



Bird migration and climate: the general picture and beyond

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As succinctly stated by Gordo (2007, this issue), the temporal shifts in migratory phenology have already been well described (Lehikoinen et al. 2004, Gienapp et al. 2007, this issue, Rubolini et al. 2007, this issue), 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. (2007) analysed available estimates of change in first arrival dates and mean/median arrival dates collected across Europe in the last 40 yr and looked for spatial and taxonomic variation, as well as intraspecific consistency. Importantly they 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. (2007) 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 (Both & te Marvelde 2007, this issue). Geographic variation is however expected, considering the spatio-temporal variation in climate change (Klein Tank et al. 2002), 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 pop-

ulation, 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 (Studds & Marra 2007, this issue). Furthermore, there are different selection pressures for arrival time in males and females (Møller 2004, 2007). Increased spring temperatures could increase pre-breeding survival rate, thereby making it possible for early arriving males competing for territories to arrive even earlier. Therefore, climate change may lead to increased time lag between male and female arrival, which is exactly what was found in a Danish barn swallow *Hirundo rustica* population (Møller 2004). However, in this issue Rainio et al. (2007) 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. Hence, we simply need more studies on how males and females respond to climate change.

Phenotypic plasticity, micro-evolution or what?

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 (Lehikoinen et al. 2004). 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 (e.g. Hüppop

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& Winkel 2006). Therefore, the adaptation of breeding time to an advancement of optimal conditions may be constrained by the migration strategy in long-distance migrants (Both & Visser 2001). 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 (e.g. Berthold 1996, Gwinner 1996), there is a growing number of studies pointing at the importance of interannual variation in winter climate as a predictor of arrival time in the summer quarters (e.g. Cotton 2003, Saino et al. 2004, 2007, this issue, Marra et al. 2005, Gordo 2007). Hence, the timing of migration may be quite flexible even in long-distance migratory birds, and the detailed studies of the American redstart *Setophaga ruticilla* 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 (Marra et al. 1998, Studds & Marra 2007).

There are also observations that are not easily explained by a simple phenotypic response. For instance, the earlier arrival of African migrants on Capri (Jonzén et al. 2006) cannot be fully explained by the climatic variables investigated so far (Saino et al. 2007). It has been suggested that the lack of explanation for the advanced arrival on Capri may be an indication of micro-evolution (Jonzén et al. 2006, 2007b), but there are potential pitfalls to make any claims about micro-evolution premature (Both 2007). 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 (Sparks & Tryjanowski 2007, this issue). Again, the data at hand do not allow any formal test of the involvement of any micro-evolutionary processes (Møller & Merilä 2004), 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, this issue). 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 two (not mutually exclusive) hypotheses (Gienapp et al. 2007). Interannual arrival data on individual birds, measured with high precision, would be useful for this purpose. Unfortunately, that kind of data is 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 (but see Sinelschikova et al. 2007). Furthermore, since the physical condition of birds can affect departure time, we clearly need experimental studies on the wintering grounds (Studds & Marra 2007) to better understand the importance of carry-over effects that may persist over several generations (Pulido 2007). Hence, we need to appreciate the whole life cycle of events and not only to study spring migration as an isolated phenomenon (Coppack & Both 2002, Hedenström et al. 2007, this issue). In that respect the timing of autumn migration and how it relates to the timing of spring migration (Péron et al. 2007, this issue), and the selection pressures involved, is of course of interest and has not received the attention it deserves.

On theory, statistics and the need for detailed data

It should now be clear that an impressive body of work exists demonstrating how avian phenology patterns—especially spring arrival time in temperate areas—have changed over the last decades. Though potentially important also for demography and population change, without any theoretical guidance these patterns cannot be interpreted and the ecological consequences remain elusive. We must start asking questions such as: If increased spring temperatures have caused an advance of the food peak date by x days, what would be the optimal shift in spring arrival time? As a first approximation it may be tempting to assume a 1:1 relationship (Visser & Both 2005), but adding opposing selection pressures (e.g. higher mortality risk early in season) would give a different answer (Jonzén et al. 2007a).

An appealing theoretical framework for interpretation of the patterns we find and predicting what to look for in the future is given by so-called annual routine models, a general approach for studying the optimal scheduling of events in a seasonal environment (Houston & McNamara 1999, McNamara & Houston 2007). The annual routine models are based on state-dependent reproductive values and, by incorporating the whole annual cycle, explicitly incorporate carry-over effects from previous seasons (Studds & Marra 2007). These models are just starting to be used in the context of climate change and the timing of biological events such as migration and breeding. The models provide testable predictions based on a sound treatment of the complex life cycles of migratory birds (Hedenström et al. 2007).

Testing any predictions of expected shifts in the timing of events requires that we can estimate the sea-

sonal distribution of that event (e.g. migration), which is not always straightforward. The data at hand are often collected for other purposes, and even long-term, standardized monitoring data from bird observatories may require special handling (Knudsen et al. 2007, this issue). Bird observatory data are typically characterized by weather-dependent, day-to-day variation that does not only reflect migration, but also the actual probability of trapping. Sample quantiles may be largely influenced by a few days of trapping because of this strong day-to-day variation. Furthermore, weather tends to affect trapping numbers of different species similarly, thereby violating any assumptions about independent observations of species on a given day (Knape et al. 2008).

These complexities, not to mention missing days and truncated seasons, call for robust approaches to the modelling of the seasonal distribution and its change. Some options are reviewed by Knudsen et al. (2007). In particular, they discuss fitting of parametric functions and smoothing methods as alternative ways for modelling the seasonal distribution of phenological events. Some of the suggested modelling approaches are difficult to handle in a frequentist setting. One option is to use Markov chain Monte-Carlo (MCMC) methods and Bayesian inference (Gilks et al. 1996). This is a flexible approach gaining in popularity in the most quantitative branches of ecology (Meyer & Millar 1999, Link et al. 2002, Clark & Gelfand 2006) and has recently been used to estimate spring arrival time in passerine birds (Jonzén et al. 2006, Saino et al. 2007). Until recently, ecologists had to select models on the basis of statistical rather than ecological considerations. This is no longer the case. When MCMC, having its origin in statistical physics, penetrated mainstream statistics in the early 1990s, it resulted in a 'model liberation movement' (Gilks et al. 1996). Not only can rather complex-structured population models be fitted to a given dataset, but also qualitatively different data sources (e.g. a time series of population density, mark-recapture data, breeding success data, etc.) can be brought together within the same statistical framework. Not surprisingly, we think this approach might be a fruitful avenue for making maximum use of available data and incorporating uncertainty and ecological complexity in a more appropriate way than what has been done in the past.

Based on the majority of the contributed papers and the discussion above, one may think that the shifted timing of biological events is the only ecological effect of climate change. However, some of the most striking patterns are species-range shifts in parallel with climate change (reviewed by Parmesan 2006). The current approach for predicting range shifts is to use so-called climate-envelope models (e.g. Pearson & Dawson

2003) that connect current species distributions to climatic variables and predict future distributions based on climate change models and the estimated relationship between species occurrence and the climatic factors. The last contribution in this issue (Mustin et al. 2007) questions the usefulness of climate-envelope models for individual species, especially when non-climatic factors such as socio-economic factors and policy responses are important for the habitat quality and habitat dynamics. Mustin et al. (2007) further argue that such details are unfortunately difficult to include in predictive models of species distribution under climate change, thereby casting some doubt on what we can really achieve. The importance of the problem should, however, provide enough motivation for future work in this area.

In conclusion, we are now—as this CR Special shows—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 microevolution) 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 is 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.

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