Bird Migration and Climate Change

Niclas Jonzén, Torbjørn Ergon, Andreas Lindén and Nils Christian Stenseth

Climate changes expose organisms to novel environmental conditions with the potential to affect the life history and demography of individuals. If they are to stay alive and reproduce, organisms must be able to cope with such environmental changes—not least with (changing) environmental stochasticity. The expression of individual traits in variable environments provides a mechanism that links variable environments and parameters such as survival and reproduction. 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, especially in the timing of migration and breeding. 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 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 general picture emerging shows that, for many species breeding in the northern hemisphere, spring arrival has advanced during the second half of the 20th century and similar patterns have recently been described in Australia. The direction of the observed changes is in agreement with global changes in spring temperature; however, detailed data revealing the underlying mechanisms have rarely been available.

In the recent contribution of Working Group II to the IPCC Fourth Assessment Report, 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 few 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 in which birds can adapt 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.

A special issue of *Climate Research*, on Bird Migration and Climate Change (Vol. 35, No. 1-2) 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. To begin with, Pulido 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 migration, and Gienapp et al. 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). Knudsen et al. note that further analysis will require methodological advances, and Hedenström et al. 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 migratory journey. Both & te Marvelde 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. To what extent recent climate change has affected the degree of protandry — earlier arrival at reproductive sites of males relative to females — in migratory songbirds, is discussed by Rainio et al. There is a growing body of literature emphasizing the importance of seasonal interactions, such as the knock-on effects of winter climate on individual performance in the breeding season. Studds & Marra study how the amount and timing of rainfall influence the food abundance and non-breeding performance in the American redstart *Setophaga ruticilla*, a species whose seasonal interactions have previously been demonstrated. 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. 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.

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. analyze a large amount of estimates of change in first arrival dates and mean/median arrival dates collected across Europe in the last 40 years and look for spatial and taxonomic variation as well as intra-specific consistency. As indicated by the impressive dataset which Rubolini et al. build upon, 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. A contribution to the field is given by Péron et al., who analyse the timing of post-nuptial migration and stopover strategy in 2 insectivorous passerine species. The last 2 contributions provide a fresh reminder of the complexity of the problem at hand: to understand and predict the ecological ramifications of climate change. Sparks & Tryjanowski study changes in spring arrival dates and how the response to temperature may change over time. In the final paper, Mustin et al. 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.

The temporal shifts in migratory phenology have already been well described, at least for spring arrival in Europe and North America, and now is the time to delve into the underlying mechanisms. Before doing that, let us have a closer look at the (rather) general patterns described so far. Rubolini et al. analysed data from both passerines and non-passerines. Overall there were rapid advances in arrival date, especially for first arrival dates in species spending the winter in Europe. The most important finding reported by Rubolini et al. was that change in spring arrival date shows a significant degree of intraspecific consistency, and can thus be regarded as a species-specific trait. In other words, different populations of the same species respond consistently, which motivates comparative analyses of interspecific differences.

The general findings reported above are complicated by the fact that there is considerable spatial variation in the observed changes in arrival time, which is true also for changes in the timing of breeding. Geographic variation is however expected, considering the spatio-temporal variation in climate change, which generates spatial variation in selection pressures and different possibilities for plastic responses depending on the time and route of migration.

If we increase the resolution and go beyond the arrival patterns based on the mean response of a population, one could think of different segments of a population responding differently to climate change. For instance, males and females often migrate during different times of the season and may also use different habitats during winter. Furthermore, there are different selection pressures for arrival time in males and females. Increased spring temperatures could increase pre-breeding survival rate, thereby making it possible for early arriving males competing for territories to arrive even earlier. However, Rainio et al. found a parallel rather than divergent shift in the timing of male and female migration in 4 songbird species detected at 5 European bird observatories. Clearly, we need more studies before we can say anything definitive about differences in how males and females respond to climate change.

Until quite recently there seemed to be a common view that species spending the winter in Europe (often referred to as short-distance migrants) are more likely than long-distance migrants to vary migration timing in response to climate change simply because they are exposed to the warming in Europe all year round. The long-distance migrants, on the other hand, are only affected by warming while migrating through Europe, and any advancement to central or northern Europe can be explained by improved environmental conditions en route. Therefore, the adaptation of breeding time to an advancement of optimal conditions may be constrained by the migration strategy in long-distance migrants. We think that it is time to revise some details of that picture.
Though the importance of endogenous control and photoperiod as

a trigger of migratory restlessness is beyond doubt, a growing number of studies point at the importance of interannual variation in winter climate as a predictor of arrival time in the summer quarters. Hence, the timing of migration may be pretty flexible even in long-distance migratory birds, and the detailed studies of the American redstart suggest that not only the speed of migration, but also the departure date can be affected by winter climate through its effect on habitat quality and thus the time needed to prepare for migration.

There are also observations that are not easily explained by a simple phenotypic response. For instance, the earlier arrival of African migrants on Capri cannot be fully explained by the climatic variables investigated so far. It has been suggested that the lack of explanation for the advanced arrival on Capri may be an indication of micro-evolution, but there are potential pitfalls to making premature claims about micro-evolution. Another interesting observation that is not easily attributed to phenotypic plasticity only is the increased response to temperature in SW Europe in the sand martin, *Riparia riparia*, which has resulted in earlier arrival in the UK at the same temperature as before. Again, the data at hand do not allow any formal test of the involvement of any micro-evolutionary processes, but they cannot be excluded either.

One may ask why we still lack conclusive evidence for evolutionary change despite selection for earlier arrival and the presence of genetic variation in the timing of migration, and plausible answers to this critical question are given by Pulido (2007). To some extent it is a data problem. Based on arrival data from bird observatories, we are not in position to differentiate between the relative roles of phenotypic plasticity and evolutionary responses, data do not unambiguously support or refute either of the 2 (not mutually exclusive) hypotheses. Interannual arrival data on individual birds, measured with high precision, would be useful for this purpose. Unfortunately, those kind of data are very scarce. However, there are other reasons why it is inherently difficult to find conclusive evidence for micro-evolution. For instance, to what extent changes in wind directions and speed can explain the earlier arrival of migratory birds is largely unexplored. Furthermore, since the physical condition of birds can affect departure time, we clearly need experimental studies on the wintering grounds to better understand the importance of carry-over effects that may persist over several generations. Hence, we need to appreciate the whole life cycle of events and not only to study spring migration as an isolated phenomenon. In that respect, the timing of autumn migration and how it relates to the timing of spring migration, and the selection pressures involved is, of course, of interest and has not received the attention it deserves.

In conclusion, we are now moving beyond the mere description of patterns and starting to think about the underlying mechanisms. Therefore, it is not surprising that we find ourselves in a situation where the importance of different processes (e.g. phenotypic plasticity and micro-evolution) are being discussed, but no consensus has yet emerged. Theoretical modelling may help us to get a better idea about the selection pressures involved in adapting to climate change and to know what to expect. However, as several of the contributed papers have pointed out, what we also need are more individual-based data and clever experiments to reveal the relative importance of the range of processes affecting how climate change shapes the timing of biological events, and consequently, the distribution and abundance of organisms.

This article is a summary of a series of scholarly articles published under the *Climate Research* Special 'Bird Migration and Climate Change' (open access).

Originally published as:

(Eds.) Niclas Jonzén, Torbjørn Ergon, Andreas Lindén, Nils Christian Stenseth. 2007. Bird Migration and Climate Change. *Climate Research*, Vol. 35, No. 1-2.

Niclas Jonzén is an Associate Professor at the Department of Theoretical Ecology, Lund University, 22362 Lund, Sweden (Niclas.Jonzen@teorekol.lu.se).

Torbjørn Ergon is a Researcher and Post-Doctoral Research Fellow at the Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biology, University of Oslo, Norway (torbjorn.ergon@bio.uio.no).

Andreas Lindén is at the Department of Biological and Environmental Sciences, Integrative Ecology Unit, Helsinki University, Finland (andreas.linden@helsinki.fi).

Nils Christian Stenseth is a Professor at the Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biology, University of Oslo, Norway (n.c.stenseth@bio.uio.no).

A New Conservation and Development Frontier: Community Protected Areas in Oaxaca, Mexico

David B. Bray, Elvira Duran, Salvador Anta, Gary J. Martin and Fernando Mondragón

Most protected areas in the world are inhabited by people. Recent figures suggest that around 11.5% of the global terrestrial area is under some form of protection but about 90% of these protected areas are in IUCN categories III-VI that allow degrees of human presence and use. In addition, some 11% of forests globally have been devolved to local communities to varying degrees by governments. Thus, the vast majority of protected areas in the world have human presence in them, although frequently with unclear rights to forests and their products when they are present.

Photo: David Barton Bray

Mexico is at the forefront of countries where local communities have direct ownership rights of their forests, with an estimated 56-80% of national forests directly owned by communities, within which extraction activities are regulated by Mexican environmental law. This process of devolution occurred as a result of a sweeping agrarian reform that took place through most of the 20th century. One outcome of this devolution has been that Mexican forest communities have gained decades of experience in managing their forests for the commercial production of timber. A recent study suggested that an estimated 2300 communities have commercial logging permits with varying degrees of vertical integration and sustainable forest management.

However, not all Mexican forest communities have commercially valuable forests and others have forest areas that are mostly inaccessible. Further, the dominance of community ownership of rural lands means that there are few opportunities for expansion of Mexico's public protected areas that do not conflict with pre-existing community ownership. These realities have led some communities to become pioneers in taking advantage of a new policy opening from the Mexican government, the possibility of officially recognized protected areas on community owned lands. According to government figures, 34 community protected areas have been recognized by the National Commission of Natural Protected Areas (CONANP) since 2003. Of these 34, 13 are in indigenous communities, and 12 of these 13 are in the state of Oaxaca, with several clustered in the Sierra Norte region. Further, a recent study by one of the co-authors and his colleagues found that Oaxacan communities are, in addition, informally protecting 236 'voluntary conservation areas' (an area of about 240,000 ha). The authors, in