

The behavioural ecology of animal movement: reflections upon potential synergies

Abstract

Animal movement acts at multiple scales: it can shape the destiny of individuals and populations, govern community and ecosystem structure, and influence evolutionary processes and patterns of biodiversity. Recent technological advances, such as the revolutionary developments in tracking technology and remote sensing, provide fresh insights and the possibility to collect detailed data on where and how animals travel through space, how they react to and/or interact with their environment and conspecifics as well as their predators and prey. Scientists from various disciplines ranging from physics to psychology develop and apply ever improving analytical techniques to observe, assess and archive animal movement across scales. As in any other field, standardising data collection is a key prerequisite in order to combine and extend dataset collections, many of which may further be utilized by behavioural ecologists to answer questions on the function and significance of animal movements. Large-scale manipulative experimental approaches have also shed new light on old questions in animal movement, and opened new and previously inaccessible perspectives to study animal movement in the context of behavioural ecology. Animal movements are intrinsic to all behavioural processes, and analysis of movement phenomena within the framework of behavioural ecology has provided rich insights into the mechanisms and functions of animal behavior for some decades. We convened an international symposium to reflect on the behavioural ecology of animal movement, asking how these two related disciplines can produce new insights and synergies. Our symposium provided a platform that brought together a diverse range of researchers working on animal movement on different taxa and a range of spatial scales to discuss how behavioural ecology can integrate with the nascent discipline of movement ecology. In this short paper we summarise the key points from this meeting, and call for a renewed focus on the behavioural processes involved in the movements of animals.

Keywords

Migration • Dispersal • Tracking • Orientation • Navigation • Commute • Foraging

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Introduction

Movement is a ubiquitous feature of the lives of animals, and is integral to many important behavioural processes. For example, animals move to feed, find mates, avoid predators, and avoid adverse (environmental) conditions. Movement decisions are therefore inextricably bound to fitness outcomes, and hence our understanding of the evolution of animal behaviour is not complete without an understanding of why and how animals move and navigate around their environments. The converse is also true: an understanding of the evolution of animal movement cannot be complete without the behavioural context that provides the substrate for all movement decisions. In our opinion, it is in this way that the tradition of behavioural ecology can and should be integrated into the more recent development of movement

ecology. In this brief ideas paper we discuss the state of the art of both disciplines, and reflect upon what behavioural ecology can contribute to our understanding of animal movements, and vice versa. We also peer into a crystal ball and speculate on what the future may hold for a synergetic approach to these two areas of enquiry, highlighting both opportunities and new research directions, and also potential pitfalls that, through an integrative approach, may be overcome.

The state that we are in: Behavioural Ecology in 2012

Behavioural ecology has now come of age: from a small pioneering subfield in the 70s and 80s, behavioural ecology is now a major field in its own right. The research landscape

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has developed from the inception of behavioural ecology, and contemporary behavioural ecology has diversified from seeking a strictly evolutionary understanding of behavior to include a desire to also understand the proximate causes of animal behavior [1,2]. It has also been acknowledged, that the two categories are not mutually exclusive [3], that behavior does not occur in a vacuum, and that new branches of behavioural ecology are interested in making more explicit links to ecological and evolutionary processes, and in harnessing behavioural insights to address conservation and other applied questions [4]. In this context movement ecology and in particular studies of connectivity have shown the importance of incorporating knowledge of habitat and space use of individuals during the non-breeding period to understand carry-over effects on both individual (i.e. body condition at winter site influences performance in breeding site) and population levels (e.g. density-dependent effects on reproduction and mortality) [5,6]. Likewise, neuroethology has become a growing research field and has brought together animal behaviourists, i.e., ethologists and neuroscientists interested in understanding the physiological and neurosensory mechanisms underlying animal behaviour, including animal movement [7]. This is specifically, but not exclusively, true for questions regarding the sensory mechanisms of animal orientation and navigation [e.g. 8].

Yet traditionally, behavioural ecology has neglected to tackle questions regarding animal movement directly. A great deal of work has, for example, focused on animal dispersal; however, much of the attention here has been on factors that shape the decision to disperse i.e. prior to dispersal (e.g. conspecific density [9]). The process of dispersal itself involving the actual movement has received significantly less attention from behavioural ecologists, and falls more into the intellectual domain of movement ecologists. Similarly, movement ecologists perhaps gloss over some of the interesting and important behavioural processes and interactions involved in, for example, migratory decisions. Hence it is our view that more integrated attention should be given to the many areas of overlap between these two fields.

Movement ecology: opportunities and challenges

Movement ecology has a venerable history that has been re-energised of late by renewed calls for an integrative approach to understanding the causes and consequences of the movement of organisms [10-12]. The trajectory of movement ecology's development has been inextricably bound to technological developments [e.g. 13,14]. These advances show great potential and have enabled new insights and a more detailed understanding of the lives of animals and how they travel through space. Here we discuss some of the opportunities and challenges associated with movement ecology today, and how these could benefit from a behavioural ecological approach.

Technology and tracking

The possibility to track individuals with various devices, which allow zooming into movement processes on a much finer and previously inaccessible scale, has revolutionised our understanding of movement ecology [14]. Experimental tracking devices get lighter, resolution increases, and they get more and more sophisticated and integrative, now not only allowing us to study the properties of the individual in multiple contexts (e.g. speed and altitude measures, pH meters to assess food intake, but also to integrate the properties of the environment (e.g. light, salinity and pressure sensors,) into our analyses. Continuous refinements in conceptual frameworks and technology will continue allowing us to decouple scales of coverage of observational data and push the limits of our understanding of movement ecology even further. It is now possible to overcome the boundaries and restriction of our "pet taxon", and not only study behavioural movement phenomena on the population and community level, but beyond that monitor different networks of species, and further consider broader ecological effects and consequences of behavioural processes [15,16]. This will allow us to gain valuable insights into broader ecological effects and to understand ecological consequences of general behavioural processes such as foraging movement, dispersal or migration. Currently, between-taxa comparisons, e.g. between birds and mammals, are still scarce.

Due to recent technological advances, the world got "tiny": we are now able to follow for example the (so far) longest recorded non-stop flight of famous E7, a bar-tailed godwit, who flew 11680 km nonstop from Alaska to New Zealand without food or rest [17]. On the other end of the scale, tracking on the millimetre scale allows us to infer new understanding of micro-organisms movements such as individual zooplankton and their responses to changes in environmental conditions [18]. Yet, whilst tracking data can produce pertinent insights into the capacities and migration patterns of a diverse array of animals, one must be cautious to not allow these innovations to take the place of clear thinking and the development of testable hypotheses. Tracking can produce fascinating descriptive data, but in order for this to advance a broader understanding of the causes and consequences of animal movement, simultaneous collection of the behavioural details is critically important. This is exemplified by recent research into the movement of groups of equids, where tracking of social groups revealed differences in how herds move around the landscape to access water resources, with two focal groups making apparently suboptimal decisions by travelling longer distances to water. Detailed behavioural observations revealed that the dominant group in the population drank at the closest water hole, together with the group at the bottom of the dominance hierarchy (but with reduced access). The intermediate groups avoided competitive interactions and their related costs, and strategically chose a watering hole farther away [D. Rubenstein, *personal communication*]. Whilst high-tech tracking can describe the movements of these animals, only behavioural observations shed light on what factors

underpinned these movement patterns. This example highlights the importance of integrating explicit behavioural observations when interpreting movement ecological data. Likewise, if we want to understand the neurobiological and physiological mechanisms underlying movement processes, like orientation and navigation, we need to study animal movement in more detail and under strictly controlled experimental conditions to draw accurate conclusions on, e.g., which compass cues were used by the animals during their movement. Thus, to gain a comprehensive understanding of animal movement ecology, it is important to integrate analyses on the behavioural, genetic, neurobiological and physiological mechanisms that govern the underlying properties for animal movement.

Datasets – storage and accessibility

Nature is too diverse to allow all questions to be answered using the same model species. For any given question, it is crucial to optimise the balance between choosing the best suited study system and available (often seductive) technology when developing the experimental design to address this question. With increasing knowledge on different taxa and species, new model animals will be established and will add extended scope and qualities to address both old and new questions. For example, recent work with cyprinids, a group of non-model fishes poorly studied in terms of migration, has shed light on the ecological trade-offs associated with migration versus residency [19,20], and also individual variation in migratory strategies [21]. In addition, hand-in-hand development of analytical tools will be needed as movement data sets are generated rapidly and need special tools to handle. However, new theoretical developments, statistical advances and the availability of massive datasets have added an improved degree of power to our analyses and our ability to extract better inference. For example, the inclusion of state-space approaches to analyse movement data allow direct modelling of movement behavior in a flexible and reliable manner providing robust methods for handling the error structure of the data [22,23]. Great care needs to be taken in handling the complexity of data, but guidelines have been provided by e.g. Jonsen et al. [24].

Understanding the drivers of input for currently available massive datasets is critically needed. We further need to store all collected material, standardise formats and enable global sharing of data between projects. This is by far not restricted to the target dataset of our tuned analyses, but equally important is the storage of supplemental material collected, which may not be key to our specific analyses, but may be of major importance for other questions in a similar context, and/or can be further exploited for meta-analyses. Global sharing of available datasets further opens the possibility to include different viewpoints from other disciplines and approaches. These collaborative enterprises have already reaped new insights. For example, analysis of EURODEER, a pan-European database which collects data on ungulate movements and distributions, has been used to identify detailed divergent inter- and intra-population modes of

movement, and to test hypotheses about the ecological drivers of such variation [25]. MAMVIS, MOVEBANK and SEATURTLE.ORG are other examples, storing movement data from birds, fish, reptiles and mammals [26,27]. In the future, we can only hope for more collaborative efforts like this, which will allow us to take the difficult logistical step and scale upwards, to allow population-level analyses of movement patterns [e.g. 28].

Individuality in movement and behaviour

A new awareness in behavioural ecology is the importance of studying animals at an individual level [29]. Consistent individual differences in behaviour (known as animal personality) have been documented in an extremely wide range of taxa [8]. Furthermore, individuality in movement patterns has also been revealed by technological advances in tracking, for example in marsh harriers *Circus aeruginosus* [30] and common roach *Rutilus rutilus* [19]. It is our view that movement ecology could benefit from following a similar, hypothesis-driven path for questions on the causes and consequences of individual differences that behavioural ecology has recently taken.

The recognition that individual variation can be important can facilitate new understanding in a number of ways. Firstly, movement ecologists can apply analytical methods developed in behavioural ecology to understand the existence of syndromes of correlated traits (“behavioural syndromes” *sensu* [29]) [31]. Very few studies have followed a ‘syndrome’ approach using migratory traits from wild animals as components of the syndrome (i.e. patterns of covariation of morphological, behavioural, life-history traits associated with the migratory phenotype), yet these data are now available for many species. For example, many populations of animals show intrapopulation variation in multiple migratory traits (differential migration), which may correlate with one another. Secondly, the importance of personality variation in explaining variation in movement patterns and strategies is poorly understood, and only a handful of pioneering studies linking dispersal [32,33] and migration [21] to personality variation exist. For example, the role of intraspecific competition in determining which individuals migrate in partially migratory populations has been hotly debated for some time [34]. In many cases surrogates of competitive ability have been used to test this hypothesis (e.g. body size), which has led to ambiguity in interpretation. Many studies have linked personality to competitive ability [35]. Explicitly measuring behaviour, rather than relying on easily measured indices of competitive ability (such as body size) which may mask important individual variation, may provide an exciting next step towards fully testing this model. Continuing with the theme of differential migration, predicting which individuals occupy high quality territories in the overwintering grounds in migrations with low population connectivity (see e.g. [5]) may benefit from an approach which aims to quantify individual variation in behaviour and link this to migratory behaviour. We can also scale down, to movements on a more local scale: what shapes individual patterns of local movement? To what extent do animals with divergent personalities have different movement

strategies during foraging, for example? Data are now emerging to suggest personality could play a key role in mediating animal movements at all scales.

Individual variation in reaction norms and trait plasticity is thought to be widespread [32], and a recent study showed how migratory fish varied in their degree of migratory consistency. A dataset which spanned a number of years for hundreds of fish showed that those individuals that were consistent in the timing of migration, were also inflexible in their destination [22]. Individual differences in responsiveness have been integrated into the personality concept via the related concept of 'coping styles' [36], but work on this in the context of animal movement is extremely scarce. Migratory animals also experience distinct habitats at different stages in the migratory cycle, spending different seasons in geographically separated regions. Each habitat poses different ecological challenges. How consistent is individual behaviour across these different contexts? Do fitness costs and benefits of animals with different personalities vary at different stages of the migratory cycle? Some work has begun to address these questions. A study that tracked the migratory behaviour of individual cranes showed that birds that hatched in low disturbance sites in Finland chose similarly undisturbed stop-over sites in Hungary [37]. These findings may also have implications for the conservation of migratory species, in addition to being of fundamental interest to both movement and behavioural ecologists.

A focus upon individuals may also elucidate the consequences of migration for fitness. Our understanding of the fitness consequences of migratory behaviour is currently limited (cf. [38]), and one could argue that the contemporary focus of migration biology tends to be upon the proximate rather than ultimate drivers of such movements. Quantifying individuality in migratory and dispersal behaviour provides an opportunity to collect data on patterns of survival and reproductive success such that we can begin to address the fitness outcomes of different strategies under different environmental conditions [39,40]. Currently, the evolutionary ecology of migration biology is poorly understood and lacks a strong empirical basis, despite its clear importance, and individual variation in migratory strategies and behaviour offers a powerful way to begin to address this fundamental gap in our knowledge. In one sense this is nothing new for some aspects of movement ecology – for example, linking dispersal ability with the evolution of life-history traits in long-term population studies has been stressed before (e.g. [41]). However, knowledge of individual movement decisions across time can inform our understanding of the evolution of movement strategies in other domains of movement ecology.

The advent of individual-based simulation modelling and continued use of game theoretical approaches in disciplines like behavioural ecology can be applied to generate novel predictions and hypotheses about the importance of different ecological factors driving the evolution of migration in different scenarios. Individual variation in migratory traits can also be a vehicle to deepen our understanding of the physiology and genetic underpinnings of migratory behaviour, as we discuss in

more detail below. It is hence our view that migration biology should take steps to follow the recent trajectory of behavioural ecology towards focussing intensively upon individual variation in migratory behaviour.

Living and moving in groups

Another research focus of behavioural ecology that has potential utility for movement ecology is the study of social interactions [42]. New analytic techniques are constantly developed to tease out the mechanisms and function of social behaviour in animals. Recent developments include social network analysis [43] and collective decision-making theory [30]. Many animals live and move in groups, and hence the social context is critical to movement decisions and navigation in many species. There are many opportunities for synergetic work here, and new tag technology can facilitate this. Tags are available now which can 'talk' to each other, essentially recording social interactions with other tagged animals by recording their presence within a certain proximity range [44]. Combining detail on social interactions with movement data can provide integrative and important insights. For example, we can develop our earlier example of evaluating the importance of individual competitive ability in migratory behaviour. By combining social network analysis with these measures of individual behaviour (i.e. competitive status/personality) we can assess the role of population structure and individual traits upon migratory variation in populations of differentially migratory animals.

Theoretical models to understand collective decision-making may also have utility in understanding migratory movements. Whilst current models for collective movement tend to deal with quite local spatial scales, there is real potential to apply these ideas to larger-scale movements [45]. Yet, although collective decisions are important, groups are often not egalitarian structures. Leaders can emerge that have a strong influence on the movements of groups [46]. Recent work in movement ecology has applied these ideas to the local movements of pigeons [47]; however, future work can focus upon the importance of leaders versus collective decisions in moving groups at larger spatial and temporal scales, such as during migratory journeys. In addition to logistically challenging empirical work, more theoretical work is also needed to scale these ideas up to migratory populations and species. Finally, how information transmits through social groups and how this affects the learning of routes and movement strategies is also an interesting area which bridges both behavioural and movement ecology [45].

Finding the way: Mechanisms of orientation and navigation

The more we learn about the impressive movements that animals are capable of, the more we also ask ourselves how they do it – not only how they physically get from A to B, but also how they solve the problems of *when*, in *what direction*, and for *how long* to move. These are classical questions best

known from bird migration research, but likewise apply to any other animal (or group of animals) moving between two points. While it has been known for quite some time that the timing and direction of migration in birds is governed by a genetic program [48], we have now entered an era where candidates for the first “migration genes” have been proposed [49,50]. Also, we are able to decipher the genetic architecture underlying the orientation systems in such detail that we can pinpoint the genes responsible for e.g., monarch butterflies to perceive polarized light and colour gradients on the sky that are part of the sky compass [51-53]. Likewise, from vague ideas and theoretical hypotheses about how animals could perceive different properties of the Earth’s magnetic field and use it for orientation and navigation, we have now come to the point where we have target receptor molecules and neural pathways supported by experimental data that are likely involved in magnetic field sensing [54-57].

During the past decade, the field of animal orientation and navigation has substantially advanced from the classical orientation studies on the organismic level to detailed investigations of the molecular, biophysical and neurosensory mechanisms of orientation. We are moving from a general understanding of the genetic basis of animal movement towards detailed knowledge on how the expression of specific genes enables animals to perceive orientation cues on a molecular level and how this information is filtered and integrated on a neuronal level to enable the animals to determine their way. But no matter how advanced the new tools and techniques are that we use, ultimately, we always have to resort to carefully designed and accurately controlled behavioural experiments to tell us whether, e.g., a newly proposed gene or neuronal pathway indeed linked to the trait in question.

The recent insights have also started to change our view on the importance of the magnetic sense not only for animal movement, but as an interface of metrics of distance, direction and position for organisms in all stages of life [58,59]. The implications have far-reaching consequences not only on how we look at animal movement, but also how we think about animals orienting and navigating in their home ranges, during foraging movements, how they approach prey when hunting, or simply how they align themselves when resting [60,61]. Cleverly designed experiments will need to investigate in what aspects of animal behaviour the magnetic field plays a role. Is this a feature that all animals possess, but that is very difficult to tease apart from other behaviours and demonstrate experimentally? Is the reception mechanism one and the same across the entire animal kingdom or did it evolve several times independently? Is it an innate trait, or can it be learned?

Unresolved questions and new directions

One may ask if any major paradigms have fallen or become re-evaluated since the research field of animal movement ecology has developed. We can certainly conclude that our view on movement ecology is no longer purely observational. Methodological and technical advances may soon allow us to

observe and capture entire networks of different individuals and their sociality from various perspectives, and thus open ways to address previously inaccessible questions, e.g., how predators and prey are moving and interacting in the African Savannah (D. Rubenstein *personal communication*) or how individuals in bird communities of known genotype and phenotype move and settle in a temperate deciduous forest [38]. Ultimately as behavioural ecologists we want to understand the properties of the individual and the properties of the environment plus their interactions to allow us to decompose the interactions. We want to understand the rate of change of the environment over time, which can be of fundamental difference on different scales, particularly as any moving animal is experiencing change per se. How can we follow and assess these changes in both time (various dimensions/directions within) and space?

The assessment of individuality and social interactions motivating particular movement strategies, dominance levels, and, for example, decisions on movement trajectories may be significantly improved by the inclusion of e.g., camera tracks of geolocated individuals in field-based study systems. The field of bio-logging has grown tremendously over recent years, and can be applied in terrestrial as well as aquatic systems [e.g. 62,63]. Both calibration of retrieved data and the accuracy of behavioural observations in the field have been of concern for some time and need to be improved (e.g. [64]). These additionally collected data will provide valuable insight into changes in landscape plus heterospecific interactions, but may also measure physiological performance, which will add an exciting new level of depth of the overall complexity of the behaviour-environmental system [e.g. 65,66]. Further technological development and improvements are to be expected in the future, and will allow us to investigate individual movements and social interactions in the previously inaccessible open field environment and beyond the uni-dimensional and rather static observational level.

For example, a technique that will likely receive more attention in movement ecological studies in the coming years as technology improves is the field of robotics. Robots may be used to experimentally manipulate the movement of animals, via providing either a social or predatory stimulus to move [67,68]. Furthermore, they can act as stimuli themselves to facilitate how information, which leads to movement decisions, transmits through social groups of animals. Related advances have led to innovative discoveries: for example, projecting computer generated ‘prey’ into a tank with a predatory fish has provided clues as to the evolution of individual and collective movement behaviours in response to selection by predators [69].

Conclusions

A highly integrative approach to study the animal movement across scales is imperative for making major advances in the field. Technology can support studies and facilitate significant conceptual advances, but questions should always be clear and driven by our desire to understand mechanisms, cause and consequences. Information on movement is important,

but so are behavioural data to properly test hypotheses about the drivers or implications of movement. Furthermore, the role of social interactions, before, during and after movement will provide clues as to the importance of social environment, and also highlight how movement can facilitate information flow, disease transmission, learning and migration, and create potential patterns of assortative mating and connectivity (e.g. [70]). Improved understanding of the underlying mechanisms of long-distance movements will subsequently allow us to transfer this knowledge to study the evolutionary dynamics of host-pathogen interactions and disease spread [71]. Rapid advances in next generation sequencing technology now allow us to investigate the genetic architecture of movement traits on a previously inaccessible scale. Therefore, critical and controversial discussion of newly emerging technology as well as careful evaluation of existing methodological and experimental approaches is a key prerequisite of progress. Small conferences, workshops and symposia provide a necessary forum for encouraging dialogue, and critical assessment of possibilities and pitfalls thereof, between researchers from different fields focussing on various taxa. These meetings facilitate direct and interactive discussions on recent progress and problems encountered, foster collaboration and promote debate. We hope that behavioural and movement ecologists

will embrace the challenges of unravelling the enduring mysteries of animal movement, and that future synergies and collaborative efforts will continue to push the frontiers of our knowledge in this fascinating and important field.

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