biology
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*Biol. Lett.* 2009 **5**, 433-435 first published online 22 May 2009
doi: 10.1098/rsbl.2009.0324

biology letters
Animal behaviour

*Biol. Lett.* (2009) **5**, 433–435
doi:10.1098/rsbl.2009.0324
*Published online* 22 May 2009

*Meeting report*

# Animal migration: linking models and data beyond taxonomic limits

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**An international workshop on animal migration was held at the Lorentz Center in Leiden, The Netherlands, 2–6 March 2009, bringing together leading theoreticians and empiricists from the major migratory taxa, aiming at the identification of cutting-edge questions in migration research that cross taxonomic borders.**

**Keywords:** evolution of migration; migration strategies; currencies of migration; predictability; tracking of migrants; graphical user interface migration models

## 1. BACKGROUND

Migration is a widespread phenomenon in the animal kingdom. During the last decades, a huge amount of empirical data have been collected to map migratory routes, to describe patterns of migration, e.g. speed and timing, use of stopover sites, and to characterize individual variation in migratory strategies. Parallel to the empirical developments, a considerable body of theory of migration has been formed. Tractable analytical models are used to derive optimal decisions on a single journey (Alerstam & Lindström 1990). Complex models of single journeys, based on dynamic programming, can investigate the effects of stochasticity in foraging or flight conditions (e.g. Bauer *et al.* 2008). More advanced models study the placement of migration in the annual cycle (McNamara *et al.* 1998; Barta *et al.* 2008).

Despite these empirical and theoretical advancements, our ability to predict the migratory movements of animals is still limited. Yet, a thorough understanding of its patterns and processes is of increasing importance, both for anthropogenic interests such as aeronautical safety, the spread of infectious diseases, pests and invasive species, as well as for the conservation of the migrants themselves. The latter is of particular concern as migrants typically rely on multiple, diverse areas throughout their annual or life-stage cycles. Habitat destruction and changing climates pose serious threats to migratory species as they result not only in the loss of habitat but a concomitant increase in distance between suitable sites, or a mismatch in timing between food sources at distant locations (Wilcove & Wikelski 2008). Models that investigate the causes, consequences, determinants and evolution of migratory behaviour may significantly enhance our understanding of animal movement, which is of fundamental importance to any conservation effort.

However, we believe that progress in migration research is hampered by the limited integration of theoretical and empirical efforts within this field and the apparent lack of awareness of such integrative efforts in other taxa. This set the background and motivation for the workshop 'Animal Migration—Linking Models and Data' at the Lorentz Center in Leiden, The Netherlands (an international centre for workshops in the sciences www.lorentzcenter.nl), which aimed at bringing together leaders in the field of theoretical and empirical approaches to migration. Emphasis was on interactions rather than presentations, with only eight major talks during this one-week meeting. The meeting started with a classification of the various modelling approaches used in migration research, showing an overwhelming taxonomic bias, with most theoretical studies conducted in birds and fishes while the other groups have been largely neglected (figure 1).

The keynote lectures covered both the general characteristics of migration in the major migratory taxa, i.e. zooplankton (e.g. Varpe *et al.* 2009), insects (e.g. Wikelski *et al.* 2006; Chapman *et al.* 2008), fishes (e.g. Fiksen *et al.* 2007; Jørgensen *et al.* 2008), turtles (e.g. Hays *et al.* 2006; Houghton *et al.* 2006) and birds (e.g. Åkesson & Hedenström 2007; Ramenofsky & Wingfield 2007), but also the important theoretical approaches to migration such as simple analytical models (Alerstam & Lindström 1990; Alexander 2002), dynamic optimization models (Houston & McNamara 1999), individual-based models (Pettifor *et al.* 2000) and models based on evolutionary methods (genetic algorithm, neural networks, e.g. Huse *et al.* 1999).

## 2. WORKGROUP DISCUSSIONS

During the meeting, considerable time was dedicated to discussing possible generalizations across taxa and ways to integrate empirical and modelling efforts.

### (a) *The evolution of migration*

In the past, many ideas have been put forward on why animals migrate. But would it be possible, with the current advanced modelling techniques, to identify the key parameters predicting an organism's optimal strategy in the face of environmental variability (i.e. stay, migrate or go dormant) and the precise strategy chosen once it decides to migrate? In this respect, the work of Alexander (2002), who addressed range limitations of migrants using simple allometric relationships for costs of transport and resting metabolic rate, was highlighted as one of the few existing examples providing an analytical analysis on the physical constraints migrants of varying size and mode of transport face. Similarly, but limited to birds, Hedenström & Alerstam (1995) used the relationship between flight

*Received* 21 April 2009
*Accepted* 1 May 2009

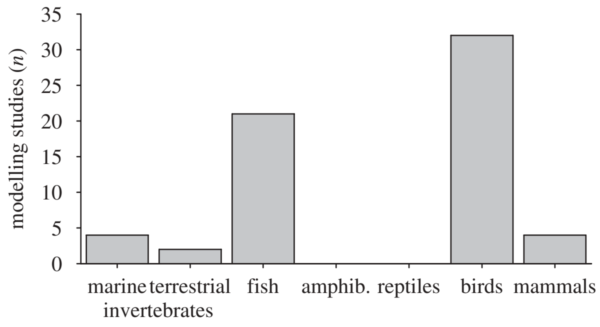


Figure 1. Results of a literature search in the Web of Science (Thomson Reuters) for migration models using the keywords 'migrat*' and 'model*'. We followed the definition of migration by Dingle (1996) and included only those theoretical studies dealing explicitly with seasonal or life-stage coupled migratory behaviour. This yielded more than 70 core publications with an enormous bias—models for birds and fish were most frequent, but invertebrates, amphibians, reptiles and mammals were heavily underrepresented in theoretical studies. Although this list of publications is probably non-exhaustive, the analysis most likely correctly identifies the taxonomic bias.

costs and airspeed to calculate a range of optimal flight speeds depending on a bird's behavioural aims, i.e. minimizing flight costs and minimizing migration time. This analysis might easily be extended to include a range of other flying, but also running and swimming, migrants. Consensus existed that it would be possible to use other analytical models and simulations to address many more ecological issues pertaining to the evolution of migration across taxa. For instance, a rather simple annual routine model might sketch the trade-off between migration and breeding, thus predicting how spatio-temporal variation in environmental conditions determines when and where reproduction occurs. Using allometric scaling similar to that of Alexander (2002), different ways of locomotion could also be investigated within this framework.

### (b) *Variation in migration strategies*

Variation in migration strategies could be explained by assuming suboptimal behaviour as well as the existence of individual optima resulting from individual (i.e. genetic and phenotypic) and environmental variation. Given the various modelling techniques that allow for incorporating individual characteristics (e.g. individual-based models, stochastic dynamic models, models based on evolutionary methods) but also the technological advancements in tracking individual animals, this is a field where major advances can be made in the near future, helping to elucidate what accounts for the variation in migration strategies and what is the ecological significance of this variation.

### (c) *Currencies of migration*

Another major issue is related to the use of 'surrogate' (or short-term) currencies in optimal migration studies. Ultimately, migratory behaviour is shaped by natural selection but evaluating migratory behaviour in terms of fitness, via e.g. dynamic programming, yields complex decision matrices that cannot easily be interpreted in terms of simple decision rules, e.g. minimizing the time spent or energy used on migration, or maximizing safety during migration. At the very least, surrogate currencies are an important heuristic tool in testing theories of optimal migration but perhaps they might be linked to the actual decision-making process of animals during migration. So far, surrogate currencies have mostly been considered in isolation and to our knowledge, only two models analytically find the optimal compromise between several currencies: Houston (1998) combined speed of migration, predation risk and arrival time, and Vrugt *et al.* (2007) used Pareto front analysis to find out whether migrating passerines minimize the time spent migrating, or the rate of energy expenditure, or behave according to a compromise. It was suggested at the meeting that dynamic programming techniques could investigate combinations of currencies and hence provide the Pareto front analysis in various settings. Overall, the Pareto front approach seems a very promising future avenue, especially if empirical research followed suit by experimentally testing what currencies 'real' animals actually optimize.

### (d) *Tracking of migrants*

Many tracking data on migrants are actually available, and given the current technological developments, the volume of data will probably increase rapidly (Rutz & Hays 2009). Nevertheless, only a handful of tracking and radar studies seem to make it into the literature and very few of these explicitly test hypotheses and model predictions (e.g. timing and speed of migration, mechanisms of orientation, migratory route and site use, decision rules). Therefore, a comparative analysis was launched comparing the ways in which migrants across taxa and size ranges, modes of locomotion and media, deal with drift.

### (e) *Predictability during migration*

The knowledge factor is a tricky aspect in many modelling studies and is often included in its extremes only, i.e. either the fact that migrants have information is ignored or the migrants' knowledge of their environment is assumed to be perfect. A migrant would have a major advantage if it had information about the potential conditions at stopover and destination sites. Environmental factors are, to some extent, spatially and temporally auto-correlated. However, the degree of auto-correlation of environmental cues in the context of migration has rarely been studied (but see Saino & Ambrosini 2008), and never in a systematic way. Notably, within the context of climate change, whether migrants are able to predict future and distant environmental conditions and which local information they use for these predictions are crucial. A call was therefore made to determine where space–time continuums are broken and use this information to make regional, seasonal and perhaps evolutionary predictions as well as potential responses to climate change scenarios. A detailed study on how predictability shapes optimal annual routines/life histories can also shed light on which species are *a priori* more vulnerable to climate change—those adapted to predictable or those adapted to more stochastic environments.

### (f) *Graphical-user-interface modelling frameworks*

Finally, it was realized that several modelling frameworks exist for animal migration, which could be made available to a wider community. Specifically, annual routine models (McNamara *et al.* 1998) and stochastic dynamic programming 'skeleton' models (Weber *et al.* 1998) are already available that allow for investigating a wide range of issues in migration ecology. It was therefore suggested that, possibly after increasing user-friendliness by, e.g., adding a graphical user interface, and flexibility of these models by building in options for additional internal state variables (e.g. immuno-competence, physiological flexibility, information status), such models should be made readily available and introduced during workshops (e.g. summer schools).

Please see http://www.lorentzcenter.nl/lc/web/2009/338/info.php3?wsid=338 for more information on the workshop. We thank all participants for inspiring discussions and the staff of the Lorentz Center, in particular G. Filippo, M. Kruk and H. Jensenius, for invaluable organizational support. The workshop received financial support by the Lorentz Center and the Netherlands Organisation for Scientific Research (NWO-grant 816.01.007 to S.B.). This is publication 4547 of the Netherlands Institute of Ecology (NIOO-KNAW).

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