



ANIMAL MOVEMENT ACROSS SCALES



Edited by Lars-Anders Hansson and Susanne Åkesson

Animal Movement Across Scales

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Preface

The evolution of a book

Animal movement has been a core research field at the Department of Biology at Lund University for decades, although studies of different taxa have traditionally been performed at different departments, using different approaches. When we received a joint, long-term Linnaeus grant from the Swedish Research Council (Vetenskapsrådet) in 2008, we decided to not only continue our individual research paths, but also aim at opening up a broader avenue by utilizing our different scientific and technical approaches, taxa, and research networks. In so doing we decided that a book would be a suitable way to synthesize, but also give our own view of, the scientific field of animal movement. Our first step was to open up for suggestions of interesting chapters and twelve of us volunteered as lead authors, and we then met at a 3-day workshop where the outline of each chapter was discussed. After the inspiring workshop, the lead authors invited co-authors for their specific chapters and an almost twelve-month writing process was initiated. A major aim with this book project has also been to involve younger researchers in the writing and discussion process; a strategy that turned out to be very successful. Following the writing process, each chapter was sent out for international review and based on those comments the final version of each chapter was submitted. Then all interested lead authors were engaged in providing input to the synthesis chapter (Chapter 14), which not only constitutes the end of the book you now hold in your hand, but also of our scientific process of synthesizing the research field of animal movement. The evolutionary process of producing this book has been very creative and inspiring for us and we hope that you as a reader will

find it useful and stimulating for your own studies and understanding of the fascinating field of animal movement across all scales! In order to guide you through the book we will below give some hints which may assist you as a reader.

To you as reader

During the writing process we decided that the target audience should be advanced undergraduate and graduate students, but a major aim has also been to provide an accessible and updated research-level text for professional researchers on animal movement, as well as established researchers from other fields entering the diverse area of animal movement. Moreover, we also wanted interested laymen to find the book engaging. In order to reach these categories of readers the chapters are written and edited in a way that makes the text as appealing and easily accessible as possible with many cross references among the chapters to make it easy to follow up intriguing subjects. To further highlight stimulating and noteworthy subjects, we have used ample illustrations to emphasize important concepts and processes. Moreover, at the end of the book we provide a glossary which hopefully will be useful for you who is new in the field of animal movement. Each chapter constitutes a unit and stands by itself, meaning that some illustrative examples or aspects of movement are taken up and discussed from different viewpoints in several chapters. This may be regarded as repetitive, although we hope you as reader will be indulgent towards this. An overall aim with this book has been to compile novel and interesting findings on movement ecology in order to stimulate and encourage the reader, rather than to provide a complete review

of the research field. We, further, had no ambition to repeat or cover identical fields as other recent and excellent reviews or books (for example Dickinson et al. 2000, Nathan et al. 2008, Milner-Gulland et al. 2011, Clobert et al. 2012; Bauer and Hoyer 2014). Instead this book has emerged through a creative process and thereby mainly reflects subjective cherry-picking by each author of especially absorbing, timely, and enlightening research. We indeed hope that you as a reader will find the subjects raised, and the viewpoints taken, as fascinating as we have found them during the writing process.

Thanks!

Just like animal movements, a book project requires a lot of energy and subsidies and this project would not have been possible without the support through our Linnaeus research platform CAnMove, funded by the Swedish Research Council (Vetenskapsrådet) and Lund University. The Royal Physiographic Society and Stiftelsen Villa San Michele provided much appreciated logistics to L-AH during the editing of the book. All chapters have been reviewed and we would like to warmly thank all reviewers for very professional inputs, which have indeed improved the quality of the book. Since some of the reviewers would like to remain anonymous, reviewer names will not be provided here. Ben B. Chapman made a linguistic check of all chapters and Maria Sol Souza drew most of the illustrations, as well as the beautiful and thought-provoking cover. Anna

Persson made the illustrations to Chapter 4. Emil Assarsson made a very professional job with the layout of the figures. Moreover, Thomas Alerstam has been supervisor or mentor for many of us and his enormous impact within the field of bird migration and navigation is clearly mirrored in the amount of citations of his work in this book. Finally, I would like to thank my wife, Ann-Christin, for fruitful discussions and ideas that would almost merit a co-editorship, and Linn, Sigrid, and Yrsa for being wonderful. The chapters of the book were written during fall 2012 and spring 2013 and edited in Askustorp, Hästveda, Sweden, and Villa San Michele, Capri, Italy, during summer 2013.

L-AH

References

- Bauer, S., and Hoyer, B. J. (2014). Migratory animals couple biodiversity and ecosystem functioning worldwide. *Science*, **344**, 1242552.
- Clobert, J., Baguette, M., Benton, T., and Bullock, J. M. (eds) (2012). *Dispersal Ecology and Evolution*. Oxford University Press, Oxford.
- Dickinson, M. H., Farley, C. T., Full, R. J., Koehl, M. A. R., Kram, R., and Lehman, S. (2000). How animals move: an integrative view. *Science*, **288**, 100–6.
- Milner-Gulland, E. J., Fryxell, J. M., and Sinclair, A. R. E. (eds) (2011). *Animal Migration—A Synthesis*, Oxford University Press, Oxford.
- Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., and Smouse, P. E. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences USA*, **105**, 19052–9.

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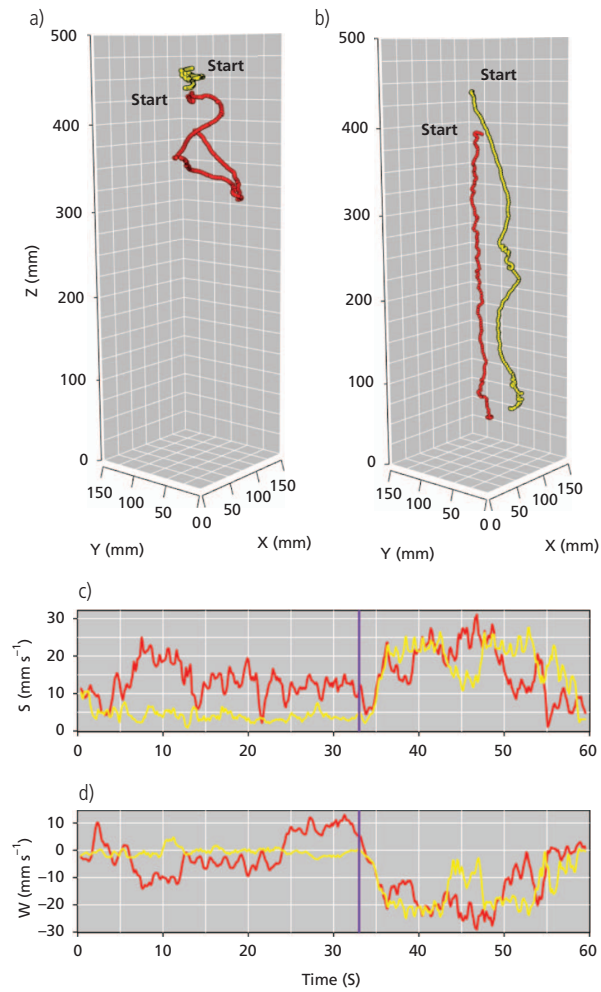


Plate 1 Tracking of the position, speed, and vertical displacement of two *Daphnia magna* individuals in the absence (a) and presence (b) of UV radiation. The animals were marked with yellow and red nanoparticles (quantum dots), and monitored simultaneously to obtain 3D trajectories. Swimming speed (S) for both animals is shown in (c) and vertical speed (w) in (d). From Ekvall et al. (2013). (See Figure 6.5)

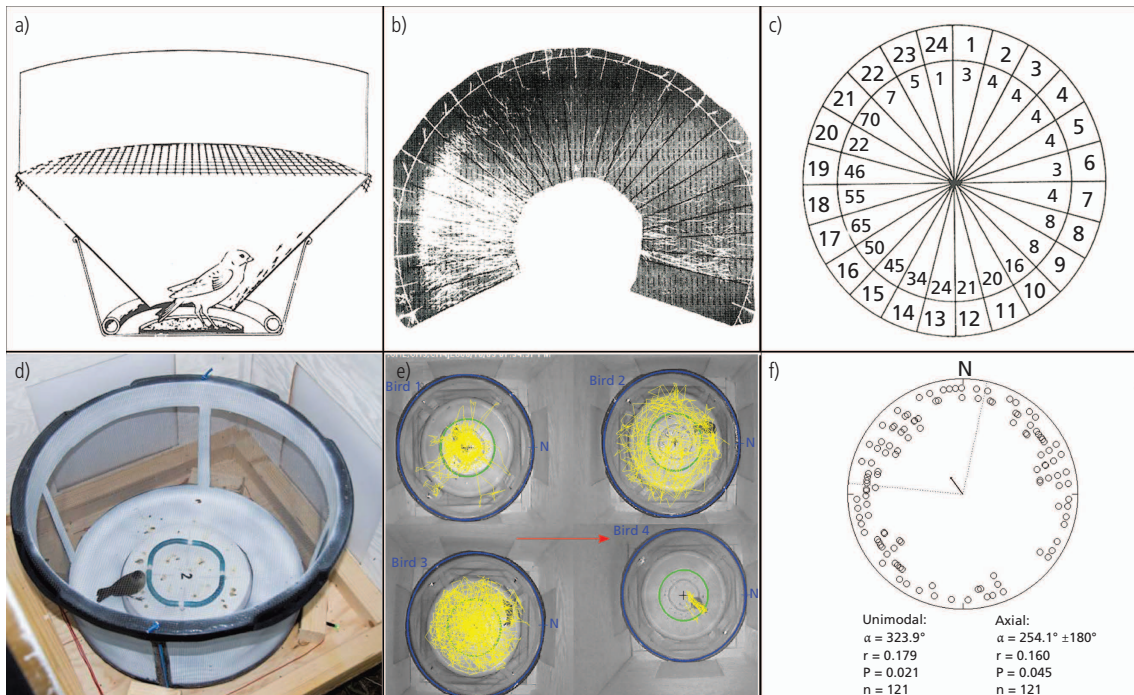


Plate 2 Various types of circular orientation cages have been designed to accurately measure and quantify the orientation preference of caged migratory birds. (a) The original orientation cage was invented by Emlen (Emlen and Emlen 1966) and is referred to as the 'Emlen funnel'. The walls of this funnel-shaped cage were covered with white blotting paper, with an ink pad placed at the bottom of the cage. Thus, a bird that is tested in this experimental setup leaves ink marks on the cage walls whenever trying to fly in a specific direction. (b) This cage design is slightly modified compared to (a), and is typically used as standard method in most orientation studies to date. Here the ink pad is removed, and the walls are covered with typewriter correction paper (e.g. white-out) or thermal paper (Mouritsen et al. 2009) whereon the birds leave scratches whenever touching the cage wall. Shown in the picture is the line-out scratch-sensitive paper (e.g. white-out or thermal paper) after a 90-min orientation experiment, spread on a light table. (c) A circular diagram divided into 24 sectors (covering 15° of the circle) showing the distribution of scratches, hand-counted on the paper shown in (b). (d) More recently, video tracking has been introduced in orientation research. Here, the movements of the birds in cages or funnels are filmed from above or below. Tracking software allows tracking the position of the bird throughout the experiment, and analysing its orientation direction. (e) Digitized orientation data of a 10-min movie interval of a bird filmed in a cage as shown in (d). (f) Orientation of the data shown in (e). Each hop of the bird from the centre (inside of the green inner circle) out to the periphery of the cage and back into the centre again counts as one data point; the position farthest away from the centre is taken as the direction of the hop (round symbols in diagram f). From all these data points (hops), the mean orientation vector with an angle α and a length r (varies between 0 and 1) is calculated. The length r can be considered as an inverse analogue of the variance (modified after Helbig 1991; Muheim, unpubl.). (See Figure 9.8)



Plate 3 Polarized light as perceived by the human eye, visible as two faint blue and two faint yellow balloons (Haidinger's brushes), aligned perpendicularly, with the blue axis indicating the axis of polarization. (See Figure 10.5)

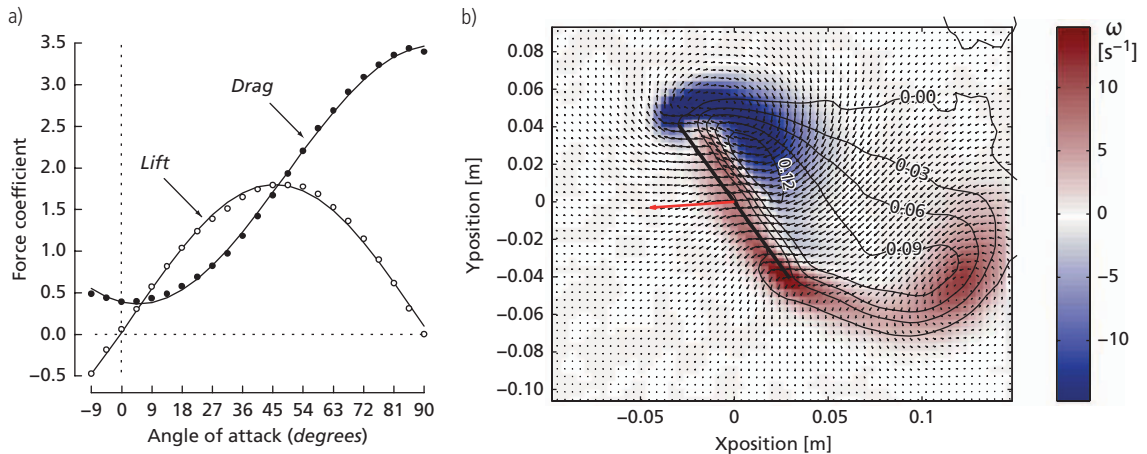


Plate 4 Steady-state lift and drag coefficients for a revolving model fruit fly wing at Reynolds number (Re) ~ 140 . (a) At this low Re , drag forces are relatively high resulting in lift-to-drag ratios ($= 1/COT_{mech}$) larger than 1 only at the angles-of-attack range of 9° – 45° (from Dickinson et al. 1999). Maximum aerodynamic efficiency occurs at post-stall angles-of-attack, (b) for which an attached leading-edge vortex occurs on the revolving wing. From Poelma et al. (2006). Reproduced with permission from Springer Science + Business Media. (See Figure 13.4)

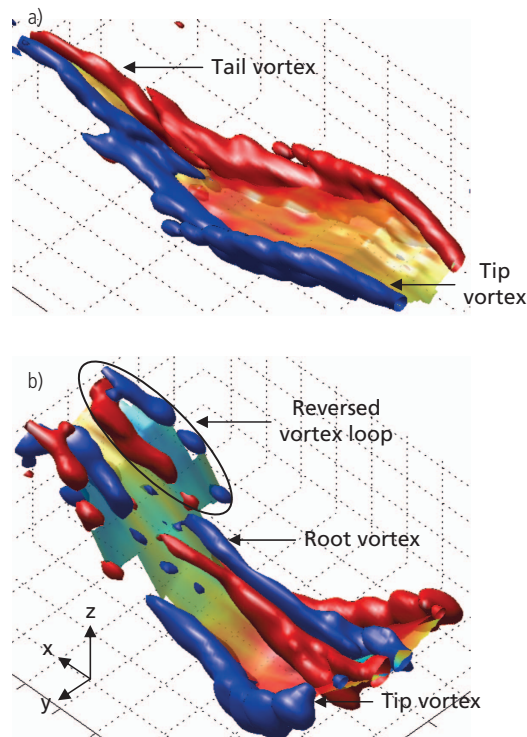


Plate 5 Wake topologies showing the vorticity iso-surfaces of the main vortex structures for one wingbeat of a pied flycatcher, *Ficedula hypoleuca* (a) and a Pallas' long-tongued bat, *Glossophaga soricina*, (b) flying to the left at 7 m/s. The strength of the vortices, measured as circulation, is proportional to the lift generated. The complexity of the wake illustrates how lift is generated by different parts of the animal at different phases of the wingbeat. For example, root vortices seen in the bat wake indicate a lower lift generation by the body than by the wings and the reversed vortex loops generated during the upstroke indicate negative lift being generated. From Muijres et al. (2012b). (See Figure 13.5)

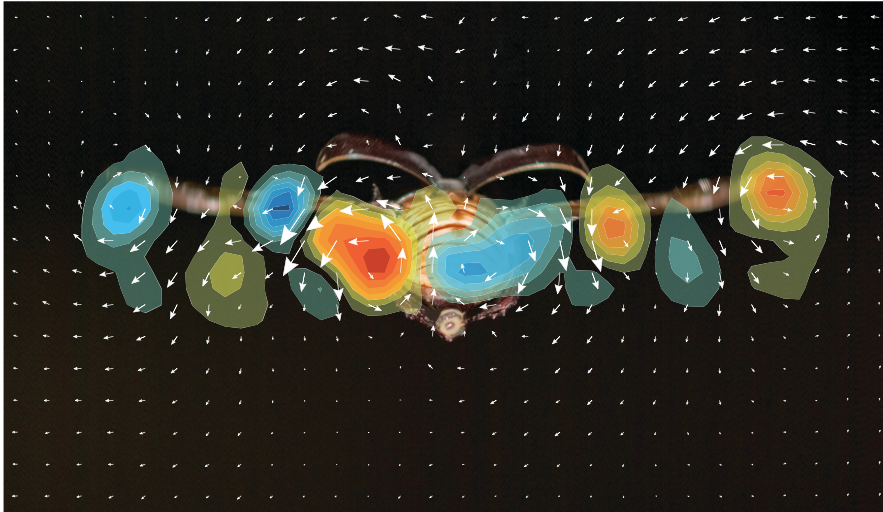


Plate 6 Velocity and vorticity measurements in the wake of a dung beetle during mid-downstroke as seen from behind. The wake contains multiple vortices along the wingspan. Going from the left wingtip to the centre of the body: wing tip vortex, interaction vortex, elytra tip vortex, and body or root vortex. The interaction vortex is the result of a negative interaction between the flow generated by the elytra and the wing, reducing the span efficiency. The strong body/root vortices show that the body does not generate significant lift forces. From Johansson et al. (2012). (See Figure 13.8)

An introduction to animal movement

Lars-Anders Hansson and Susanne Åkesson

All organisms on our planet move at some stage of their life cycle and animal movements on land, in air, and in water are therefore pervading features of animal life. Movements covering just a few, to many thousands of body lengths are performed by a variety of organisms—from the smallest protozoans to the largest whales, and can extend over widely different spatial and temporal scales, from the millimetre to global scale and from seconds to months. Animal movement is also a general feature of our everyday life, since even people living a modern, urban lifestyle cannot avoid seeing amazing examples of animal movement, such as bumblebees finding a flower with a surplus of nectar in a park, mosquitoes efficiently finding blood in our veins, and swifts (*Apus apus*) targeting their nest entrances under rooves with an astonishing precision and speed after an endurance flight lasting several days. Despite all those astounding achievements taking place around us, we rarely give a thought to how these animals manage, and how and why they move. Consider, for example, the never-ending row of ants walking the same path 24 h a day on the wall of the little house in Italy as shown in Fig. 1.1. Irrespective of whether the sun is burning or if it is completely dark, they just continue moving along their invisible track. Obviously they are not using the sun or the Earth's magnetic field to navigate, but rather their track is laid out with odour, allowing all individuals to follow the same, safe way (Fig. 1.1). Apart from a sophisticated odour detection system they also need morphological adaptations for locomotion to be able to walk along the wall without falling down. Hence, even those tiny

organisms have unbelievable adaptations to not only handle chemical information for finding their way, but also to secure attachment and proprioceptors (stretch receptors) to successfully fight physical laws for moving up a wall!

Given such astonishing examples, it is not surprising that animal movement has, throughout our history (Nussbaum 1978), fascinated laymen as well as researchers. Similarly, it is not surprising that research on animal movement ecology is now entering a new era with the development of novel molecular, electronic, and other technical methods, which allows analysis of the movements of individual animals in the context of the complex variety of ecological trade-offs that determine the evolution of movement habits. In this book we aim at addressing how and why animals move and in what ways they differ in their locomotion and navigation performance. Our ambition is that the book will provide considerable synergistic connections both between studies performed on different taxa and between different spatial and temporal scales. Throughout the book we suggest that optimization is a useful approach for understanding the evolution of movement patterns among different animals, as well as their travelling performance, movement strategies, and paths followed. Taking foraging movements and dispersal into account as well as migration (see Box 1.1) is crucial for a detailed understanding of the spatial scale of adaptation, and also for analysing the consequences of movement at the population and community level, in the context of landscape and climate change as regarding the spread of invasive species.

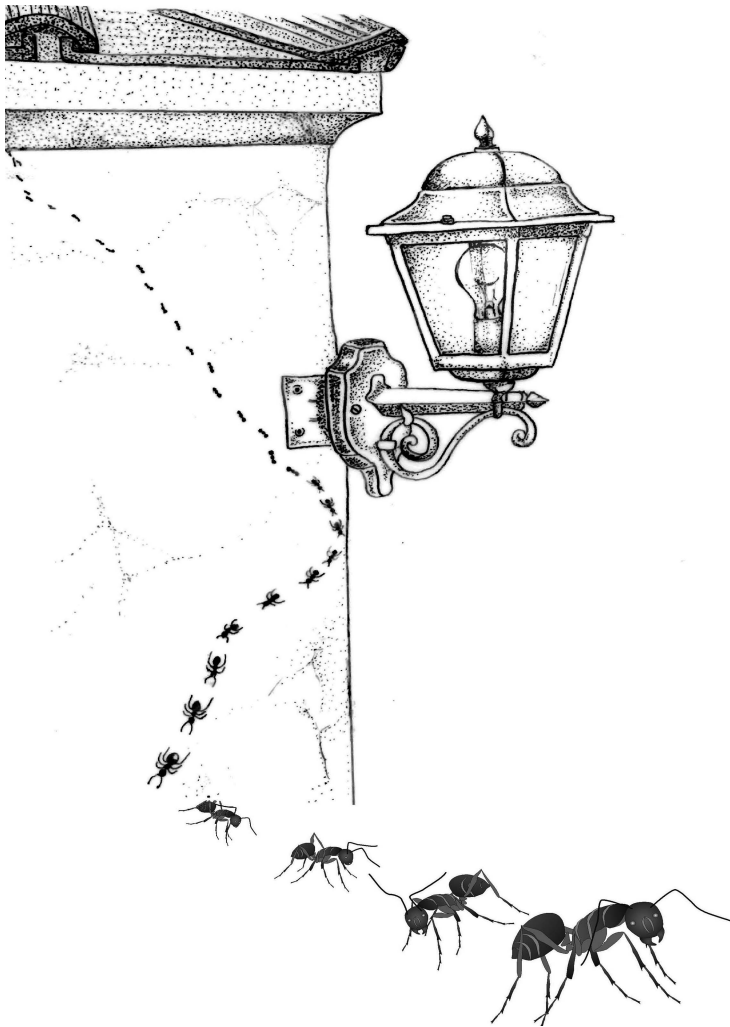


Figure 1.1 Ants on a wall in southern Italy are an illustrative example of locomotion on vertical surfaces, endurance movements, and the use of chemical senses in navigation. Artwork by Maria Sol Souza.

1.1 To move or not to move

To minimize energy expenditure, and thereby optimize its performance, an organism might reduce its movement, which is the case in, for example, terrestrial plants and also many marine invertebrates. Although the seeds or progeny can be highly mobile, adult stages of plants and sedentary animals generally live their lives at the place where they are born or settled and make the best of that situation by using nutrients available in the soil where they stand, and fighting enemies and grazers without moving from that site. Actually, by just considering

trees, for example those beech trees, *Fagus* sp., that have been standing for more than 70 years outside the window of the room where this text is being written without moving at all, an immobile strategy seems rather successful. In contrast, the pied flycatcher, *Ficedula hypoleuca*, is constantly moving while vigorously defending his nestbox hanging in the closest beech tree, simultaneously singing and catching mosquitoes. On the other hand, the lake we can glimpse between the beech trees contains cyanobacteria (or blue-green algae, as they are also called), which are evolutionarily older than most other life on Earth, but are, just as the pied

Box 1.1 Movement terminology

The reasons for animal movements differ widely, from daily foraging movements to long distance migrations or dispersals over unknown lands and waters. In order to set the frame for the chapters in this book, we have used the following very broad definitions:

Movement. Individuals or populations (or parts of populations) that change position at any temporal or spatial scale. Movement includes all other ways of displacement.

Dispersal. Individuals or populations (or parts of populations) that move to reach new areas, but do not return.

Migration. What constitutes animal migration is a matter of some debate, with many definitions in the literature (Baker 1978, Dingle and Drake 2007, Brönmark et al. 2014). We have here used the following, rather broad, definition: Individuals or populations (or parts of populations) that move between two well-defined habitats on a temporally (reasonably) predictable basis. Migration includes, e.g., the seasonal migrations of birds between wintering and reproduction areas, fish migrations from lakes to streams (see Chapman et al., Chapter 2), but also the once-a-lifetime migration of eels

from freshwaters to their natal marine habitat to spawn and then die (Aarestrup et al. 2009).

Homing. Refers to when an animal returns to a known goal, e.g. its home.

Foraging movements. Individuals that move between resting places, nest sites, etc., and feeding grounds in a temporally reasonably predictable way, e.g. bees moving from flower fields to the hive or bird parents feeding their nestlings. These types of movements are difficult to distinguish from migration, but generally occur at a shorter time scale. The most striking difficulty when distinguishing between migration and feeding movements is the very well known diel vertical migrations (DVM) of aquatic zooplankton. This type of movements may actually fit better as 'feeding movement' or as diel vertical movements, than as actual 'migration'. However, the term diel vertical migration is so established as a research area that any attempts to re-categorize it would lead to a revolution. Hence, in order to avoid such responses, we will here adopt the traditional view while noting the difficulties with such distinctions.

flycatcher, able to move in order to gather resources. Hence, mobility may not necessarily be a trait that has evolved *from* sedentary living, but instead may be one type of life strategy; that is, sedentary life is not necessarily inferior to being able to move! Actually, based on the number of beech trees compared to pied flycatchers outside the window suggests that the fitness of the sedentary life strategy is by no means worse than the mobile way of living! Hence, we may conclude that sedentary and mobile life strategies are both successful, suggesting that mobility comes with costs in comparison to a sedentary strategy, and vice versa. Such costs of movement include, for example, the machinery behind morphological adaptations for movement, such as legs, wings, and fins, but also knowing where to go, i.e. having sensory equipment to sense resources, threats, or mates. Sedentary organisms can instead spend the energy required for such movements on growth and reproduction.

Although most plants are in their adult stage sedentary or, with respect to aquatic habitats, free-floating

without movement organelles, most animals are able to move as adults. Actually, the earliest invertebrate animals that evolved in the sea more than 500 million years ago appeared as two kinds: those that stayed put and waited for food to come to them, and those who moved to get it. In aquatic systems a sessile way of animal living is generally more fruitful than in terrestrial systems as a result of its three-dimensional food space and currents transporting suitable food-packages for consumption. Hence, not unexpectedly, sessile animal life is more common in aquatic than in terrestrial systems. However, in contrast to the generally sessile life-forms of plants, movement is the norm in the animal kingdom in both terrestrial and aquatic systems. Animals spend a considerable amount of time and energy on movement directed towards resources, such as food, shelter from predation, or sites suitable for reproduction. If these resources are of higher quality and more easily available elsewhere at certain times of the year or day, movement, dispersal, or regular migrations might be favoured by natural selection.

1.2 Overview of the book

In order to facilitate reading, the chapters of this book are separated into three major sections: In the first, which we have called ‘Large-Scale Patterns of Movement’, we address temporal and spatial patterns of movement at different scales, as well as how these might change in the future. Within the four chapters constituting the section ‘Movement Strategies and Adaptations’ we discuss alternative strategies to optimize movements, and, finally, ‘The Mechanisms and Codes of Navigation and Movement’, focusing on navigation, senses, locomotory energetics, and the genetics behind movement and migration.

1.2.1 Large-scale patterns of movement

In this section we address how migration has evolved many times independently and is an extremely widespread strategy in nature to combat predictable adverse changes in environmental conditions in time and space. This suggests that although there are no strong taxonomic constraints to the evolution of migration, migratory behaviour is to some degree evolutionarily unstable. A frequent observation, which is, among other aspects, discussed in Chapter 2 by Chapman et al., is therefore that animals move within relatively narrow time windows and in steps with circannual (seasonal) and circadian (daily) rhythms. Although temporal patterns of movement are diverse among life-forms there are many common themes which apply across temporal scales. Moreover, partial migration, i.e. when some but not the whole population migrate, may affect large-scale movements and migratory patterns in most species (Chapman et al., Chapter 2). Animals on the move are often vulnerable to abiotic as well as biotic threats, including human-induced phenomena, such as climate change and habitat fragmentation. Obviously, species with specific ecological traits are more prone to such threats than others. In the chapters by Lindström et al. and Smith et al. (Chapters 3 and 4, respectively), we highlight how different types of human-induced changes may alter the movements and migratory patterns we are used to seeing in, e.g., birds and insects. Finally, based on long-term data sets, we

also provide a future perspective on how patterns of animal migration may change over time together with the potential evolutionary consequences thereof (Chapman et al., Lindström et al., Smith et al.; Chapters 2–4).

1.2.2 Movement strategies and adaptations

In this section we focus on what long journeys may teach us about life strategies in general and optimal movement and migration theory in particular. Different migratory strategies have most likely evolved because they conveyed improved survivorship to individuals that migrated in relation to those that stayed all year around at one site. The individuals migrating or dispersing may in this way have reached sites more suitable for reproduction, or providing higher food quantity and quality. When a moving strategy is adopted, animals migrate or disperse according to some alternative rules, for example minimizing the cost or duration of transport, or the total risk of predation during the journey (Hedenström and Lindström, Chapter 5). Although there might be some general rules for optimizing a dispersal or migratory journey, there are considerable differences between species, and even within species and populations at an individual level, e.g. between animals with differing personalities. The consequences of such personalities are discussed in Nilsson et al. (Chapter 6). Moreover, in Westerdahl et al.’s chapter (Chapter 8), we discuss the often neglected aspect that the moving animal may bring pathogens from one place to another and thereby spread diseases. From the viewpoint of the pathogenic micro-organism hitch-hiking on larger animals, this movement constitutes an efficient way of dispersal, whereas from the viewpoint of the host, migrating or dispersing may be a strategy to avoid pathogenic infections (Westerdahl et al., Chapter 8).

1.2.3 The mechanisms and codes of navigation and movement

Within the five chapters constituting this section, we discuss that all types of self-generated movements come with costs and the animal must produce forces to overcome resistance and gravity (Johansson et al., Chapter 13). For terrestrial locomotion, this

is achieved by generating ground reaction forces, while in air and water this is done by generating fluid dynamic forces. Moving across scales thus has consequences for our expectations regarding the animal movement, including the occurrence of seasonal migrations, which may be limited by the speed and cost of locomotion (Johansson et al., Chapter 13). Here we discuss how animals move and address adaptations to generate forces and mechanisms to reduce the cost of transport. However, to overcome resistance and produce enough energy to actually move forward is not enough; an animal must also properly navigate in order to fulfil the actual reason for movement: to reach desired resources. Our understanding of the sensory systems behind animal movement has improved considerably during the past decades, including, for example, a better understanding of alternative compass mechanisms, including the magnetic compass, as well as strategies used for navigation, which are described in Åkesson et al. (Chapter 9) and Muheim et al. (Chapter 10). In addition to magnetic senses, moving animals may also use polarized light, the sun, and celestial navigation to find their way (Åkesson et al., Chapter 9, and Muheim et al., Chapter 10) and a considerable amount of taxa also utilize odour for navigation (Svensson et al., Chapter 11). For example, insects use odours to find mates or food, but even some birds use ‘the smell-scape’ to find their nests or patchy food (Svensson et al., Chapter 11). Actually, the olfactory system was probably one of the first senses that evolved among animals on our planet; i.e. olfaction is possibly the oldest and most widespread sensory modality. However, despite that chemical communication may be the most potent and widespread form of information transfer in nature, the research field of chemical ecology is historically young. Although there are several reasons for this, such as the problems in analysing odour chemicals, a major reason is likely that we as humans have a poorly developed sense of olfaction and therefore find it more familiar to study how animal behaviour is influenced by our own major senses: visual and auditory cues. Hence, in this section of the book we aim at illustrating that moving animals are not relying on only one navigation instrument, but have an array of, more or less, reliable ‘compasses’. In particular

we describe how an animal needs a combination of at least one compass sense and a map to find their way back to a known site, or how they may rely on path integration and an ego-centric navigation system, measuring their own movements relative to the starting point (Åkesson et al., Chapter 9).

Another proximate cornerstone of animal movement research is the quest to understand the genetics behind movement and migration, including gene flow and local adaptations (Liedvogel and Lundberg, Chapter 12, and Hollander et al., Chapter 7). Movement and migratory strategies vary considerably between major groups of organisms, but also between closely related species or even within populations of the same species. From quantitative genetic analyses of cross-breeding and selection experiments, we know that a considerable proportion of the variance in a migratory phenotype has a genetic basis, but the number and identity of genes involved in modulating the migratory phenotypes are still largely unknown. In Chapter 12 by Liedvogel and Lundberg, we outline our current understanding of the genetic architecture of migratory phenotypes. We introduce molecular genetic tools and highlight how recent achievements in genomics potentially provide previously inaccessible ways to generate fully sequenced and annotated genomes of migratory species in the near future. Moreover, within the frame of the genetic code, an organism may be rather plastic and adjust its movement performance to the current environment. Such phenotypic plasticity may affect the ability for, e.g. local adaptations and dispersal (Hollander et al., Chapter 7).

1.3 Costs and benefits of movement

Despite the advantages of being mobile, any kind of active movement, whether in terms of running, swimming, or flying, comes with energy expenditure costs (Johansson et al., Chapter 13) and few organisms have adaptations that make them experts in more than one of the forms of movement. Hence, to become the best flyer, runner, or swimmer requires costly, specific adaptations, and having evolved such a specific morphology might not allow for further specializations from an energetic point of view. Moreover, there may also be

trade-offs between adaptive traits so that the organisms specialized in one trait may be really bad at the others. Actually, this seems to be the general case and, e.g. the common swift, *A. apus*, lives the major part of its life flying (see, e.g., Hedenström and Lindström, Chapter 5), but can effectively not walk or swim. The cheetah, *Acinonyx jubatus*, is one of the fastest runners, but rarely tries to fly or swim, and a blue-finned tuna, *Thunnus thynnus*, is a very fast swimmer, but few people have seen it walk or fly. In contrast to these specialists, most organisms are more of generalists in their movement strategy and have spent their 'evolutionary energy' on developing capabilities for more than one way of movement. Hence, by graphically describing this thought experiment in a three-dimensional way, we observe most organisms being able to do,

but not exceptionally good at, two, or even three ways of moving, whereas the real specialists mastering only one, but doing it really well, are few, represented by symbols tightly fitted to either the swim, run, or flying axes (Fig. 1.2). Hence, we find the symbols for most organisms in a swarm in the space between the axes in such a conceptual graph, whereas relatively few, the specialists, reach far out along one single axis (Fig. 1.2). The reason for this pattern is likely that the cost of evolving and managing specific motoric adaptations for, e.g., excellent flying involves trade-offs which are suboptimal for excellence in swimming and running, putting limits to the evolution of a super-organism mastering all means of movement to perfection. However, one way to approach being a super-organism is to use a specific morphological

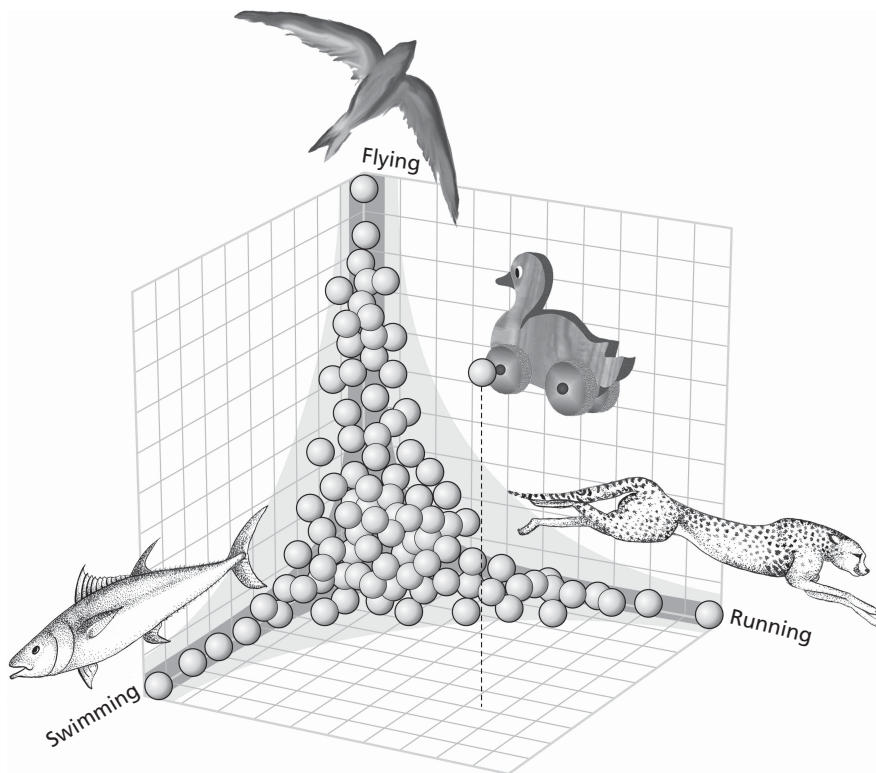


Figure 1.2 A conceptual illustration of different movement modes (running, swimming, flying), showing that few organisms are specialists in only one mode, and those that are generally have a weak performance for the other modes. In contrast, the majority of organisms are generalists and are reasonably good at several modes, as illustrated by the swarm of dots in the volume between the axes. A potential specialist on all modes may be the imaginary toy duck which is fast in air, water and on land. Note that this is a conceptual figure not based on data, but meant as a thought experiment.

adaptation to enhance movement efficiency when moving in different ways, for example as in the common guillemot (*Uria aalge*; Åkesson et al., Chapter 9), which is a reasonably good flyer, is a very good swimmer and diver, and is able to walk, albeit not very well. The trick here is that they use their feet and wings not only for walking and flying, respectively, but also for diving, i.e. using them as fins. In this way they reduce the cost (and space!) of mastering movement in several ways. Hence, it might be difficult to find, and even to imagine, a super-organism that could master all ways of moving. One possible imaginary super-organism may actually be the little yellow toy-duck on the back cover of this book, and also inserted in Fig. 1.2. We can see that it has probably long, pointed wings, which ensures rapid flight (Johansson et al., Chapter 13), it has large wheels which, for sure, will allow it to reach a high speed on flat ground, and it can obviously swim and even dive. Finally,

it has a compact and strong body that can harbour a metabolism providing energy for the different adaptations. However, evolution has not yet combined all these features within the same taxa and we are therefore left to our imagination.

References

- Aarestrup, K., Okland, F., Hansen, M. M., et al. (2009). Oceanic spawning migration of the European eel (*Anguilla anguilla*). *Science*, **325**, 1660.
- Baker, R. (1978). Demystifying vertebrate migration. *New Scientist*, **80**, 526–8.
- Brönmark, C., Chapman, B., Hansson, L.-A., Hulthén, K., Skov, C., and Nilsson, P. A. (2014). There and back again: migration in freshwater fishes. *Canadian Journal of Zoology*, **92**, 467–479.
- Dingle, H. and Drake, V. A. (2007). What is migration? *Bioscience*, **57**, 113–21.
- Nussbaum, M. C. (1978). *Aristotele's de motu animalum*. Princeton University Press, Princeton, NJ.

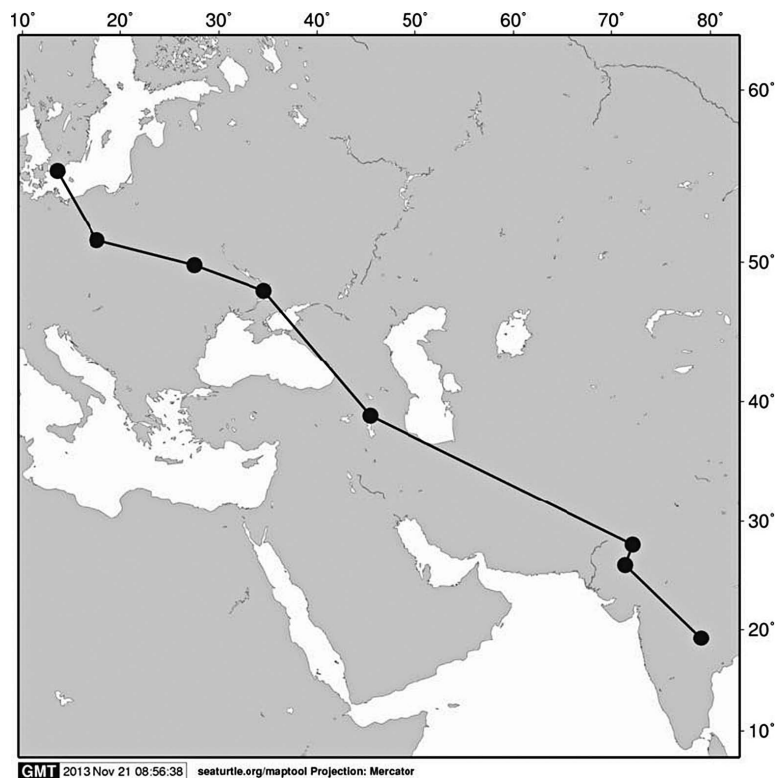
PART I

Large-Scale Patterns of Movement

Chapter 2. Patterns of animal migration

Chapter 3. Movement and migration in a changing world

Chapter 4. Beyond dispersal: the role of animal movement in modern agricultural landscapes



A migratory path from Scandinavia to India of little ringed plover, *Charadrius dubius*. Courtesy of Anders Hedenström.

Patterns of animal migration

Ben B. Chapman, Kaj Hulthén, Maren Wellenreuther, Lars-Anders Hansson, Jan-Åke Nilsson, and Christer Brönmark

Animal migration is a fabulously rich and varied tapestry of behaviour, encompassing a diverse range of movements. Migration often evokes images of the spectacular seasonal journeys of birds from their European breeding grounds to the food-rich African plains and forests; or the leaping of Pacific salmon as they fight the river currents to return to their natal streams to reproduce and then die; or the teeming herds of wildebeest as they migrate across the Serengeti. Yet these iconic epitomes of animal migration tend to focus upon the seasonal, long-distance migration of charismatic species. The true diversity of migratory patterns in nature is far broader than these examples would suggest, with migration occurring at an astonishing range of spatial and temporal scales. From the seasonal journeys of Arctic terns, *Sterna paradisica*, that fly thousands of kilometres from the high Arctic to the South Pole (Fig. 2.1; Egevang et al. 2010), one can scale down to short distance migratory movements of blue tits, *Cyanistes caeruleus*, that migrate less than 100 km (Nilsson et al. 2008), and even further to the daily migrations of micro-organisms such as zooplankton which move mere metres vertically in the water column in response to daily environmental fluctuations in predation risk and light (Hansson and Hylander 2009). One can also scale up, in time, to migrations that occur just once in a lifetime, such as in many semelparous fishes that migrate from the ocean to breed in freshwater habitats and then perish. Or we can consider the transgenerational migrations of insects such as the painted lady butterfly, *Vanessa cardui*, where it takes six generations to complete the migratory

cycle from Europe to Africa and back again (Stefanescu et al. 2012).

In order to make sense of the bewildering complexity and heterogeneity of migratory patterns in nature it is critical that we classify some of the variation observed in the wild. In this way we can begin to conjecture and test hypotheses about the evolution of different migratory patterns. Furthermore, a clear understanding of the sheer variety of migratory behaviour will assist us to conserve migratory species and the habitats they rely upon in an ever-changing world (Smith et al., Chapter 4; Lindström et al., Chapter 3). In this chapter our aim is to highlight the diversity of migratory patterns in nature and categorize some of these patterns. To achieve this we discuss taxonomic, population-level, temporal and spatial patterns of migration. Throughout the chapter we will also discuss the evolutionary processes postulated to have shaped the different forms of migration. By doing this we hope to highlight that an understanding of the patterns of migration that can be found in the natural world requires an evolutionary approach, assessing the costs and benefits of different strategies through the collection of field and experimental data, and the testing of theoretical models. Finally we discuss evidence of changing patterns of migration, in response to both anthropogenic and natural processes (see also Lindström et al., Chapter 3).

2.1 The evolution of animal migration

For migration to evolve via natural selection the fitness benefits of migration must outweigh those of