Challenging claims in the study of migratory birds and climate change
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APPENDIX S3. THEORY FOR STUDYING BIRD MIGRATION AND CLIMATE CHANGE

The timing of migration, or arrival date at a given place, is affected by (1) departure time, (2) migration distance and (3) migration speed. The timing of migration can be treated as a classical life-history problem to be solved using optimization. To predict potential climate-induced shifts in the timing of bird migration, it is necessary to understand the factors and trade-offs involved in determining migration timing. Literature on the optimal timing of life-history events includes both general theory (Roff, 1983; Williams & Nichols, 1984; Iwasa & Levin, 1995) and theory geared towards bird migration (Hedenström et al., 2007; Jonzén, Hedenström & Lundberg, 2007).

In contrast to most current studies, a theoretically sound approach should not consider the timing of migration separately from other life-history events in the annual cycle that may influence the predicted timing of migration. Changing migration patterns involve coupling between seasonal events that might considerably affect the general patterns. Typical factors that can affect the optimal timing of migration in birds are establishment of territory, mating, reproduction and moult, each of which have their own constraints and optimal timing, depending on climate (McNamara, Welham & Houston, 1998; Hedenström et al., 2007; Jonzén et al., 2007). These are factors that are highly dependent on the life history of the species in focus. In observational studies, we recommend simultaneous comparison of the timing of several important events in the annual cycle and the timing between them. Annual routine models (McNamara & Houston, 1996) provide a theoretical framework where seasonal interactions (Norris & Marra, 2007) can be incorporated, as well as seasonally fluctuating selection pressures. In these models, state-dependent reproductive values are...
modelled and a fitness measure is maximised by finding the combined optimal scheduling of important biological events (McNamara et al., 1998; Barta et al., 2008).

Some theory has been put forward on the issue of migration speed. In optimal migration theory it is assumed that an individual optimizes its performance with respect to one or several currencies (e.g. energy, time or survival). Often, natural selection is assumed to select for high migration speed and, given a continuous distribution of resources in space, the overall migration speed can be expressed as a function of flight speed, gross rate of energy accumulation at stopovers, the rate of energy consumption when at stopovers, and the rate of energy expenditure during flight. Potential effects of climate change on the timing of migration can be addressed by considering how these factors may be affected by climate change (Hedenström et al., 2007). Similarly, it is possible to formulate a simple analytical expression for the instantaneous migration speed when resources occur at discrete points in space (Alerstam & Hedenström, 1998). Climate change may for instance affect the space-time patterns of resources available, which would affect the daily rate of fuel accumulation, and lead to changes in the use of staging areas (Houston, 1998) and hence the arrival date observed along the migration route (Hedenström et al., 2007).

REFERENCES


