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EDITORIAL

Stuck in motion? Reconnecting questions and tools in movement ecology

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Introduction

Is science mostly driven by novel ideas or by new tools? Whilst in certain areas of science or at specific times new ideas might have led to new understanding and even changed entire fields of research (e.g. Dyson 2012), for the field of movement ecology, 'tools' [tracking devices, computing power and statistical/mathematical methods, Geographical Information Systems (GIS) and remote sensing data] have led to an ongoing revolutionary progress lasting many decades. There has been a down side, however, to this increasingly rapid development of new methods. It is becoming more and more challenging to match research questions with the appropriate tools, especially with the increasing availability of high-resolution animal movement data sets. Thus, discussions among ecologists often become entirely focussed around methodological aspects (Hebblewhite & Haydon 2010), losing track of the fact that it is the research questions that dictate the most appropriate sampling design and methods to use (Fieberg & Börger 2012).

This Special Feature guest edited by Bram van Moorter, Manuela Panzacchi, Francesca Cagnacci and Mark S. Boyce aims to address this disconnect between research questions and tools in movement ecology. It arose from a workshop of the same name that took place in Hedmark University College in Norway (11–17 August, 2012) organized by the Guest Editors. All six papers of this Special Feature focus on an ecological question, ranging from the relationship between habitat selection and population abundance to the spatial partitioning of behaviours along the movement trajectory. One or more methodological approaches are discussed, their performances evaluated using simulated and/or real movement data, and documented software codes are provided to allow the readers to repeat all analyses.

In this editorial for the Special Feature, I firstly briefly review the major milestones in tool development for movement ecology research, from the first mark–recapture techniques to the current techniques allowing users to collect high-frequency movement data and high-resolution environmental data, as well as the methods for statistical and mathematical analyses. I then briefly describe the methods covered in the Special Feature and conclude with a brief outlook on ongoing and future developments.

Key tool development milestones in movement ecology

Fundamental questions about animal movements, such as migration, were first posed by luminaries including Aristotle and Pliny the Elder, but it was only in early 1800, when the naturalist John James Audubon attached strings to the legs of migratory birds, that it became possible to demonstrate that it is the same individuals which tend to return the following spring. This led to the development of mark–recapture or resight methods, originally to study bird migration as it formed the basis of the many bird ringing/banding schemes set up since around 1900, but since then used for many animal taxa (e.g. Letcher *et al.* 2015). Coupled with appropriate sampling designs (e.g. mass mark–recapture) and the development of increasingly sophisticated statistical and mathematical methods, such as the random walk and diffusion-based methods, sparked by the seminal paper by Kareiva & Shigesada (1983), these data have allowed ecologists to answer fundamental questions about animal movements and population redistribution (Turchin 1998). Thanks to the ready availability of high-performance computers, combined with sophisticated pattern-matching algorithms such as those used in astronomy (Arzoumanian, Holmberg & Norman 2005), in recent years it has been possible to extend mark-resight methods to unmarked animals by using photo-identification methods (e.g. Holmberg, Norman & Arzoumanian 2009), camera trap sensor arrays (Yu *et al.* 2013), individual song identification (Petrusková *et al.* 2015) and non-invasive genetic sampling (Sawaya *et al.* 2011).

Charles Darwin discussed fundamental ideas about the effects of individual movements on ecological and evolutionary processes long before these could be tackled. For example in the 3rd edition of the *Origin of Species* (Darwin 1861) he discusses how the commonly observed tendency of animals to restrict their movements to relatively small 'home areas' (today called home ranges, reviewed in Börger, Dalziel & Fryxell 2008) fundamentally affects the interactions between individuals and hence natural selection processes at the local level,

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ultimately scaling up to the rate of population spread and the diffusion of new genotypes. Addressing such questions requires the ability to collect more frequent and individual-based location data than most mark–recapture methods can provide. This became possible with the use of radiotransmitters, developed since the late 1950s to track animal movements and survival (Kenward 2001). These systems are based on electronic tags which emit a radio signal [typically a very high frequency (VHF) – signal] that can be used to locate the position of an animal from distance, without the need to see the individual. Arguably, this has been one of the most important methodological advancements in movement ecology, and since then measures of animal movement behaviour are at the basis of fundamental ecology theories (e.g. Emlen & Oring 1977; Johnson 1980; Clutton-Brock 1989) and are essential for managing wildlife populations (Claudet *et al.* 2010) or predict disease transmission rates (Fèvre *et al.* 2006). And still today, for many questions VHF-based systems are the most efficient solution (Hebblewhite & Haydon 2010), especially when combined with automated monitoring systems (Cooke *et al.* 2004; Mennill *et al.* 2012b). For example using data on home range overlap in cougars, Elbroch *et al.* (2015) recently showed that the Resource Dispersion Hypothesis (Macdonald 1983), commonly applied to social carnivores, may be relevant also for solitary species.

In the late 1970s, researchers started fitting animals with tags linked to the ARGOS satellite system, which opened up the possibility of tracking animals remotely across the globe, without the need to locate the signal by the researcher. This revolutionized the study of long distance movements, for example of marine predators (Weimerskirch 2009), especially when combined with depth recorders to measure diving behaviour (Burger & Wilson 1988; Laplanche, Marques & Thomas 2015). In the late 1980s, researchers started to develop tags linked to the GPS satellite system, allowing the collection of high-frequency accurate location data (Tomkiewicz *et al.* 2010). Thanks to increased storage capacities and smaller batteries, high-frequency locations can now be collected for many animals species, allowing researchers to answer increasingly sophisticated questions (Cagnacci *et al.* 2010). How to efficiently use such data is one of the aims of this Special Feature. Small animals and marine animals cannot be tracked using satellite-based tags, but the development of light-level geolocators (Wilson *et al.* 1992) made it possible to collect movement data from these species also. These tags measure light levels, used to estimate sunrise and sunset times, which can then provide an estimate of the movement of the animal. They are very lightweight, inexpensive, and are the only method for these smaller/marine species, however, there is a cost of high positional error and low frequency of locations (Winship *et al.* 2012). Conversely, on small, local scales, songbird movements can be tracked without using any tags, by setting up an array of directional microphones, combined with song recognition algorithms (Blumstein *et al.* 2011; Mennill *et al.* 2012a),.

Animal movements are fundamentally determined by the interaction between the external environment and the characteristics and needs of each individual (Nathan *et al.* 2008), thus obtaining precise and appropriate information about the environment is essential. The ready availability of GIS with which to manage and combine movement and environmental data coupled with the availability of remotely sensed environmental data with global coverage (Neumann *et al.* 2015) allow unprecedented possibilities for understanding the relationship between environmental and movement dynamics (Hebblewhite, Merrill & McDermid 2008; Willems, Barton & Hill 2009; Morellet *et al.* 2013; Kranstauber *et al.* 2015). Accordingly, four of the papers in this Special Feature present new methods for investigating resource selection and the relationship between animal movements and landscape characteristics.

In parallel with the massive increase in the capacity to collect animal location and environmental data, there has been an equally large increase in the number and complexity of statistical and mathematical methods available, for analysing movement data. Examples include mathematical ('mechanistic') methods (Moorcroft & Lewis 2006; Codling, Plank & Benhamou 2008; McClintock *et al.* 2012; Bauer & Klaassen 2013; Potts & Lewis 2014; Schlägel & Lewis 2014; Bateman *et al.* 2015), hierarchical models such as linear and nonlinear mixed models and state-space models (Jonsen, Flenming & Myers 2005; Patterson *et al.* 2008; Börger & Fryxell 2012; Beyer *et al.* 2013; Blackwell *et al.* 2015; van de Kerk *et al.* 2015), new approaches for estimating resource selection functions (Matthiopoulos *et al.* 2011; McDonald *et al.* 2013; Potts *et al.* 2014; Thurfjell, Ciuti & Boyce 2014), individual-based models (Mitchell & Powell 2004; Wang & Grimm 2007; Rubin *et al.* 2015), new space use estimation methods (Horne, Garton & Rachlow 2008; Benhamou 2011; Downs & Horner 2012; Fleming *et al.* 2015), flexible machine learning methods (Dalziel, Morales & Fryxell 2008; Li *et al.* 2012; Bracis *et al.* 2015), network analysis methods (Jacoby *et al.* 2012) or methods for modelling group dynamic movements (Langrock *et al.* 2014). Similarly, there has been a large increase in the number of dedicated software packages for movement analyses (Calenge 2006; Kranstauber & Smolla 2013; Johnson 2015). Choosing an appropriate method is hence becoming more difficult and at times the important link with the specific research question is lost. Providing examples on how to establish this link is one of the main aims of this Special Feature.

Questions and topics covered by papers in the Special Feature

This Special Feature comprises six contributions, of which five present novel analyses and approaches and one is a literature review. Four papers address questions related to habitat selection: Boyce *et al.* (2015) review the literature asking if and when habitat selection can be used to predict species abundances in heterogeneous environments; Van Moorter *et al.* (2015) present a new theoretical framework linking individual movement responses to environmental heterogeneity to the emergent habitat selection and space use patterns; Panzacchi *et al.* (2015) show how a combination of step-selection functions and a novel method, the Randomized Shortest Path (RSP) algorithm, can be used to identify corridors and barriers between habitat patches in fragmented landscapes; and Beyer *et al.* (2014) develop a new step-selection function framework to simultaneously estimate, from a time series of locations, not only habitat selection and movement ability but also the permeability of landscape barriers for individual animals. The remaining two contributions both address the classification or segmentation of movement paths into different types or behavioural sections. Cagnacci *et al.* (2015) present a comparison of three methods to identify migratory movement paths, often not a straightforward task for partially migratory populations, and quantify migration parameters. Gurarie *et al.* (2015) conclude the section with a comparison of four approaches for identifying behavioural phases in movement tracks.

I now briefly describe in more detail the questions and topics addressed by the papers of this Special Feature. A fundamental aim of much movement research is to quantify and predict habitat (resource) selection by animals (Johnson 1980; Arthur *et al.* 1996; Rhodes *et al.* 2005; Christ, Hoef & Zimmerman 2008; Moorcroft & Barnett 2008; Matthiopoulos *et al.* 2015), which is also closely related to predicting species geographical distributions (McDonald *et al.* 2013). In particular, according to ecological theory there is a close correspondence between habitat selection, species abundance and population dynamics, yet there are no practical methods to quantify and model these relationships (but see Matthiopoulos *et al.* 2015). Accordingly, in the first paper of this Special Feature Boyce *et al.* (2015) review the literature to ask if habitat selection can predict abundance. At carrying capacity (or in an ideal-free distribution), habitat selection metrics can be used to estimate abundance. Under non-equilibrium conditions, however, this direct relationship breaks down (see also Fronhofer, Kropf & Altermatt 2015) and Boyce *et al.* (2015) conclude that a mechanistic understanding of population dynamics is required to predict abundance from habitat data; an observation to consider in relation to the mathematical framework developed by Matthiopoulos *et al.* (2015) to link habitat selection to density-dependent population growth.

A fundamental concept of the movement ecology framework is that the interactions between individual conditions and the characteristics and dynamics of the external environment generate the structure and geometry of movement paths (Nathan *et al.* 2008). In turn, individual movements lead to the emergence of habitat selection and space use patterns at larger scales (Johnson 1980; Moorcroft & Lewis 2006; Börger, Dalziel & Fryxell 2008). A coherent theoretical and methodological framework to mechanistically link individual movements, landscape characteristics, habitat selection and space use was, however, missing and Van Moorter *et al.* (2015) present one based on two key movement mechanisms and apply it to a moose (*Alces alces*) GPS-tracking data set. In heterogeneous environments, animals can maximize the utilization of preferred habitat by increasing the time they remain in preferred habitat patches (Benhamou & Bovet 1989) or by increasing the frequency of returns to the latter (Riotte-Lambert, Benhamou & Chamaillé-Jammes 2013). The key contribution of Van Moorter *et al.* (2015) is to show that quantifying the spatial distribution of these two movement types and relating it to the observed landscape structure allows us to directly link individual movements to second-order and third-order habitat selection (location of home ranges and selectivity within home ranges respectively).

Human-induced land-use change is increasingly modifying landscapes and restricting animal movements. Accordingly, many researchers are attempting to identify the barriers impeding animal movements, or the landscape sections that connect fragmented habitat patches ('corridors'). Panzacchi *et al.* (2015) take a different approach by highlighting that barriers and corridors are not different entities but are two extremes among a continuum of landscape structures. The authors first use step-selection functions, an increasingly popular method which allows to jointly estimate movement propensity and habitat selection from individual movement paths (Fortin *et al.* 2005; Forester, Im & Rathouz 2009; Potts *et al.* 2014; Thurfjell, Ciuti & Boyce 2014), to create a 'friction' map for animal movements, using a data set of migratory wild reindeer (*Rangifer t. tarandus*) as a case study. Second, they introduce the RSP algorithm, a new approach which combines optimal movement and random walk methods, to identify the best areas for strategic movements between functional areas/habitat fragments. Using model calibrations, the authors demonstrate that the RSP approach outperforms optimality or random-walk-based methods and, interestingly, provide evidence to suggest that reindeer may trade-off between-movement optimization and exploration during migration.

Whilst there might indeed be a continuum between barriers and corridors, a specific type of barrier is of particular interest for basic and applied movement research, namely semi-permeable barriers, defined as features that cannot be circumnavigated but may be crossed (e.g. rivers, roads, fences). Such barriers fundamentally affect animal movements both through proximity effects (altered movement/habitat selection close to the barrier) as well as permeability effects (reduced probability of moving between the areas on both sides of the barrier). Beyer *et al.* (2014) develop a new extension of step-selection functions to address the question of how individual movement capacities, proximity to the barrier and habitat preference interact in determining the probability of crossing a barrier. Using simulations and an application to data on migratory reindeer, the authors demonstrate that the approach is unbiased and precise, if sufficient barrier crossing events and locations close to the barrier have been recorded. Biologically, the authors highlight the strong individual differences among reindeer in the avoidance of, and probability to, cross roads; thus, the approach will prove useful for exploring the mechanisms driving patterns such as age-dependent movement strategies in response to road density (Singh *et al.* 2012). Importantly, the barriers need not be permanent but could also be dynamic, for example as those found in the aerial environment (Shepard *et al.* 2013; Lambertucci, Shepard & Wilson 2015).

Quantifying the degree of variability in the propensity to migrate, and estimating migration parameters for the migratory set of a population, are two long-standing questions in animal movement research (Mayr & Meise 1930), yet it is often a tricky task for partially migratory populations (Börger *et al.* 2011). Cagnacci *et al.* (2015) compare the performance of three contrasting methods, applied to the same large data set of over 100 individual trajectories of deer from three different populations. Interestingly, all methods provided very similar results for fully migratory populations, whereas the agreement was markedly lower in partial migratory populations, suggesting the need to compare the results of different methods and combine it with sensitivity analyses.

Finally, a key assumption of the movement ecology framework is that animal movements are fundamentally characterized by facultative switches between distinct movement modes (Fryxell *et al.* 2008) and many different methods have been developed to identify and segment movement paths into different behavioural sections (Barraquand & Benhamou 2008; Beyer *et al.* 2013). Gurarie *et al.* (2015) use simulated and real animal movement data to compare the performance of four contrasting methods. The simulations highlight the sensitivity of methods to model mis-specification, such as spatial bias or autocorrelation, with different assumptions impacting the ability to correctly identify specific characteristics of the movement path (e.g. orientation). Importantly, with the application to real data, Gurarie *et al.* (2015) highlight important trade-offs between the strength of *a priori* assumptions, model complexity and explanatory power of the methods, impacting the ability to detect structure in the movement paths. In general, the authors highlight a point of central importance for this Special Feature: before fitting complex movement models, it is advisable to do a detailed exploratory analysis of the characteristics of the data. The Gurarie *et al.* (2015) paper provides important general principles for doing so.

Future outlook

Connecting 'tools' with the research questions asked will become increasingly important in the future. There will be an unprecedented increase in the availability of movement data thanks to upcoming technological developments which will allow us to track from space a large number of animal species (Wikelski *et al.* 2007). Multichannel biologging sensors combined with dead reckoning methods (Wilson *et al.* 2007; Laplanche, Marques & Thomas 2015) already allow us to track animal movements at subsecond scales (e.g. 40 Hz), hence recording the actual true trajectory and not a sample of points.

Furthermore, multi-channel loggers recording body acceleration or magnetic orientation allow researchers to infer body posture, behavioural states, individual conditions and even relative energy expenditure (Wilson *et al.* 2013, 2014), hence solving effectively the fundamental limitation of location-only data (Börger *et al.* 2011). Movement research has so far ignored a key determinant, the energetic cost of movement through a dynamic landscape, but thanks to these technological developments an exciting new era lies ahead (Shepard *et al.* 2013), which will require the development of new theoretical/mathematical methods to incorporate the new possibilities offered by these technologies. For example the Lévy walk is a popular (e.g. Auger-Méthé *et al.* 2015), albeit increasingly controversial (Pyke 2015), method for modelling animal movements. The method focuses exclusively on the distribution of step lengths, as many other random walk methods, assuming a uniform distribution of turning angles. Using the new opportunities proved by multi-channel loggers Wilson *et al.* (2013) could demonstrate a fundamental failure of these approaches, to ignore that the main source of energy expenditure in movement paths is given by the turn costs, not by the distribution of step lengths. Interestingly, the authors also show that the importance of turn costs is predicted by basic Newtonian mechanics.

In conclusion, research in movement ecology is certainly driven by technological development, allowing us to answer long-standing questions. Establishing a closer connection between questions and tools is, however, crucial to efficiently use the opportunities offered by these new tools, and will be even more important in the future. It may even lead to the emergence of new theories and ideas.

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