



# Introduction

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Climate changes expose organisms to novel environmental conditions, with the potential to affect life history of individuals and demography of populations (Stenseth et al. 2002). If they are to stay alive and reproduce, organisms must be able to cope with the changes in the distribution and co-variation of environmental variables (Lande et al. 2003). The expression of individual traits in variable environments provides a mechanism that links variable environments and variable vital rates (e.g. survival and reproduction; Tuljapurkar 1990). After all, how well a species is able to cope with environmental changes depends on its potential to adapt to new environmental conditions.

Some of the most striking examples of rapid changes in life history traits due to climate change are found in migratory birds, not the least in the timing of migration (Hüppop & Hüppop 2003) and breeding (Dunn 2004). The combined effect of the public's fascination for birds, a general interest in the phenomenon of migration and the long history of systematic recording of arrival and departure of migratory birds (reviewed by Lehikoinen et al. 2004) have generated a wealth of potentially valuable data that can shed light on how bird migration patterns are affected by climate change and variability. The picture emerging shows that, for many species breeding in the northern hemisphere, spring arrival has advanced during the second half of the 20th century (Lehikoinen et al. 2004), and similar patterns have recently been described in Australia (Beaumont et al. 2007). The direction of the observed changes in spring arrival is in agreement with global changes in spring temperature; however, detailed data revealing the underlying mechanisms have rarely been available (but see Both et al. 2006).

In the recent contribution of Working Group II to the IPCC 4th Assessment Report (IPCC 2007), it is stated with high confidence that 'Ecosystems and species are very likely to show a wide range of vulnerabilities to climate change, depending on imminence of exposure

to ecosystem-specific, critical thresholds'. The wide range of vulnerability, as highlighted by the IPCC, is mirrored by the inter-specific variation in changing phenology patterns shown by migratory birds in the last decades. Focussing on arrival time only, there is considerable variation among species despite the general trend towards earlier arrival. Moving beyond the simple demonstration of earlier spring migrations, more systematic studies are required if we are to understand the nature of variation both within and between species. In order to identify the ways birds can adapt to, or are constrained from adapting to, climate change, we need to investigate such issues as the extent to which adaptation differences reflect systematic differences between the migration strategies, food preferences or taxonomic grouping of birds.

Since the publication of the special volume of *Advances in Ecological Research* on 'Birds and climate change' (Møller et al. 2004), several papers have presented new empirical results verifying or challenging previous conclusions. Most importantly, researchers have started to move beyond the mere description of phenology patterns. Recent publications have addressed fundamental questions of how to interpret the observed shifts in phenologies (Visser & Both 2005, Jonzén et al. 2007a), and to what extent the advanced arrival of birds migrating from Africa to Europe is the result of phenotypic plasticity or micro-evolution (Jonzén et al. 2006, 2007b, Both 2007). Also the heritable tendencies for phenotypic plasticity may be under selection (Nussey et al. 2005).

This Climate Research Special includes 13 contributions on various aspects of bird migration and climate change. Collectively these papers add significantly to our understanding of how climate change affects migratory birds. Pulido (2007, this issue) demonstrates that we are still lacking conclusive evidence for evolutionary change, despite selection for earlier arrival and the presence of genetic variation in the timing of

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migration, and Gienapp et al. (2007, this issue) point out that we need to investigate to what extent existing changes in phenology are consistent with evolutionary explanations. Among the contributions is also a review of why bird migration dates are shifting (Gordo 2007, this issue). Knudsen et al. (2007, this issue) notes that further analysis will require methodological advances, and Hedenström et al. (2007, this issue) highlight the need for a properly developed theoretical framework for interpretation of patterns, as well as predictions of what to look for in the future.

The migration schedule of birds will be modulated by the environmental conditions experienced throughout the migration. Both & te Marvelde (2007, this issue) investigate how spatiotemporal spring temperature patterns affect geographical variation in laying date in 2 contrasting species, one spending the winter in Europe and the other migrating to West Africa. We expect to find not only inter-specific differences with respect to change in timing of migration, but also differences between males and females migrating at different times of the season and facing different selection pressures (Møller 2004, 2007). To what extent recent climate change has affected the degree of pro-tandry—earlier arrival to reproductive sites of males relative to females—in migratory songbirds, is discussed by Rainio et al. (2007, this issue).

There is a growing body of literature emphasizing the importance of seasonal interactions (Webster et al. 2002), such as the knock-on effects of winter climate on individual performance in the breeding season (e.g. Saino et al. 2004, Norris & Marra 2007). Studts & Marra (2007, this issue) study how the amount and timing of rainfall influence the food abundance and non-breeding performance in the American redstart *Setophaga ruticilla*, a species for which seasonal interactions have previously been demonstrated (Marra et al. 1998). Whereas the winter ecology of American redstarts has been studied in detail for some time, much less is known about the climate impact on the non-breeding performance of birds wintering in Africa. Saino et al. (2007, this issue) focus on how rainfall and temperature patterns in Africa influence the timing of spring arrival of birds on the island of Capri in southern Italy.

Whereas detailed studies of single species are often informative, coarse scale information on a wide range of species allows for interesting comparison and the search for general patterns. Rubolini et al. (2007, this issue) analyze a large amount of estimates of change in first arrival dates and mean/median arrival dates collected across Europe in the last 40 yr and look for spatial and taxonomic variation as well as intra-specific consistency. As indicated by the impressive dataset which Rubolini et al. used, there has been a strong

emphasis on the timing of spring migration. Considerably less is known about how climate change has affected autumn migration phenology (Jenni & Kéry 2003). A contribution to the field is given by Péron et al. (2007, this issue), who analyse the timing of post-nuptial migration and stopover strategy in 2 insectivorous passerine species.

The last 2 contributions to this CR Special provide a fresh reminder of the complexity of the problem at hand: to understand and predict the ecological ramifications of climate change. Sparks & Tryjanowski (2007, this issue) study changes in spring arrival dates and how the response to temperature may change over time. In the final paper, Mustin et al. (2007, this issue) use migratory shorebirds as an example and discuss whether predictive models of climate impact at the species level may require ecological details that are difficult to include.

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#### LITERATURE CITED

- Beaumont LJ, McAllan IAW, Hughes L (2006) A matter of timing: changes in the first date of arrival and last date of departure of Australian migratory birds. *Glob Change Biol* 12:1339–1354
- Both C (2007) Comment on 'Rapid advance of spring arrival dates in long-distance migratory birds'. *Science* 315:598b
- Both C, te Marvelde L (2007) Climate change and timing of avian breeding and migration throughout Europe. *Clim Res* 35:93–105
- Both C, Bouwhuis S, Lessels CM, Visser ME (2006) Climate change and population declines in a long-distance migratory bird. *Nature* 441:81–83
- Dunn PO (2004) Breeding dates and reproductive performance. *Adv Ecol Res* 35:69–87
- Gienapp P, Leimu R, Merilä J (2007) Responses to climate change in avian migration time—microevolution versus phenotypic plasticity. *Clim Res* 35:25–35
- Gordo O (2007) Why are bird migration dates shifting? A review of weather and climate effects on avian migratory phenology. *Clim Res* 35:37–58
- Hedenström A, Barta Z, Helm B, Houston AI, McNamara JM, Jonzén N (2007) Migration speed and scheduling of annual events by migrating birds in relation to climate change. *Clim Res* 35:79–91
- Hüppop O, Hüppop K (2003) North Atlantic Oscillation and timing of spring migration in birds. *Proc R Soc Lond B Biol Sci* 270:233–240
- IPCC (2007) *Climate change 2007: impacts, adaptation and vulnerability*. Parry ML, Canziani OF, Palutikof JP, van der Linden PJ, Hanson CE (eds) Contribution of Working Group II to the 4th Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge
- Jenni L, Kéry M (2003) Timing of autumn bird migration

- under climate change: advances in long-distance migrants, delays in short-distance migrants. *Proc R Soc Lond B Biol Sci* 270:1467–1471
- Jonzén N, Lindén A, Ergon T, Knudsen E and others (2006) Rapid advance of spring arrival dates in long-distance migratory birds. *Science* 312:1959–1961
- Jonzén N, Hendenström A, Lundberg P (2007a) Climate change and the optimal arrival of migratory birds. *Proc R Soc Lond B Biol Sci* 274:269–274
- Jonzén N, Lindén A, Ergon T, Knudsen E and others (2007b) Response to comment on 'Rapid advance of spring arrival dates in long-distance migratory birds'. *Science* 315:598c
- Knudsen E, Lindén A, Ergon T, Jonzén N and others (2007) Characterizing bird migration phenology using data from standardized monitoring at bird observatories. *Clim Res* 35:59–77
- Lande R, Engen S, Sæther BE (2003) Stochastic population dynamics in ecology and conservation. Oxford University Press, Oxford
- Lehikoinen E, Sparks TH, Zalakevicius M (2004) Arrival and departure dates. *Adv Ecol Res* 35:1–31
- Marra PP, Hobson KA, Holmes RT (1998) Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science* 282:1884–1886
- Møller AP (2004) Protandry, sexual selection and climate change. *Glob Change Biol* 10:2028–2035
- Møller AP (2007) Tardy females, impatient males: protandry and divergent selection on arrival date in the two sexes of the barn swallow. *Behav Ecol Sociobiol* 61:1311–1319
- Møller AP, Fiedler W, Berthold P (eds) (2004) Birds and climate change. *Adv Ecol Res* 35:1–251
- Mustin K, Sutherland WJ, Gill JA (2007) The complexity of predicting climate-induced ecological impacts. *Clim Res* 35:165–175
- Norris DR, Marra PP (2007) Seasonal interactions, habitat quality, and population dynamics in migratory birds. *Condor* 109:535–547
- Nussey DH, Postma E, Gienapp P, Visser ME (2005) Selection on heritable phenotypic plasticity in a wild bird population. *Science* 310:304–306
- Péron G, Henry PY, Provost P, Dehorter O, Julliard R (2007) Climate changes and post-nuptial migration strategy by two reedbed passerines. *Clim Res* 35:147–157
- Pulido F (2007) Phenotypic changes in spring arrival: evolution, phenotypic plasticity, effects of weather and condition. *Clim Res* 35:5–23
- Rainio K, Tøttrup AP, Lehikoinen E, Coppack T (2007) Effects of climate change on the degree of protandry in migratory songbirds. *Clim Res* 35:107–114
- Rubolini D, Møller AP, Rainio K, Lehikoinen E (2007) Intraspecific consistency and geographic variability in temporal trends of spring migration phenology among European bird species. *Clim Res* 35:135–146
- Saino N, Szép T, Romano M, Rubolini D, Spina F, Møller AP (2004) Ecological conditions during winter predict arrival date at the breeding quarters in a trans-Saharan migratory bird. *Ecol Lett* 7:21–25
- Saino N, Rubolini D, Jonzén N, Ergon T, Montemaggiori A, Stenseth NC, Spina F (2007) Temperature and rainfall anomalies in Africa predict timing of spring migration in trans-Saharan migratory birds. *Clim Res* 35:123–134
- Sparks T, Tryjanowski P (2007) Patterns of spring arrival dates differ in two hirundines. *Clim Res* 35:159–164
- Stenseth NC, Mysterud A, Ottersen G, Hurrell JW, Chan KS, Lima M (2002) Ecological effects of climate fluctuations. *Science* 297:1292–1296
- Studds CE, Marra PP (2007) Linking fluctuations in rainfall to nonbreeding season performance in a long-distance migratory bird, *Setophaga ruticilla*. *Clim Res* 35:115–122
- Tuljapurkar S (1990) Population dynamics in variable environments. Springer-Verlag, Berlin
- Visser ME, Both C (2005) Shifts in phenology due to global climate change: the need for a yardstick. *Proc R Soc Lond B Biol Sci* 272:2561–2569
- Webster MS, Marra PP, Haig SM, Bensch S, Holmes RT (2002) Links between worlds: unraveling migratory connectivity. *Trends Ecol Evol* 17:76–83