Impacts of climate change on upland birds: complex interactions, compensatory mechanisms and the need for long-term data.

This is the author’s manuscript

Original Citation:

Availability:
This version is available http://hdl.handle.net/2318/139619 since

Published version:
DOI:10.1111/ibi.12070

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http://onlinelibrary.wiley.com/doi/10.1111/ibi.12070/abstract;jsessionid=1714158C47E8B64CEC82F4FE0550027B.f01t02
The study of phenology, the timing of events in an organism’s life cycle, has been one of the cornerstones of research into the impacts of climate change on biodiversity. There have been widespread changes to the phenology of biological systems (Parmesan & Yohe 2003, Parmesan et al. 2007, Thackeray et al. 2010) which have been most apparent in the Northern Hemisphere (Schwartz et al. 2006). There is good evidence from Europe and North America that many bird species now breed earlier in the year as a result of warmer spring weather. Such changes may not in themselves be harmful, but when organisms at different trophic levels respond at different rates, community interactions can be disrupted (Walther 2010). Some of the best examples of such phenological mismatches come from birds. Studies of a number of woodland insectivorous passerines such as Pied Flycatcher Ficedula hypoleuca (Both & Visser 2005) and Great Tit Parus ater (Visser et al. 1999, Husby et al. 2009) have shown that breeding success has been reduced as a result of differential warming effects on birds and their caterpillar prey. These effects are not ubiquitous, however, and other studies have failed to detect such mismatches, even in other populations of woodland birds (Creswell & McCleery 2003, Waite & Strickland 2006, Wesolowski & Maziarz 2009, Vakta et al. 2011).

Phenological mismatch is just one of many ways in which climate change may impact upon bird populations (Mustin et al. 2007, Geyer et al. 2011). Climate-driven changes in prey abundance
(e.g. Frederiksen et al. 2006), competition (Ahola et al. 2007), disease (Benning et al. 2002), predation (Martin 2007), browsing pressure (Martin & Maron 2012) and agricultural management (Kleijn et al. 2010) may all drive changes in some bird populations. Severe cold weather (Robinson et al. 2007), flooding (Gilbert et al. 2010) or heat stress (McKechnie et al. 2012) may impose more direct effects. Recent evidence suggests that the majority of detrimental climate change impacts will occur through altered species interactions (Cahill et al. 2013), but we are only scratching the surface in our understanding of the many possible ways in which climate change may affect bird populations. Few studies have considered the potential for multiple mechanisms to impact on particular populations. Research to identify the most important mechanisms therefore remains an urgent priority for the academic community, not least because such information may guide conservation intervention (Pearce-Higgins et al. 2011).

Much knowledge of the impacts of phenological changes on terrestrial bird populations comes from deciduous woodland, yet upland birds, which we broadly define as those breeding in open habitats at relatively high altitudes, are regarded as particularly vulnerable to climate change (Şekercioğlu et al. 2008, Chamberlain et al. 2012). These are species that are adapted to live in cold environments, and therefore might reasonably be expected to decline in abundance as a result of rising temperatures. There is, however, relatively little understanding of climate change impacts on birds in these environments, due largely to the practical difficulties of working in what are typically harsh and remote locations and the subsequent paucity of long-term monitoring data (Chamberlain et al. 2012). Much of the existing evidence comes from the UK, and suggests that many upland species, such as Common Sandpiper Actitis hypoleucos (Dougall et al. 2005), Black Grouse Tetrao tetrix (Ludwig et al. 2006), Meadow Pipit Anthus pratensis and Dipper Cinclus cinclus (Sparks et al. 2006), have advanced their breeding seasons over the past few decades, although phenological trends in others have not been statistically significant (e.g. Ring Ouzel Turdus torquatus, Beale et al. 2006, Sparks et al. 2006).

Rather fewer studies have tried to assess whether such changes have resulted in detrimental effects due to the impacts of phenological mismatch. These habitats are highly seasonal, with relatively short breeding seasons constrained by spring temperatures or snow cover (e.g. Byrkjedal 1980) and seasonal peaks in invertebrate availability (Coulson & Whittaker 1978, Pearce-Higgins & Yalden 2004), so the potential for phenological mismatch appears high. However, population changes in Golden Plovers Pluvialis apricaria (Pearce-Higgins et al. 2010) and variation in the breeding success of Ring Ouzels (Beale et al. 2006) and productivity of Common Sandpipers (Pearce-Higgins et al. 2009) all appear to be unrelated to indices of mismatch, although any future divergence in phenological trends between predators and prey in response to further warming may
cause impacts of mismatch to occur (Pearce-Higgins et al. 2005). It is important also to examine the potential for climate change to affect vulnerable upland populations through other mechanisms. Although Pearce-Higgins et al. (2010) found no evidence of trophic mismatch having driven changes in a Golden Plover population, they found strong evidence of negative impacts of summer warming, mediated through a strong negative correlation between August temperature and the abundance of craneflies (Tipulidae), a key prey group. Hot August weather leads to the drying out of the surface layers of blanket peat, causing high mortality of larval craneflies. Similarly, despite the apparent lack of trophic mismatch effect, Beale et al. (2006) suggested that Ring Ouzel population declines may be linked to rising summer temperatures in the UK. Conversely, for Common Sandpiper, warming during the chick rearing period is likely to have boosted breeding success (Pearce-Higgins et al. 2009). Such immediate positive effects of breeding season temperature upon productivity are widespread amongst upland birds (Pearce-Higgins 2011) and probably result from reduced thermoregulatory requirements and increased prey activity. It is therefore necessary to consider a wide range of potential climate change impacts when analysing population time-series to identify a climate change effect, which has rarely been achieved.

The work of Fletcher et al. (2013), published in this issue of Ibis, adds significantly to this literature by describing the ways in which recent climate change has affected the breeding phenology and success of a population of Red Grouse Lagopus lagopus scotica in the Scottish Highlands over a 20-year period. First, Fletcher et al. (2013) assessed how warming has influenced the breeding phenology of Red Grouse using changes through time in mean first egg date of the population as a whole and for a sub-population of radio-tagged females. In common with many other bird species, Red Grouse showed an advance in lay dates of c. 0.5 days per year over the period of study, apparently driven by a trend to warmer springs, a pattern broadly in line with other studies of northern and upland birds (see above), and indeed with those from other habitats (Dunn & Winkler 2010). Moreover, individual radio-tagged females followed in different years were able to adjust their lay dates according to spring temperatures, and showed roughly the same patterns as the population as a whole. This adds to the number of studies in which most of the observed change in population-level laying date can be attributed to the phenotypic plasticity of individuals (Nussey et al. 2007, Weidinger & Král 2007, Charmantier et al. 2008) and suggests that there is a degree of innate flexibility in a species’ response to a changing climate.

The most important aspect of Fletcher et al. (2013), however, is that they then examined the potential impacts that these phenological changes may have had on Red Grouse breeding success, alongside a number of other potential mechanisms of climate change impact. Specifically, they assessed whether changes in laying date affect clutch size, which tends to be negatively correlated
with laying date in single-brooded species (Crick et al. 1993). In addition, since craneﬂies make up an
important part of Red Grouse chick diet (Park et al. 2000), Fletcher et al. additionally tested whether
 craneﬂy phenology (indexed by May temperature; Pearce-Higgins et al. 2005), and the interaction
 between laying date and May temperature (as an index of likely phenological mismatch), also
signiﬁcantly inﬂuenced chick survival. May temperature and rainfall were also used to estimate the
vulnerability of Red Grouse chicks to poor weather conditions after hatching (Erikstad 1985),
variables which may also inﬂuence the incidence of parasitic infection by the nematode
Trichostrongylus tenuis (Cattadori et al. 2005). Finally, the effect of August temperature in the
previous year was also assessed to account for potential reductions in craneﬂy abundance following
hot summer weather (Pearce-Higgins et al. 2010). As expected, clutch size was negatively related to
ﬁrst egg-date, as was chick survival, indicating that the earliest nests in a year tended to be most
productive. However, there was no signiﬁcant trend in clutch size through time that could be related
to temperature, although regression coefﬁcients were suggestive of a 0.4 egg per decade increase in
clutch size, or a 0.14 egg increase per degree C. Chick survival was strongly negatively related to both
May and August temperature in the previous year, but not May rainfall or the interaction between
ﬁrst egg date and May temperature.

These results can be used to draw a number of inferences. First, there was no evidence that
Red Grouse were strongly affected by the index of phenological mismatch. Although annual
breeding success was higher in years with a cold May and so later emergence of tipulids, this effect
was not dependent upon mean laying date. This apparent lack of phenological mismatch may be
regarded as surprising, given the seasonal nature of the upland environment in which Red Grouse
breed, with a highly synchronised emergence of their main prey, but matches previous studies in
these environments. Although there is variation in the importance of different invertebrate prey
between Red Grouse populations (Park et al. 2000), the relationship between May and August
temperature and survival suggests that craneﬂies were indeed the key prey type in this study,
although May temperature may also affect grouse productivity through variation in the rate of
infection by Trichostrongylus tenuis (Cattadori et al. 2005).

The second major inference is that despite a shift in phenology, there were no apparent
negative effects on Red Grouse, suggesting that this population is currently able to cope with
changing climatic conditions without detrimental impacts. Instead, the negative correlation between
chick survival and August temperature in the previous year matches that previously identiﬁed for
Golden Plovers by Pearce-Higgins et al. (2010), and suggests a signiﬁcant impact of variation in prey
abundance. Thus, after hot summers when the survival of early larval craneﬂies is likely to be low, it
appears that the reduced availability of adult craneﬂies for both Golden Plover and Red Grouse
chicks to feed on will reduce their productivity. However, there was no warming trend for either
August or May temperatures, unlike the Golden Plover study, which stresses the importance of
relatively small-scale variations in climatic trends, and suggests that caution must be taken when
applying models derived from one location to make predictions in another (e.g. Whittingham et al.
2007).

The study of Fletcher et al. (2013) emphasises the need to collect long-term demographic
monitoring data in order to understand fully the potential impacts of climate change on species.
Furthermore, such data should be analysed for evidence of a range of potential mechanisms through
which climate change might impact species. In the case of Red Grouse, warming may lead to
increased clutch size and enhanced chick survival through an advance in laying date, but a decrease
in productivity, such as through reductions in the availability of tipulid prey as well as other
mechanisms. Any future impact of warming on the population as a whole will therefore depend
upon the relative strength of these positive and negative impacts. For example, were the negative
effects of temperature upon chick survival to outweigh the positive effects of earlier laying,
significant negative impacts of future warming on Red Grouse populations would result, in the same
way as for Golden Plover (Pearce-Higgins et al. 2010). Despite the lack of current negative impacts
of climate change, continued monitoring of these potentially vulnerable populations is necessary.

More broadly, the study of Fletcher et al. adds to the evidence that the impacts of climate
change on populations may occur through altered species interactions, rather than direct effects
(Cahill et al. 2013). Although many upland birds appear to show immediate benefits in terms of
improved productivity or survival as a result of warmer weather, there is increasing evidence that
negative impacts of climate change will occur through altered prey availability. This does not appear
to result from trophic mismatches caused by divergent phenological trends between predators and
more direct effects on prey populations and availability, as shown for Golden Plovers (Pearce-Higgins
et al. 2010) and Red Grouse (Fletcher et al. 2013), and inferred for Ring Ouzel (Beale et al. 2006),
Golden Eagle Aquila chrysaetos (Watson et al. 2003) and a wide range of insectivorous upland birds
(Pearce-Higgins 2010). Long-term monitoring of key food resources for upland birds should
therefore also be a priority. The complex interactions and compensatory mechanisms revealed by
the work of Fletcher et al. suggest that if scientists are to understand fully the impacts of climate
change on birds, they will require very long runs of data on a range of demographic rates and their
drivers, a salutary lesson in a warming world in which funding cuts enforce ever shorter research
projects.
The authors are grateful to Paul Donald for the invitation to write this commentary, and for commenting on earlier drafts.

REFERENCES


