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

DOI:10.1111/ibi.12070

Running head: Climate change and upland birds

COMMENTARY

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

DAN CHAMBERLAIN[1*] & JAMES PEARCE-HIGGINS[2]

[1]*Dipartimento di Scienze della Vita e Biologia dei Sistemi, Università di Torino, Via Accademia Albertina 13, 10123 Torino, Italy*

[2]*British Trust for Ornithology, The Nunnery, Thetford IP24 2PU, UK*

*Corresponding author.

Email: dan.chamberlain99@gmail.com

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 (Paremsan & 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, Wesołowski & 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 prey (Beale *et al.* 2006, Pearce-Higgins *et al.* 2009, 2010, Fletcher *et al.* 2013), but instead through 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

Ahola, M.P., Laaksonen, T., Eeva, T. & Lehikoinen, E. 2007. Climate change can alter competitive relationships between resident and migratory species. *J. Anim. Ecol.* **76**: 1045-1052

Beale, C.M., Burfield, I.J., Sim, I.M.W., Rebecca, G.W., Pearce-Higgins, J.W. & Grant, M.C. 2006. Climate change may account for the decline in British ring ouzels Turdus torquatus. *J. Anim Ecol.* **75**: 826–835.

Benning, T.L., LaPointe, D., Atkinson, C.T. & Vitousek, P.M. 2002. Interactions of climate change with biological invasions and land use in the Hawaiian Islands: Modeling the fate of endemic birds using a geographic information system. *PNAS* **99**: 14246-14249.

Both, C., Bouwhuis, S., Lessels, C.M. & Visser, M.E. 2006. Climate change and population declines in a long-distance migratory bird. *Nature* **441**: 81–83.

Both, C. & Visser, M.E. 2005. The effect of climate change on the correlation between avian life-history traits. *Glob. Change Biol.* **11**: 1606-1613.

Both, C., van Asch, M., Bijlsma, R.G., van den Burg, A.B. & Visser, M.E. 2009. Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? *J. Anim Ecol.* **78**: 73–83.

Byrkjedal, I. 1980. Nest predation in relation to snow-cover – a possible factor influencing the start of breeding in shorebirds. *Ornis Scand.* **11**: 249-252.

Cahill, A.E., Aiello-Lammens, M.E., Fisher-Reid, M.C., Hua, X., Karanewsky, C.J., Ryu, H.Y., Sbeglia, G.C., Spagnolo, F., Waldron, J.B.,Warsi, O., & Weins, J.J. 2013. How does climate change cause extinction? *Proc. Roy. Soc. B.* **280**: 21231890

Cattadori, I.M., Haydon, D.T. & Hudson, P.J. 2005. Parasites and climate synchronize Red Grouse populations. *Nature* **433:** 737-741.

Chamberlain, D.E., Arlettaz, R., Caprio, E., Maggini, R., Pedrini, P., Rolando, A. & Zbinden, N. 2012. The altitudinal frontier in avian climate impact research. *Ibis* **154**: 205-209.

Charmantier, A., McCleery, R. H., Cole, L. R., Perrins, C., Kruuk, L. E. B., & Sheldon, B. C. 2008. Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science* **320**: 800–803.

Coulson, J.C. & Whittaker, J.B. 1978. The ecology of moorland animals. In Heal, O.W. & Perkins, D.F. (eds). *Production ecology of British Moors and Mountain Grasslands*: 52-93. Berlin Heidelberg New York: Springer.

Cresswell, W. & McCleery, R. 2003. How great tits maintain synchronization of their hatch date with food supply in response to long-term variability in temperature. *J. Anim. Ecol.* **72**: 356–366

Crick, H.Q.P. 2004. The impact of climate change on birds. *Ibis* **146**: 48–56.

Dougall, T.W., Holland, P.K., Mee, A. & Yalden, D.W. 2005. Comparative population dynamics of common sandpipers *Actitis hypoleucos*: living at the edge. *Bird Study* **52**: 80–87

Dunn, P.O. & Winkler, D.W. 2010. Effects of climate change on timing of breeding and reproductive success in birds. In Møller, A.P., Fiedler, W. & Berthold, P. (eds). *Effects of Climate Change on Birds*: 113-128. Oxford, UK: Oxford University Press.

Erikstad, K.E. 1985. Growth and survival of Willow Grouse chicks in relation to home range, brood movements and habitat selection. *Ornis Scand.* **16**: 181-190.

Fletcher, K., Howarth, D., Kirby, A., Dunn, R. & Smith. A. (2013) Effect of climate change on breeding phenology, clutch size and chick survival of an upland bird. *Ibis* **155**: xx-yy.

Commento [p1]: In this issue

Frederiksen, M., Edwards, M., Richardson, A.J., Halliday, N.C. & Wanless, S. 2006. From plankton to top predators: bottom-up control of a marine food web across four trophic levels. *J. Anim. Ecol.* **75**: 1259-1268.

Geyer, J., Kiefer, I., Kreft, S., Chavez, V., Salafsky, N., Jeltsch, F. & Ibisch, P.L. 2011. Classification of climate-change-induced stresses on biological diversity. *Cons. Biol.* **25**: 708-715.

Gilbert, G., Brown, A.F. & Wotton, S.R. 2010. Current dynamics and predicted vulnerability to sea-level rise of a threatened Bittern *Botaurus stellaris* population. *Ibis* **152**: 580-589.

Huntley, B., Green, R.E., Collingham, Y.C. & Willis, S.G. 2007. *A Climatic Atlas of European Breeding Birds.* Barcelona, Spain: Lynx.

Husby, A., Kruuk, L.E.B. & Visser, M.E. 2009. Decline in the frequency and benefits of multiple brooding in great tits as a consequence of a changing environment. *Proc. Roy. Soc. B* **276**:1845–1854.

Kleijn, D., Schekkerman, H., Dimmers, W.J., van Kats, R.J.M., Melman, D. & Teunissen, W.A. 2010. Adverse effects of agricultural intensification and climate change on breeding habitat quality of Black-tailed Godwits *Limosa l. limosa* in the Netherlands. *Ibis* **152**: 475-486.

Ludwig, G. X., Alatalo, R.V., Helle, P., Lindén, H., Lindström, J. & Siitari, H. 2006. Short- and long-term population dynamical consequences of asymmetric climate change in black grouse. *Proc. Roy. Soc. B* **273**: 2009-2016.

Martin, T.E. 2007. Climate correlates of 20 years of trophic changes in a high-elevation riparian system. *Ecology* **88**: 367-380.

Martin, T.E. & Maron, J.L. 2012. Climate impacts on bird and plant communities from altered animal-plant interactions. *Nature Climate Change* **2**: 195-200.

McKechnie, A.E., Hockey, P.A.R. & Wolf, B.O. 2012. Feeling the heat: Australian landbirds and climate change. *Emu*: **112**, i-vii

Mustin, K., Sutherland, W.J., Gill, J.A. 2007. The complexity of predicting climate-induced ecological impacts. *Climate Research* **35**: 165-175.

Nussey, D. H., Wilson, A. J. & Brommer, J. E. 2007. The evolutionary ecology of individual phenotypic plasticity in wild populations. *J. Evol. Biol.* **20**: 831–844.

Park, K.J., Robertson, P.A., Campbell, S.T. Foster, R., Russell, Z.M., Newborn, D. & Hudson, P.J. 2001. The role of invertebrates in the diet, growth and survival of red grouse (*Lagopus lagopus scoticus*) chicks. *J. Zool Lond* **254**: 137-145.

Parmesan, C. 2007. Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Glob. Change Biol.* **13**: 1860–1872.

Parmesan, C. & Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**: 37–42.

Pearce-Higgins, J.W. 2010. Using diet to assess the sensitivity of northern and upland birds to climate change. *Climate Research* **45**: 119-130.

Pearce-Higgins, J.W. 2011. How ecological science can help manage the effects of climate change: a case study of upland birds. In Marrs, S.J., Foster, S., Hendrie, C., Mackey, E.C. & Thompson, D.B.A. (eds). *The Changing Nature of Scotland*: 397-414. Edinburgh, UK: TSO Scotland.

Pearce-Higgins, J.W., Bradbury, R.B., Chamberlain, D.E., Drewitt, A., Langston, R.H.W. & Willis, S.G. 2011. Targeting research to underpin climate change adaptation for birds. *Ibis* **153**: 207-211.

Pearce-Higgins JW, Dennis P, Whittingham MJ, Yalden DW. 2010. Impacts of climate on prey abundance account for fluctuations in a population of a northern wader at the southern edge of its range. *Glob. Change Biol.* **16**: 12–23.

Pearce-Higgins, J.W. & Yalden, D.W. 2004. Habitat selection, diet, arthropod availability and growth of a moorland wader: the ecology of European Golden Plover *Pluvialis apricaria* chicks. *Ibis* **146**: 335–346

Pearce-Higgins, J.W., Yalden, D.W., Dougall, T.W. & Beale, C.M. 2009. Does climate change explain the decline of a trans-Saharan Afro-Palaearctic migrant? *Oecologia* **159**: 649-659.

Pearce-Higgins, J.W., Yalden, D.W. & Whittingham, M.J. 2005. Warmer springs advance the breeding phenology of golden plovers *Pluvialis apricaria* and their prey (Tipulidae). *Oecologia* **143**: 470-476.

Robinson, R.A., Baillie, S.R. & Crick, H.Q.P. 2007. Weather-dependent survival: implications of climate change for passerine population processes. *Ibis* **149**: 357-364.

Şekercioğlu, C.H., Schneider, S.H., Fay, J.P. and Loarie, S.R. 2008. Climate change, elevational range shifts and bird extinctions. *Cons. Biol.* **22**: 140-150.

Sparks, T.H., Collinson, N., Crick, H., Croxton, P., Edwards, M., Huber, K., Jenkins, D., Johns, D., Last, F., Maberly, S., Marquiss, M., Pickup, J., Roy, D., Sims, D., Shaw, D., Turner, A., Watson, A., Woiwod, I. & Woodbridge, K. 2006. *Natural Heritage Trends of Scotland: phenological indicators of climate change*. Edinburgh, UK: Scottish Natural Heritage Commissioned Report No. 167 (ROAME No. F01NB01).

Thackeray, S.J., Sparks, T.H., Frederiksen, M., Burthe, S., Bacon, P.J., Bell, J.R., Botham, M.S., Brereton, T.M., Bright, P.W., Carvalho, L.C., Clutton-Brock, T., Dawson, A., Edwards, M., Elliott, M., Harrington, R., Johns, D., Jones, I.D., Jones, J.T., Leech, D.I., Roy, D.B., Scott, W.A., Smith, M., Smithers, R.J., Winfield, I.J. & Wanless, S. 2010. Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Glob. Change Biol.* **16**: 3304–3313.

Schwartz, M.D., Ahas, R. & Aasa, A. 2006. Onset of spring starting earlier across the Northern Hemisphere. *Glob. Change Biol.* **12**: 343-351.

Vatka, E., Orell, M. & Rytkönen, S. 2011. Warming climate advances breeding and improves synchrony of food demand and food availability in a boreal passerine. *Glob. Change Biol.* **17**: 3002-3009.

Visser, M.E., van Noordwijk, A.J., Tinbergen, J.M. & Lessels, C.M. 1998. Warmer springs lead to mistimed reproduction in great tits (*Parus major*). *Proc. Roy. Soc. B* **265**:1867–1870.

Waite, T.A. & Strickland, D. 2006. Climate change and the demographic demise of a hoarding bird living on the edge. *Proc. Roy. Soc. B* **273**: 2809–2813.

Walther G-R. 2010. Community and ecosystem responses to recent climate change. *Phil. Trans. Roy. Soc. B* **365**:2019–2024.

Watson, J., Fielding, A.H., Whitfield, D.P., Broad, R.A., Haworth, P.F., Nellist, K. & Macdonald, E.J. 2003. Golden eagle (*Aquila chrysaetos*) breeding performance in relation to climate in western Scotland during the period 1981-2000. In Thompson, D.B.A, Redpath, S.M., Fielding, A.H., Marquiss, M. & Galbraith, C.A. (eds) *Birds of Prey in a Changing Environment*: 149-161. Edinburgh: The Stationary Office.

Weidinger, K. & Král, M. 2007. Climatic effects on arrival and laying dates in a long-distance migrant, the Collared Flycatcher *Ficedula albicollis*. *Ibis* **149**: 836-847.

Wesołowski, T. & Maziarz, M. 2009. Changes in breeding phenology and performance of wood warblers *Phylloscopus sibilatrix* in a primeval forest: a thirty-year perspective. *Acta Ornithologica* **44**: 69-80.

Whittingham, M.J., Krebs, J.R., Swetnam, R.D., Vickery, J.A., Wilson, J.D. & Freckleton, R.P. 2007. Should conservation strategies consider spatial generality? Farmland birds show regional not national patterns of habitat association. *Ecol. Lett.* **10**: 25-35.