.M. & Lessells, C.M. 1998. Warmer springs lead to mistimed reproduction in great tits (*Parus major*). *Proc. R. Soc. Lond. B* 265: 1867–1870.
- Visser, M.E., Holleman, L.J.M. & Caro, S.P. 2009. Temperature has a causal effect on avian timing of reproduction. *Proc. R. Soc. Lond. B* 276: 2323–2331.
- Visser, M.E., Caro, S.P., van Oers, K., Schaper, S.V. & Helm, B. 2010. Phenology, seasonal timing and circannual rhythms: towards a unified framework. *Philos. Trans. B*, in press.

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