Case study: Long-tailed tits in the Rivelin Valley: investigating the effects of climate change

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Since 1994, a team of researchers from the University of Sheffield led by Ben Hatchwell has been studying long-tailed tits *Aegithalos caudatus* in the Rivelin Valley, Sheffield. The project has been funded primarily by a series of grants from the Natural Environment Research Council, with some additional funding from the Nuffield Foundation, Association for the Study of Animal Behaviour, and the University of Sheffield. The principal reason for starting the project was that long-tailed tits have a social system that is globally rare and unique among British birds. They are cooperative breeders in which some adults that have failed to breed successfully, redirect their reproductive effort to help another pair raise their offspring. Such behaviour poses many interesting evolutionary questions, addressing which requires collection of behavioural and life history data from individually marked birds whose pedigree is known. Therefore, in each year since the start of the project, with the help of undergraduate and postgraduate students, research assistants and post-doctoral researchers, the breeding attempts and survival of over 5,000 individuals have been closely monitored. These data have allowed us to answer many questions relating to the evolutionary and ecological causes and consequences of their extraordinary social system, but they also allow us to investigate other problems, including the effect of our changing climate on this population of long-tailed tits.

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The effect of climate change on biodiversity is typically manifest in shifts in the distribution of species and changes in the timing of annual events such as breeding or flowering, i.e. phenological shifts. National data collected by the British Trust for Ornithology (BTO) over a 43-year period shows that the timing of breeding of long-tailed tits has advanced by 15 days, more than any other UK bird. Using long-term data collected over a 19-year period, Philippa Gullett (PhD student; supervised by Ben Hatchwell and Karl Evans from the University of Sheffield, and Rob Robinson from the BTO) set out to investigate the effects of weather on breeding phenology in more detail, and also to examine the effect of climate variables on key population parameters in the Rivelin Valley long-tailed tits.

The start of egg-laying varied by more than 3 weeks across years and, as suggested by national data, this variation was related to mean March temperatures with earlier breeding in warmer years. Similarly, annual variation in the mean date on which breeding terminated was predicted by mean April temperatures, with pairs finishing earlier in warmer years. Long-tailed tits prey heavily on defoliating caterpillars when provisioning nestlings, so the latter pattern is probably caused by more rapid larval development and hence an earlier peak in caterpillar abundance in warm years; indeed, direct sampling of caterpillars over a 4-year period revealed earlier peak abundance in warmer springs. Importantly, since April temperatures have warmed more rapidly than March temperatures during the course of our study, the length of the breeding season has contracted by about one third between 1995 and 2011 (Gullett *et al*. 2013).

The window of opportunity for reproduction is clearly sensitive to a warming climate, but what about the impact of climate on other stages in the long-tailed tit life history? Weather during the breeding season has negligible effects on either clutch or brood size, nor on hatching and fledging success, which are instead determined primarily by nest predation. However, the survival of offspring from fledging to the following breeding season (i.e. recruitment) was affected negatively by warm March temperatures, but positively by warmer May temperatures. The mechanisms underlying these effects are not completely understood but may be attributable to the effects of weather on food availability at crucial stages of the season (Gullett *et al*. 2015). Finally, much of the annual variation in the survival rate of adult long-tailed tits could be explained by temperature and rainfall. Specifically, adult survival increased following warm, dry springs and warm autumns. Surprisingly, winter weather had little effect on this key population parameter (Gullett *et al*. 2014). We speculate that the characteristic flocking behaviour of long-tailed tits, and especially their communal roosts, during the winter helps to reduce their susceptibility to the adverse effects of harsh weather.

Results from the intensive study of long-tailed tits in the Rivelin Valley have several implications for studies of the impacts of climate change at a national scale. First, the local model of the timing of breeding predicted phenology at a national scale over several decades, demonstrating that such studies can be extrapolated at much larger geographic scales. Second, the opposing effects of weather in different months highlight the importance of examining uneven rates of warming through the year when predicting climate change impacts. Third, historical climate data suggests that adult survival would have been enhanced by warming over the past four decades, during which the UK long-tailed tit population has doubled. This population trend is predicted to continue under a range of future climate scenarios.

References

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