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## Trackable life: Data, sequence, and organism in movement ecology

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### ABSTRACT

Over the past decade an increasing number of ecologists have begun to frame their work as a contribution to the emerging research field of movement ecology. This field's primary object of research is the movement track, which is usually operationalized as a series of discrete "steps and stops" that represent a portion of an animal's "lifetime track." Its practitioners understand their field as dependent on recent technical advances in tracking organisms and analyzing their movements. By making movement their primary object of research, rather than simply an expression of deeper biological phenomena, movement ecologists are able to generalize across the movement patterns of a wide variety of species and to draw on statistical techniques developed to model the movements of non-living things. Although it can trace its roots back to a long tradition of statistical models of movement, the field relies heavily on metaphors from genomics; in particular, movement tracks have been seen as similar to DNA sequences. Though this has helped movement ecology consolidate around a shared understanding of movement, the field may need to broaden its understanding of movement beyond the sequence if it is to realize its potential to address urgent concerns such as biodiversity loss.

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### 1. Introduction

Since the early 2000s, a number of ecologists have rallied around the banner of movement ecology, a nascent and perhaps ephemeral subfield organized around a newly salient object of inquiry.<sup>1</sup> The object in question is the movement path, trajectory, or track, typically operationalized as a sequence of discrete "steps and stops" taken by an organism within a Cartesian space on time scales ranging from minutes to decades.<sup>2</sup> Although distinctive in its focus, movement ecology is not an isolated development. It is one of a number of data-centric approaches that have emerged in recent

decades across the life sciences as the amount of data that can be collected and stored and the computing capacity to analyze them have grown exponentially.<sup>3</sup> As "big data" are mobilized to address concerns about biodiversity conservation and wildlife management, movement ecology is coming to serve in many cases as a useful conceptual framework, methodological toolkit, and epistemic community. A close examination of its primary object of concern, the track, as revealed through the discourse of some of the subfield's leading figures and through the design of its primary data repository, offers insight both into the practice of data-centric science and into its potential to pose long-standing ecological

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<sup>1</sup> For overviews, see Holyoak, Casagrandi, Nathan, Revilla, & Spiegel (2008); Kays et al. (2015).

<sup>2</sup> Nathan et al. (2008), p. 19053.

<sup>3</sup> On big data and data-centric methods in the life sciences and ecology, see Aronova, Baker, & Oreskes (2010); Strasser (2012); Leonelli (2012, 2014); Stevens (2013); Sepkoski (2013). On histories of data in science, see Daston (2012); Gitelman (2013).

questions in new ways—in particular, its potential to shift attention from the relationship between populations and territories to the dynamic interaction of bodies moving in space.<sup>4</sup>

It has been suggested that data-centric or data-intensive science renders traditional models of the scientific method obsolete by replacing hypothesis-testing with pattern-identification.<sup>5</sup> Such claims are clearly exaggerated; in practice, data-centric or data-intensive sciences show no sign of abandoning hypothesis-testing. Nonetheless, data-centric approaches do tend to shift the focus from a search for underlying causes to the reliable identification of recurring surface patterns. This means that research in fields such as movement ecology often begins, even if it does not end, with agnosticism as to the causal forces that produce a particular observable pattern. What matters in the first instance is that the pattern is identifiable. For movement ecology, the primary object of investigation and site of pattern-seeking is the track. Once identified and characterized, the track may be brought into relation to other variables or causal models, but the initial goal is to understand it on its own terms. By privileging the observable track over the “deeper” evolutionary or ecological processes that divide the living from the non-living and various forms of living things from each other, movement ecologists have been freed to search for commonalities in surface patterns of motion across widely disparate domains: the Brownian motion of particles, the dispersal of wind-borne seeds, the territoriality of rodents, the migrations of birds, and so forth.

This approach to understanding organisms as a subset of a broader class of bodies in motion has important implications both for how research is done and for how it is deployed to address problems of biodiversity and biosecurity. Historians of laboratory-based experimental biology have shown that one of the preconditions for the success of such research is that the organisms under investigation are, or can be rendered, tractable. The “doability” and ultimate success of biological research is tightly tied to the choice of the proper research organism. At the same time, the choice of tractable organisms places more or less well-recognized limits on the ability of scientists to generalize their results.<sup>6</sup> Unlike laboratory biologists, movement ecologists do not attempt to standardize their organisms, but they do focus on organisms that make their research doable, and they do intervene in their lives in ways that expand or improve their suitability for study. The key criterion for them is not tractability but *trackability*: the ability of an organism, as it has been selected, modified, or instrumented for research purposes, to produce movement paths or tracks that can be recorded and analyzed in productive ways.<sup>7</sup> This focus on trackability has significant consequences beyond the practice of ecological science. As movement ecologists make an increasing number of organisms trackable by developing ever-smaller radio-tags, geolocators, and other devices and techniques, they are also changing the affordances available for the management of individuals and populations in space.

Because movement ecology and related approaches are becoming increasingly important for the scientific understanding and management of life, their core ontologies—that is, the fundamental scientific objects around which they are organized—deserve close scrutiny. The need to operationalize abstractions such as movement in concrete practices of data collection, management, and analysis means that contingent choices must be made as to the properties of those objects that will be considered most important. These choices are not an inevitable consequence of the focus on movement. They are the path-dependent products of technological advances, research programs, funding opportunities, personal idiosyncrasies, and chance. In the case of movement ecology, the most important historical condition has been the explosion of research in genomics and bioinformatics since the 1990s, which has provided movement ecologists with powerful data-processing tools and perhaps even more powerful metaphors. The metaphor of the sequence, in particular, has helped movement ecologists make strong claims about the commensurability of different kinds of movement, but it has also oriented the field toward certain understandings of movement and away from others. The remainder of this paper explores the origins of movement ecology, its operationalization of tracks and of trackability in the shadow of genomics, and the way in which those choices have influenced the field’s understanding of the organism.

## 2. The data-centrism of movement ecology

The term “movement ecology” can be found in the scientific literature as early as the 1970s, but it was only in the 2000s that it began to circulate widely as a label for a coherent domain of inquiry.<sup>8</sup> Since then, a small but very active network of ecologists has rapidly constructed the apparatus of a subfield around it, starting with special sections of prominent journals such as *Science* (2006) and the *Proceedings of the National Academy of Science* (2008) on themes of movement, dispersal, and migration. Growing interest in the field has resulted in the establishment of a centralized data repository called Movebank (launched in 2007), a dedicated journal, *Movement Ecology* (launched in 2013), and several large research centers. Two of the most active of these centers are the Department of Migration and Immuno-Ecology led by Martin Wikelski at the Max Planck Institute for Ornithology in Radolfzell, Germany, since 2008 and the Minerva Center for Movement Ecology led by Ran Nathan at the Hebrew University of Jerusalem since 2012. A series of workshops, symposia, and conferences—such as the Symposium on Animal Movement and the Environment held at the North Carolina Museum of Natural Sciences in 2014—have helped knit an international community of movement ecologists together.<sup>9</sup>

<sup>4</sup> The following analysis is based on a close reading of the published scientific literature in movement ecology and of public statements on the state and goals of the subfield by some of its leading figures. It also draws on a growing body of work examining the history and present role of movement-tracking techniques in conservation biology; see Mitman (1996); Benson (2010, 2011, 2014); Koelle (2012); Reinert (2013); Blavascunas (2013); Stokland (2014); Whitney (2014).

<sup>5</sup> E.g., Anderson (2008).

<sup>6</sup> On doability and the importance of the choice of the right organism, see Clarke & Fujimura (1992); Lederman & Burian (1993). On model organisms, see Bolker (1995); Joyce & Palsson (2006); Leonelli & Ankeny (2012).

<sup>7</sup> I use the term *trackability* here rather than *traceability* to emphasize the specifically spatial nature of the object that is the focus of movement ecology; cf. the discussion of biological tracers in Griesemer (2007) and Creager (2013).

<sup>8</sup> The term can be found in the ecological literature as early as the 1970s with many of the same meanings and connotations that it holds today, including a close connection to technological developments in animal tracking and an interest in drawing generalizable, cross-species conclusions about motion (Brown & Parker, 1976). A search of the ISI Web of Science citation database with the phrase “movement ecology” as topic conducted on 22 October 2014 resulted in 204 results. More than half of the articles using this term have been published since 2011. Movement ecologists have recently begun to reflect on the origins of the field. Fagan & Calabrese (2014) argue that an article by Kareiva & Shigesada (1983) on correlated random walks provided an important model for movement ecologists of how abstract spatial models could be brought into relation to empirical data.

<sup>9</sup> Relevant links: the Minerva Center: <http://move-ecol-minerva.huji.ac.il/>; Wikelski’s department: <http://www.orn.mpg.de/wikelski>; the 2014 North Carolina workshop: <http://amovee2014.com/>; the *Movement Ecology* journal: <http://www.movementecologyjournal.com/>; Movebank: <https://www.movebank.org/>.

The emergence of movement ecology as a self-conscious sub-field or research program at this particular historical moment is often described by practitioners as a result of technological advances that fall into two broad areas: the collection of data and the analysis of data. On the collection side, technological advances have made it possible to acquire an unprecedented amount of detailed data about the movements of individual organisms. While electronic tracking devices have been in use among animal ecologists since the 1960s, the range of environments and animals to which they can be applied has long been limited by their weight and size and by the labor-intensive process of collecting tracking data by hand.<sup>10</sup> More recently, miniaturized radio-tags, geolocators, and data loggers, non-tagging-based techniques such as isotope-based tracking, and expanded surveillance and communications infrastructures, including both specialized scientific observation networks and general-purpose telecommunications networks, have greatly expanded the variety of trackable organisms.<sup>11</sup>

With smaller tags, expanded infrastructures, and automated data collection, it has become increasingly plausible—if still far from realized in practice—to see individualized tracking as a technique applicable to organisms generally and trackability as a basic criterion for research. Martin Wikelski, for example, has suggested that the extension of tracking techniques to ever-smaller organisms may “solve some of the longest-standing biological enigmas across a range of disciplines and provide a much sought-after tool for experimental biologists of all fields.”<sup>12</sup> The emphasis on experimentation is significant: rather than simply expanding the observational powers of field researchers, tracking promises to allow laboratory-like experimentation to take place on a global scale.<sup>13</sup> To accelerate this process, Wikelski and others have sought to develop new tracking infrastructures. The International Cooperation for Animal Research Using Space (ICARUS) project, for example, aims to place a new generation of highly sensitive animal-tracking receivers on orbiting satellites; it has recently received large-scale support from the German and Russian science and space agencies.<sup>14</sup> Such projects pose trackability as a criterion dividing living things into those that can be studied by movement ecologists at the present moment and those which will become available for study once the necessary techniques and infrastructures have been developed.<sup>15</sup>

In addition to enhanced data collection capabilities, the other major area of technological development seen by movement ecologists as crucial to the emergence of their field is an increased capacity for data storage, dissemination, and analysis. From a strictly technological point of view, the decreasing cost of digital storage media, the ease and speed of transmitting data across long distances via the Internet, and increasing computational power have made it feasible to employ complex algorithms on massive collections of tracking data. As with data-gathering technologies, most of these developments initially represent changes in quantity that gradually lead to changes in quality.<sup>16</sup> Digital computers have been used to process, analyze, and even simulate animal-tracking

data since the 1960s, but the earliest such examples required each data point to be entered onto a punched card by hand before being submitted to a mainframe computing center for processing.<sup>17</sup> In contrast, much of today's tracking data is initially recorded in digital form on devices wired into global telecommunications networks. By lowering transaction costs, the digitization of data collection is facilitating the emergence of databases that aggregate tracking data from many different investigators, studies, and species. These databases, in turn, provide opportunities to generalize models of movement across species, genera, and even higher taxonomic levels.<sup>18</sup> When combined with increasingly sophisticated algorithms for processing movement data and relating it to environmental factors and other variables, they provide the technical foundation for a new class of researcher in animal ecology, the data specialist.<sup>19</sup>

Developing and deploying these technological developments does not come cheap, and movement ecologists have offered a number of reasons why research sponsors should invest their limited resources in the field. Arguments for the practical benefits mix the discourse of biological security with that of nature preservation; they include the management of risks, such as the transmission of diseases by migrating birds and the spread of invasive species, as well as the preservation of value, particularly that of organisms that migrate long distances and the ecosystems they depend on.<sup>20</sup> The initial grant application for the data repository Movebank to the U.S. National Science Foundation in 2007, for example, claimed that “[s]tudying animal movement is of critical importance to addressing environmental challenges including invasive species, infectious diseases, climate and land-use change.”<sup>21</sup> What movement ecology offers in comparison to other methods of addressing such concerns is an understanding of ecological space in terms of organismic tracks. Rather than dividing the landscape into territories occupied by populations, as was common in ecology in the twentieth century, movement ecology maps the “quilt” or “tapestry” woven together from the paths followed by individual bodies.<sup>22</sup> For the advocates of movement ecology, this approach promises to allow for the management of risk and preservation of biodiversity with an unprecedented level of precision and responsiveness to change.<sup>23</sup>

Aside from such practical concerns, movement ecology has been offered as a synthetic framework that unifies and clarifies existing research interests within ecology while also building bridges beyond it into neighboring fields. The website of the Minerva Center, for example, claims that its research will elucidate “the fitness consequences of lifetime movement, the secrets of animal navigation, and the drivers of inter-continental bird migration.”<sup>24</sup> By focusing on movement per se, movement ecology promises to bring insights developed in one scientific domain to another so that, for example, statistical models developed for understanding the Brownian movement of particles or the tropisms of single-celled organisms can be adapted to the study of complex,

<sup>10</sup> Benson (2010).

<sup>11</sup> See, e.g., Cagnacci, Boitani, Powell, & Boyce (2010); Kays et al. (2015).

<sup>12</sup> Wikelski et al. (2007), p. 183.

<sup>13</sup> On the history of attempts to bring laboratory-like practices into the field, see Kohler (2002).

<sup>14</sup> Max Planck Institute for Ornithology (2014).

<sup>15</sup> For a discussion of the impact of technological advances on bird-tracking, for example, and the need for satellite-based systems that can track very small birds, see Bridge et al. (2011); see also Pennisi (2011). On model organisms and tractability, see Ankeny & Leonelli (2011).

<sup>16</sup> On the relatively conservative way in which computers were initially incorporated into biological research, see Agar (2006).

<sup>17</sup> Siniff & Tester (1965).

<sup>18</sup> On data processing and management in movement ecology, see Urbano et al. (2010).

<sup>19</sup> These data specialists often have skills that cross over biological domains. The lead author of one study of elephant movements, for example (Boettiger et al. 2011), was trained in a biophysics department and works primarily on gene expression.

<sup>20</sup> On discourses of biosecurity, see Lakoff and Collier (2008).

<sup>21</sup> Kays (2011b).

<sup>22</sup> Such textile metaphors can be found in Nathan et al. (2008), p. 19052.

<sup>23</sup> On the importance of movement ecology for understanding disease transmission, for example, see Altizer, Bartel, & Han (2011).

<sup>24</sup> Minerva Center for Movement Ecology (n.d.).

multicellular organisms operating on human-like temporal and spatial scales. At the same time, by focusing on the movements of individuals who make decisions in response to environmental conditions, it builds bridges from ecology to ethology, psychology, and animal behavior studies. Finally, it offers a framework for integrating existing approaches to movement within ecology that have tended to be considered in isolation. These include the physics of locomotion, stochastic movement processes, individual decision-making, and the evolutionary consequences of different movement strategies. Movement ecology thus promises to generate new scientific insights by unifying research across different forms of life, across different disciplinary approaches to understand individual lives, and across different methodological approaches within the ecological study of movement.<sup>25</sup>

Despite their focus on movement as a phenomenon of interest in its own right, movement ecologists are not uninterested in the evolutionary and ecological processes that influence it. On the contrary, they describe their approach as potentially illuminating long-standing questions about those processes that have not been resolved by previous methods. The Minerva Center for Movement Ecology, for example, includes “elucidat[ing] the links between movement patterns and their underlying processes” as one of its primary aims.<sup>26</sup> The director of the center, Ran Nathan, has offered an influential theoretical framework for movement ecology that explicitly identifies the kinds of causal processes that ecologists need to take into account to produce a truly explanatory and predictive, rather than merely descriptive, science.<sup>27</sup> More broadly, movement ecology emerges partly from the growth in interest since the 1990s in so-called mechanistic models of animal movement and distribution, which aim to explain observed patterns in terms of detailed mathematical models of “underlying” behavioral, physiological, and environmental factors.<sup>28</sup>

Nonetheless, there is a significant ontological shift involved in the identification of movement per se as the phenomenon of interest. Just as a focus on the dynamics of population growth abstracts from the underlying causes driving the rise and fall of any particular population and encourages scientists to search for patterns that hold across populations, so does a focus on movement abstract from the underlying causes leading an individual to move in a particular way.<sup>29</sup> The first step of an ecologist interested in foraging as an evolutionarily significant behavior might be to identify behaviors of particular evolutionary or ecological significance and then develop an observational or experimental protocol to collect data about that behavior. In contrast, the movement ecologist might start with an observed pattern of movement over a given time interval—perhaps even a “lifetime track”—which he or she would then divide into qualitatively different segments on the basis of surface characteristics, perhaps with the aid of partially automated statistical algorithms that are applicable regardless of the nature of the body that is in motion.<sup>30</sup> Only subsequently are certain of these segments identified as associated with foraging, mating, migrating, etc., and linked to evolutionary or ecological factors. It is for this reason that statistical models of random walks or Markov chains have so often served as the starting point for

analyses in movement ecology: they can be applied just as easily to albatrosses as to ants, to sea lions as to seed pods.<sup>31</sup>

There are several consequences of this approach for the way movement ecology is practiced. One is the privileging of minimalist explanations of animal behavior—that is, explanations whose null hypothesis is that animal movement is entirely random. This “behavioral minimalism” puts the burden of proof on those who seek to explain movement as the result of complex organism-environment interactions rather than simple stochastic processes.<sup>32</sup> Another consequence is to highlight the existence of movement patterns whose function is unclear. Like noncoding or junk DNA in genomics, these apparently nonfunctional movements come under scrutiny precisely because it is the movement path as a whole and as such that is the object of investigation, rather than movement only inasmuch as it can be understood as the ephemeral surface expression of deeper, more meaningful causes. Perhaps the most important consequence, however, is to facilitate comparisons across diverse species and even across the living/non-living divide.

### 3. The track as sequence

The commensurability of the tracks of different objects cannot be taken for granted, but instead has to be produced via a standardized conceptualization of movement that allows, for example, the tracks of widely varying biological species to be incorporated into a single database or plotted on a single map. For contingent reasons, even though movement ecology draws heavily on physical and statistical models of movement, the metaphor of the genomic sequence has played a key role in making movements commensurable in this way in movement ecology. The influence of the genomic model is not something that requires especially subtle analysis or behind-the-scenes investigation to uncover. It is often either explicit or self-evident, as with the most ambitious and, to date, successful repository in movement ecology, Movebank, whose name is modeled on that of the first major repository of genetic data, GenBank.<sup>33</sup> As with GenBank and other scientific data repositories (and collections in general), the success of Movebank depends on establishing agreement about the kinds and formats of objects to be deposited.<sup>34</sup>

Movebank was initially funded by the U.S. National Science Foundation through a grant to Roland Kays, then curator of mammals at the New York State Museum, and Martin Wikelski, then at Princeton University. From 2007 to 2011, NSF awarded more than \$1.1 million under its Advances in Biological Informatics program for the construction of the repository, in addition to funding for related animal-tracking projects. For technical expertise in database design and analysis, Kays and Wikelski turned to computer scientists at the San Diego Supercomputer Center and the University of Illinois at Urbana-Champaign. By the end of the initial grant period, Movebank included about 10 million location data points from more than 17,000 animals, with 18 million additional non-location data points from accelerometers and other sensors.<sup>35</sup>

<sup>31</sup> For a survey of the use of random-walk methods in animal ecology, see [Turchin \(1998\)](#).

<sup>32</sup> On the figure of the “minimal animal,” see [Benson \(2014\)](#). The term “behavioral minimalism” is developed in [Lima & Zollner \(1996\)](#).

<sup>33</sup> This influence was even more evident at the beginning of the project, when the name of the repository was styled MoveBank. For an example of the initial GenBank-like orthography, see [National Science Foundation \(n.d.\)](#). References to GenBank can also be found elsewhere in the movement ecology literature; see, e.g., [Cagnacci et al. \(2010\)](#), p. 2159.

<sup>34</sup> On the history of GenBank, see [Hilgartner \(1995\)](#); [Strasser \(2008\)](#); [Stevens \(2013\)](#).

<sup>35</sup> [Kays \(2011b\)](#).

<sup>25</sup> The theme of unification is widespread but particularly evident in [Nathan et al. \(2008\)](#).

<sup>26</sup> [Minerva Center for Movement Ecology \(n.d.\)](#).

<sup>27</sup> [Nathan et al. \(2008\)](#).

<sup>28</sup> [Moorcroft & Lewis \(2013\)](#).

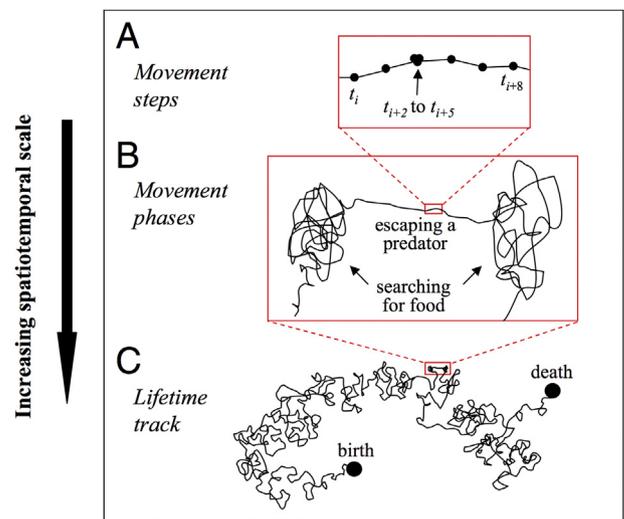
<sup>29</sup> On the history of population ecology, see [Kingsland \(1985\)](#).

<sup>30</sup> E.g., [Eliezer Gurarie, Russel D. Andrews, and Kristin L. Laird, “A Novel Method for Identifying Behavioural Changes in Animal Movement Data,” \*Ecology Letters\* 12, no. 5 \(2009\): 395–408.](#)

Movebank is now hosted by the Max Planck Institute for Ornithology in Germany, one of whose departments is lead by Wikelski. It has continued to grow, aided by the fact that some funding agencies and journals now either encourage or require data to be publicly archived. It has also added new tools, such as the Env-DATA system, which makes it possible to automatically annotate movement tracks with weather and other environmental data.<sup>36</sup>

Despite the incorporation of non-location data into Movebank, the track as a sequence of coordinates plotted in a Cartesian space over time remains the central data object around which other sorts of data are assembled. This operationalization of movement as sequence has been heavily influenced by genomics. In the case of GenBank and similar genetic databases that emerged in the 1980s and 1990s, the literal encoding of genetic data as computable sequences helped consolidate an informatic understanding of DNA as the “code” of life and of genetics as a science of decoding—an understanding that has been simultaneously radicalized and questioned in various postgenomic fields as well as in synthetic biology, which aims to identify and reengineer the “building blocks” of life.<sup>37</sup> This privileging of DNA-as-sequence provided the computational commensurability across individuals and species that made it possible for bioinformatics per se to emerge as a distinctive area of expertise. Similarly, for ecologists, the operationalization of movement as sequence holds out the promise of abstracting away the contextual factors that might otherwise make, say, the continent-spanning migrations of a bird difficult to understand within the same framework as the foraging flights of a mosquito or the seed-dispersal strategies of a flowering plant.<sup>38</sup> Ecological or evolutionary factors can subsequently be used to explain why, in fact, different organisms move differently, just as they can be used to explain why genomes differ, but the operationalization of movement as sequence is the initial step that makes underlying commonalities visible. The commensurable sequence becomes a kind of “scaffold” for other, perhaps less commensurable data that are assembled around it.<sup>39</sup>

The parallels between the track and the DNA sequence, between movement ecology and genomics, and between movement and inheritance have been explicitly articulated by Nathan, who suggests that spatial coordinates at particular times can be seen as the metaphorical equivalent of DNA base pairs. Much like the DNA sequence, he suggests, the track is made up of smaller elemental units (i.e., locations in time and space), but it is nonetheless the smallest unit that is biologically meaningful. At a higher level of organization, the discrete points sampled from a continuous movement path can be clustered into movement phases, which correspond metaphorically to genes and reflect the different patterns of movement that emerge in light of the organism’s changing goals—e.g., feeding, mating, or avoiding predators. Movement phases, in turn, can be clustered into a single “lifetime track,” which is the movement-ecological equivalent of an individual genome (see Fig. 1). The genomic metaphor gives Nathan the opportunity to suggest movement ecology’s revolutionary potential: “improved tracking technology promises to do for movement ecology what genetic sequencing did for molecular genetics: to provide an



**Fig. 1.** Nathan et al.'s 2008 visualization of the movement path at increasing spatiotemporal scales, which shows the influence of the genomic model. The movement path is defined as “a sequential collection of steps and stops” (Nathan et al., 2008, p. 19053, Fig. 1). Reproduced with permission of the Proceedings of the National Academy of Sciences of the United States of America.

elemental view of a movement track, in the same way that a nucleotide sequence provides an elemental view of a DNA string. The scientific revolution potentiated by genome sequencing can be compared with insights about movement drawn from mapping every step and stop of an individual during its lifetime track from birth to death.”<sup>40</sup>

Such discretized “step and stop” representations of movement predate the recent emergence of movement ecology by decades; they are a precondition rather than a product.<sup>41</sup> Nonetheless, the expansion of electronic tracking methods since the 1960s and their accelerating computerization in the past several decades have generalized a practice that was once limited to only a few of the most easily trackable species under particular environmental conditions. The key shift has been the transition from mapping a distribution of locations at which a marked or otherwise recognizable animal has been observed to mapping trajectories followed by an individual. Previously, such trajectories were mappable in the field only when individual animals could be followed visually for extended periods of time or when they left detectable tracks in snow, mud, or other substrates. The introduction of radioisotope and dye tracers in the 1940s and 1950s, and then of radio-tracking devices in the 1960s, made it possible to generate “tracks” even for animals that left no visible marks. Since the 1990s, the increasing affordability and miniaturization of Global Positioning System (GPS)-enabled tags and data loggers has made highly detailed tracks increasingly easy to collect. Partly as a result, representations of movement in terms of sequences are now being granted a new ontological status as instances of a data object, the track, around which a new set of practices can be developed.<sup>42</sup> Like other kinds of data objects, the track is simultaneously a construction meant to mirror something in the world—in this case, the physical but intangible and ephemeral movement of an organism—and an

<sup>36</sup> Dodge et al. (2013).

<sup>37</sup> On genetics as code, see Kay (2000); Keller (2000, 2002); Stevens (2013). On synthetic biology, see Roosth (2013).

<sup>38</sup> On the red knot, a migrating shorebird, see Whitney (2014).

<sup>39</sup> For the idea of DNA sequence as scaffold, see Stevens (2013), p. 205. On the insufficiency of location coordinates for capturing the full range of ways in which locality enters into ecological research, see Shavit & Griesemer (2009, 2011). On the limits of databases more generally, see Bowker (2000, 2005). For a more skeptical take on the ability of data structures to determine scientific ontologies, see Hine (2006).

<sup>40</sup> Nathan et al. (2008), p. 19053. The genomic metaphor is also deployed in a recent overview of movement ecology by Kays et al. (2015), p. 2.

<sup>41</sup> On the development of statistical models of animal movement in the 1950s and 1960s, see Benson (2014).

<sup>42</sup> On the impact of GPS on wildlife tracking, see Cagnacci et al. (2010); Urbano et al. (2010).

object with its own structures and affordances. These structures and affordances are related to, but not reducible to, either the material form in which data is recorded and communicated or the information that is conveyed.

The formulation of the movement path or track as a sequence of discrete “steps and stops” has important implications both for data collection and for data analysis. On the data collection side, it forces the researcher to make decisions about sampling rates that can influence the movement paths that result. Increasing the frequency of sampling inevitably raises costs and runs up against material limits: transmitter batteries are exhausted, bandwidth proves insufficient, and storage media fill up. Moreover, frequent sampling can pose problems for analysis methods that are based on the assumption that each successive step is a statistically independent event. On the other hand, sampling at a lower rate can obscure ephemeral or rapidly changing movement phenomena, such as quick out-and-back foraging trips. The most appropriate rate of sampling depends on the movement of interest. A snowshoe hare attempting to evade a fox will move at a different rate than one foraging or resting, for example, and will therefore require a correspondingly different minimum frequency of sampling. Even in a world of abundant data, movement ecologists working with discretized movement paths as their primary data object are forced to make decisions about the temporal and spatial scale of the phenomena they wish to observe. Statistical methods for modeling the unobserved times between two data-points in continuous time and space have been developed, but they too require scientists to see animal use of space “not as a geometry to be discovered but as a biological construct inextricably linked to a question or hypothesis.”<sup>43</sup>

The theory-laden nature of animal-tracking data challenges one of movement ecology’s most appealing characteristics: its ability to generate models and explanations of movement that are general enough to cross species borders while also taking into account environmental, physiological, and other factors. As a thought experiment, consider the kinds of “decisions” that lie behind the movements of a migratory bird sampled either on an hourly or on a monthly basis. On an hourly basis, the movement of the bird is likely to be determined by food availability, predation threats, mating opportunities, and other short-term factors. On a monthly basis, however, movement is likely to be determined primarily by seasonal changes in daylight, temperature, or vegetation cover. At each scale, errors in measurement can lead to significant qualitative shifts in the observed patterns of movement.<sup>44</sup> Moreover, as the interval between observations increases, so can the uncertainty about the path that connects the two locations.<sup>45</sup> Models developed to explain movement on one temporal–spatial scale can be largely irrelevant to explaining movement on other scales; movement ecologists admit that they “do not yet know the best temporal ‘scale’ to sample different species to ensure inferences from such statistical approaches match with ‘real’ behaviors.”<sup>46</sup> On a more technical level, as one group of movement ecologists has recently argued, “inferences from discrete-time models are not time scale-invariant.”<sup>47</sup> As a result, there is no straightforward way in many cases of comparing the movement processes along two supposedly

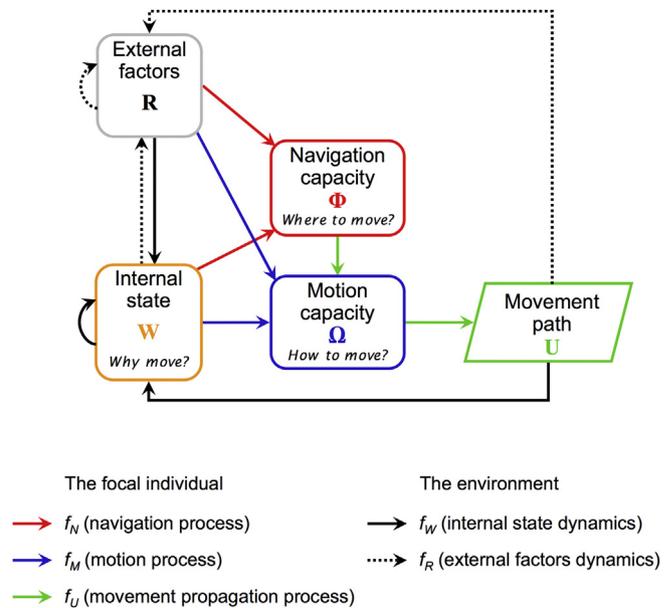


Fig. 2. Nathan et al.'s 2008 model of a “general conceptual framework for movement ecology,” showing how the movement path emerges from the interaction of four factors: external environment, internal state, motion capacity, and navigation capacity (Nathan et al., 2008, p. 19054, Fig. 2). Reproduced with permission of the Proceedings of the National Academy of Sciences of the United States of America.

comparable tracks sampled at different rates, even for a single species.

This scale-dependence suggests one important difference between genomics and movement ecology: unlike DNA sequences, it is not obvious how to divide the trajectories of animals (or plants) into discrete chunks.<sup>48</sup> Kays and other movement ecologists suggest that increasing the frequency of sampling so that the time intervals become shorter than any possibly relevant movement phenomenon will render this question moot, but the solution comes at the cost of reducing the variety of organisms that can be effectively tracked, since higher-frequency sampling over a given time period generally requires heavier batteries, storage media, or both.<sup>49</sup> One must choose between two kinds of incommensurability: either one can track a wide range of organisms at time intervals that place a priori constraints on the phenomena that can be observed, or one can track a limited range of organisms at very high temporal frequency. Neither choice provides the evidentiary basis to make unqualified claims about movement as such.

A comparison with model organism databases is instructive. While such databases face a number of challenges, many of those challenges are simplified by the fact that each database, by definition, focuses on a single type of organism—the thale cress, for example, or the zebra fish. Moreover, model organisms concern a “subgroup of organisms that have been standardized to fit an integrative and comparative mode of research.”<sup>50</sup> Although databases centered on model organisms face the challenge of integrating varying kinds of data about the organism in question and extrapolating beyond it, this selection and standardization means that there is a single, agreed-upon object of concern about which a variety of different kinds of data can be collected and compared.<sup>51</sup>

<sup>43</sup> Quote from Lyons, Turner, & Getz (2013). For an alternative method of dealing with discrete measurements of tracks, which also suggests the importance of non-organic models of movement for understanding organisms in movement ecology, see Kranstauber, Kays, LaPoint, Wikelski, & Safi (2012).

<sup>44</sup> See, e.g., Bradshaw et al. (2007).

<sup>45</sup> Horne, Garton, Krone, & Lewis (2007), pp. 2361–2362.

<sup>46</sup> Hebblewhite & Haydon (2010), p. 2309. For one strategy for accounting for multiple scales, see Benhamou (2013).

<sup>47</sup> McClintock, Johnson, Hooten, Ver Hoef, & Morales (2014), p. 13.

<sup>48</sup> Geneticists have also realized that much happens around DNA strands that cannot easily be captured in a sequence database; see Keller (2000, 2002).

<sup>49</sup> Kays et al. (2015), p. 3.

<sup>50</sup> Ankeny & Leonelli (2011), p. 313.

<sup>51</sup> On model organisms, see Bolker (1995); Joyce and Palsson (2006).

No such selection of organisms, let alone standardization, takes place in the case of a generalized movement ecology database. What have been standardized instead are space, time, and the discrete form in which the movement track is represented. Because inferences about mechanism are not independent of time scale in discrete-time models, however, such standardization does not necessarily entail comparability. When movement databases are confined to certain kinds of species, certain temporal-spatial scales, and certain kinds of research questions or hypotheses, they may indeed be able to generate new integrative insights within a limited domain.<sup>52</sup> But in doing so they relinquish movement ecology's ambition to provide insight into the fundamental principles of biological movement (see Fig. 2). Drawing synthetic conclusions from studies of wildly disparate forms of life requires not only unifying theoretical frameworks but also compatible data structures.<sup>53</sup> Without them, a repository such as Movebank risks becoming, in effect, a repository of repositories focused on distinctive and incommensurable times scales, organisms, and research questions.

#### 4. The trackable organism

Movement ecology is one of a number of sites today where organisms of all kinds—including the human organism—are being reimagined and newly operationalized in light of unprecedented varieties and quantities of data. For movement ecology, in particular, the importance of data per se is not new; what is new is that vast amounts of fine-grained digital data on location are now available at relatively low cost, which has opened up new fields of investigation. By using this data to make movement the primary phenomenon of interest and the movement track the primary object of concern, movement ecology is redefining what it is that matters about organisms.<sup>54</sup> Movement can thus be seen as a “defining characteristic of animals,” as Roland Kays and his colleagues have argued, or even as “a fundamental characteristic of life,” as Ran Nathan has argued, rather than a result of other, more fundamental processes.<sup>55</sup> The ontological privileging of movement and the track has opened up connections not solely to the statistical physical sciences but also to the broader question of mobility, a theme of increasing interest across a number of scientific and humanistic disciplines. Rendered at least partially independent from questions of evolutionary adaptation and physiological processes, movement is becoming a phenomenon that potentially unifies concerns that cross between animals, machines, and humans. Freed from a commitment to a deep ontology of the organism that would tie them to specific biological questions and theoretical frameworks, movement ecologists become capable of expanding into and borrowing from a variety of neighboring domains. Some interdisciplinary collaboration around themes of movement and mobility are already underway.<sup>56</sup>

Within biology and ecology, the focus on movement entails a transformed understanding of the relationship of the organism to its surroundings. Since the nineteenth-century work of Claude

Bernard and other physiologists, the organism has often been understood as an entity that maintains an internal environment or *milieu intérieur* as a way of adapting to its external environment or conditions of life.<sup>57</sup> In other words, the organism has been posed as the mediator between vital processes and the contexts in which they operate. Whereas physiology has focused on the organism's internal environment, ecology has focused on the organism's relationship to its external environment, understood as including both abiotic factors and other organisms.<sup>58</sup> In a subfield such as ecosystem ecology, this focus on external factors can lead to a view of the organism as a little more than a passage-point for processes that recirculate energy and matter through systems. The movement of an organism, from this perspective, is a mechanism for transferring energy and matter from one location to another as part of a system of dynamic feedback and control whose real units are trophic levels or ecosystem functions.<sup>59</sup> Population ecology similarly displaces the organism in favor of a focus on reproducing groups of organisms (i.e., populations) defined in reproductive or spatial terms. In this case, movement becomes a mechanism for redistributing genes and populations across landscapes.<sup>60</sup> In movement ecology, in contrast, the organism remains at the center of the frame—not as a physiologically homeostatic unit or as a fitness-maximizing individual, but in the form of a body in motion through space.

Movement ecology is also producing a new understanding of the kind of organism that is best suited to scientific research. Without the ability to collect and analyze large amounts of movement data of a particular kind, this approach to the organism would be of only limited interest, as it has been for most of the history of modern biology. The rapid accumulation of such data in the past several decades has, however, opened up a new field for scientific exploration. Whereas one of the practical criteria for an organism to become a “model organism” for laboratory research is that it be experimentally tractable, for an organism to become suitable for movement ecology it must above all be trackable—that is, capable of being used to reliably generate the track as a data object. Trackability, like experimental tractability, thus becomes a hidden criterion for the inclusion of an organism in the field of objects about which knowledge can be produced. Just as fruit flies and Norway rats were well-suited to the laboratory environments in which they became crucial components of experimental systems for genetics and physiology in the twentieth century, so are certain kinds of organisms particularly well-suited to being the trackable organism of twenty-first-century movement ecology studies. Birds, for example, continue to be central to movement ecology despite the field's universalizing aims. This is partly because the temporal and spatial scale of their movements, the medium through which they move, and the size of their bodies in relation to those of humans makes them relatively easy and scientifically rewarding to track using existing technologies.<sup>61</sup>

Movement ecology's focus on movement per se as the phenomenon of interest and on trackability as a criterion for inclusion in scientific studies has consequences not only for the practice of scientific research but also for practical problems such as biodiversity loss. Just as fascination with charismatic megafauna shaped conservation throughout the twentieth century and continues to do so today, movement ecology's privileging of the trackable organism

<sup>52</sup> See, e.g., the Census of Marine Life, briefly described in O'Dor (2004).

<sup>53</sup> For a detailed analysis of data structures and models in climate science, see Edwards (2010).

<sup>54</sup> On the imagination of the “minimal animal” that is associated with this approach, see Benson (2014).

<sup>55</sup> Kays et al. (2015), p. 1; Nathan et al. (2008), p. 19052.

<sup>56</sup> See, e.g., Demšar et al. (2015). There are also as-yet-unexplored resonances between movement ecology and sociological studies of mobility; e.g., Urry (2007). Movement ecologists' openness to non-organic models of movement processes is particularly evident in studies of seed dispersal; see, e.g., Levin, Muller-Landau, Nathan, & Chave (2003).

<sup>57</sup> Holmes (1986).

<sup>58</sup> Nyhart (2009).

<sup>59</sup> On ecosystem ecology, see Hagen (1992); Bocking (1997).

<sup>60</sup> On population ecology, see Kingsland (1985).

<sup>61</sup> On the history of bird tracking, see Barrow (1998); Wilson (2010); De Bont (2011).

has the potential to reorient policy and public interest around organisms that can be used to generate abundant and easily narrativized tracks—much as *Drosophila melanogaster*, the fruit fly, became central to twentieth century genetics in part because of its capacity to rapidly produce mutations.<sup>62</sup>

In some cases, an organisms' existing charisma may serve as the driver of expanded trackability: elephants, for example, have been tracked in detail in recent decades in part because they have long been seen as impressive, dangerous, and endangered. Detailed tracking, in turn, has helped solidify their reputation as organisms with rich individual biographies and complex social lives that come into close contact with those of humans.<sup>63</sup> In other cases, tracking may bring attention to organisms whose lives had previously been difficult to render charismatic, either because they were elusive or because they were enacted on inhuman scales. An example of a secretive creature rendered charismatic through tracking is the fisher, which has been tracked with high spatial resolution radio-collars by Roland Kays, one of the co-founders of Movebank, in upstate New York. The process and results of this research were documented in a series of blog posts in the *New York Times* in 2011, giving the rarely seen species an unprecedented level of press exposure.<sup>64</sup> If photogenicity was crucial to the charisma of twentieth-century wildlife, trackability may be the key in the twenty-first century.<sup>65</sup>

Movement ecology's concern with movement per se, its construction of the track as its primary data object, and its efforts to make organisms trackable also have other implications for the management of life. In the twentieth century, biologists developed new tools for understanding and managing the relationships between populations and territories. These tools were easily transferred between human and nonhuman domains, so that an expert on butterfly population ecology such as Paul Ehrlich could become a leading neo-Malthusian advocate for human population control as well as a proponent of biodiversity conservation through the establishment of protected areas.<sup>66</sup> Movement ecology is still in the making and its future contributions to policy remain uncertain, but it is already clear that it offers a different set of possibilities for the management of life than did population ecology.

One can see these possibilities in the way Movebank's potential practical applications are discussed. On the one hand, one of its most promising applications is the use of multispecies tracking data to identify critical areas to be protected; in this way it simply extends the existing populational-territorial paradigm. On the other hand, movement ecology emphasizes the dynamic nature of organismic movements, which shift seasonally and in response to changes in climate, population density, and other factors; it also makes visible the wide range of variability among individuals within a population or species. A repository such as Movebank thus offers conservationists and land managers the possibility of managing life as a dynamic lacework of intersecting movement paths in relation to changing environmental conditions rather than as the growth and decline of populations within or across static territorial

containers. While new biopolitical configurations are still in the making, there is no reason to suspect that techniques for the study and management of organisms-in-motion will be any less portable across the human-animal divide in the twenty-first century than the study and management of populations-in-territories was in the twentieth century.<sup>67</sup>

## 5. The limits of sequence

Noting the inapposite aspects of the genomic metaphor and the practical difficulties for analysis that are produced by operationalizing movement tracks as sequences of discrete location–time pairs, one might be tempted to conclude that movement ecology should broaden its framework to consider other approaches to the phenomenon of movement—including approaches that are not limited to data collected through radio-tracking and GPS tags and other forms of remote, discretized sampling of movement tracks. In fact, within the fields of ecology and wildlife biology, movement ecology's preoccupation with the technical aspects of data collection and analysis has been criticized by those who believe that “much research devoted to collecting more location data and analyzing them with ever-better statistical procedures is misguided until we understand better what, exactly, we are estimating.”<sup>68</sup> Mammalogists Roger Powell and Michael Mitchell have argued that beginning one's analysis by “simply plotting time spent in different places” and only subsequently looking for ecological or evolutionary explanations is less useful than beginning with “the biological, fitness-driven reasons behind animals' use of space.”<sup>69</sup> In an argument that resonates with Jakob von Uexküll's early twentieth-century approach to the animal *Umwelt*, Powell and Mitchell suggest approaching movement not as an objective path through Cartesian space but rather as a subjective relationship between the organism and its environment—defining “home range,” for example, not in terms of quantitative measures of observable movement but in terms of an animal's cognitive map of space.<sup>70</sup>

The approach they are criticizing is, of course, the basic methodological innovation of movement ecology, which privileges the “superficial” movement track over “deeper” causes and operationalizes movement as a discrete sequence. How or whether movement ecologists will be able to incorporate such critiques into their evolving practices remains to be seen, but the challenge is not trivial: it goes to the very heart of the question of whether movement as such is a phenomenon that can be productively studied.<sup>71</sup> In the meantime, the acceleration of data collection and the development of ever-more sophisticated statistical techniques for identifying patterns in movement tracks continue apace. For movement ecologists, the possibility of obtaining more data about a wider variety of species—particularly songbirds, rodents, flying insects, and other small animals that have hitherto been difficult to track because existing tags are too heavy or bulky for them to carry—suggests a sense in which the idea of movement as sequence can be taken to its limit and perhaps beyond. As the feasibility of high-frequency short-interval measurement of animal movement on a global scale increases and as millions of data points become as easy to handle computationally as hundreds or thousands, the

<sup>62</sup> Kohler (1994).

<sup>63</sup> Mitman (2005). For a movement ecology approach to studying elephants, see Boettiger et al. (2011).

<sup>64</sup> Links to Roland Kays' blog posts for the *New York Times* and other information about his fisher research can be found at: <http://rolandkays.com/fisher/>. This work was carried out in collaboration with one of his graduate students, Scott LaPoint. For a blog post that discusses the use of Movebank to archive tracking data, see Kays (2011a). On the combination of GPS- and accelerometer-based methods used to track the fishers with very high spatial resolution, see Brown et al. (2012).

<sup>65</sup> On the importance of photography, film, and television in generating interest in and support for conservation of wildlife in the twentieth century, see Mitman (1999); Bousé (2000); Gouyon (2011).

<sup>66</sup> On Ehrlich, see Sabin (2013).

<sup>67</sup> On population and territory in twentieth-century conservation biology, see Benson (2015). For a recent example of conservation-relevant movement ecology, see Cushman, Lewis, & Landguth (2013).

<sup>68</sup> Powell & Mitchell (2012), p. 948.

<sup>69</sup> Powell & Mitchell (2012), p. 956.

<sup>70</sup> Uexküll (2010 [1934]).

<sup>71</sup> For a more narrowly targeted critique of the statistical assumptions that movement ecologists often make, see Pozdnyakov, Meyer, Wang, & Yan (2014).

question of the appropriate sampling interval promises to recede in importance, even as new problems of data management emerge.<sup>72</sup> With short enough sampling intervals, the difference between discrete and continuous measurement may become irrelevant, inasmuch as all phenomena of interest to the biologist will take place at frequencies higher than those which can be effectively characterized given the sampling rate. Thus a quantitative increase in data could, perhaps, lead to a qualitative shift in the epistemological obstacles faced by movement ecologists.

This appealing scenario is, however, likely to remain in the realm of the ideal for several reasons. First, while it is thinkable that animals above the size of the smallest songbird or perhaps even larger insects could be tracked with modest refinements of currently available technologies, that is still a rather generous lower limit given the diversity of life.<sup>73</sup> Detailed tracking of the movements of ants, for example—one of the most numerous, successful, and ecologically influential forms of life on Earth— will require currently unforeseeable technical developments.<sup>74</sup> Even with recent advances in miniaturization, it has been estimated that 70 percent of bird species and 65 percent of mammal species still cannot be actively tracked.<sup>75</sup> Second, even if such techniques are developed, scientific ambition leads almost inevitably to an ever-lengthening ladder of observational achievement. As tags become more powerful and efficient, the animals capable of carrying larger tags are burdened with additional sensors, longer-lived batteries, more powerful transmitters, and so forth. Thus the materiality of tracking and the variability of organic bodies in motion make true commensurability practically unlikely, even if theoretically possible.

Finally, much work remains to be done both by ecologists and by scholars in the humanities and social sciences to understand how data-centric approaches to phenomena such as movement are being brought to bear on contemporary problems such as biodiversity loss or biosecurity threats. Under such conditions, it is unusual for any single ontology to dominate; the question is rather how multiple ontologies are coordinated or come into conflict.<sup>76</sup> Elephant movements in northern Kenya, for instance, have been studied intensively by “wildlife biologists” for decades but have only recently been tracked in great detail with the use of GPS collars by researchers who self-identify as “movement ecologists.” Such studies are not unsophisticated; by attempting to model movement as the result of individual elephant decision-making in response to environmental and social conditions, they go well beyond characterizing the superficially observable aspects of movement patterns.<sup>77</sup> One of the striking findings of this research is that, for at least one variety of statistical model it is much easier to predict elephant movements in areas distant from human settlements than it is in human-dominated areas, “probably because movement behavior [is] reactive to the presence, movements, and threats of humans and livestock in such areas.”<sup>78</sup>

In other words, neither the null hypothesis of behavioral minimalism (i.e., completely random movement) nor the use of environmental factors to predict movement are sufficient: multispecies

interactions that are social, historical, and contingent are also in play. Pastoralists, cattle, and elephants each bring their own kinds of “data” and their own understandings and embodiments of movement to these interactions. To the extent that this result holds more broadly, movement seems poised to become ever more unpredictable within the framework of models that are based on a single, reductionist ontology of movement. Thus the very problems that movement ecology promises to help humanity address may make some of its methods for understanding “animal ecology in the Anthropocene” obsolete.<sup>79</sup> Within these zones of unpredictability, however, there may be other methods that can provide traction. The more movement ecology can complement the powerful tools that it has developed in the past several decades for the analysis of movement as sequence with methods sensitive to historically specific contexts for and understandings of movement, the more valuable it may become, and the more it may serve as a model for other data-centric sciences aiming to contribute to the solution of urgent problems.<sup>80</sup>

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<sup>72</sup> On this shift from sampling to data-management challenges, see Cagnacci et al. (2010).

<sup>73</sup> Bumblebees have been successfully tracked using extremely miniaturized telemetry tags; Hagen, Wikelski, & Kissling (2011).

<sup>74</sup> Such tracking has been accomplished in the laboratory setting (Mersch, Crespi, & Keller, 2013), but field studies remain infeasible.

<sup>75</sup> Some of these species can be tracked using devices that must be physically recovered in order to read off the stored location data; see Kays et al. (2015), p. 3.

<sup>76</sup> Thompson (2002).

<sup>77</sup> Wittemyer, Polansky, Douglas-Hamilton, & Getz (2008); Boettiger et al. (2011).

<sup>78</sup> Boettiger et al. (2011), p. 1656.

<sup>79</sup> Kays et al. (2015), p. 7.

<sup>80</sup> For a survey of some alternative methods that have emerged with cultural anthropology, see Kirksey and Helmreich (2010).

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