Evaluating Contributions of Recent Tracking-Based Animal Movement Ecology to Conservation Management

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The use of animal-born sensors for location-based tracking and bio-logging in terrestrial systems has expanded dramatically in the past 10 years. This rapid expansion has generated new data on how animals interact with and respond to variation in their environment, resulting in important ecological, physiological, and evolutionary insights. Although understanding the finer details of animal locations has important management relevance, applied studies are not prominent in the movement ecology literature. This is despite the long history of applied studies of animal movement and the urgent and growing need for evidence-based conservation guidance, especially in the challenging field of human-wildlife interactions. The goal of this review is to evaluate the realized contribution of tracking-based animal movement ecology to solving specific conservation problems, and to identify barriers that may hinder expansion of that contribution. To do this, we (a) briefly review the history and technologies used in animal tracking and bio-logging, (b) use a series of literature searches to evaluate the frequency with which movement ecology studies are designed to solve specific conservation problems, and (c) use this information to identify challenges that may limit the applied relevance of the field of movement ecology, and to propose pathways to expand that applied relevance. Our literature review quantifies the limited extent to which research in the field of movement ecology is designed to solve specific conservation problems, but also the fact that such studies are slowly becoming more prevalent. We discuss how barriers that limit application of these principles are likely due to constraints imposed by the types of data used commonly in the field. Problems of scale mismatch, error compounding, and data paucity all create challenges that are relevant to the field of movement ecology but may be especially pertinent in applied situations. Finding solutions to these problems will create new opportunity for movement ecologists to contribute to conservation science.

Keywords: animal movement, biologging, conservation biology, data paucity, error compounding, radio telemetry, scale mismatch, wildlife management

INTRODUCTION

The use of animal-born sensors for location-based tracking and bio-logging in terrestrial systems has expanded dramatically in the recent past (Kays et al., 2015). This rapid expansion has resulted in important insights into ecology and physiology, especially in documenting how animals interact with and respond to variation in their environment. These recent developments have, in many cases, been seen through the theoretical lens of movement ecology (Nathan et al., 2008).

Although this work has led to basic scientific advances, understanding the finer details of animal locations and state also has important applied or management relevance (Wilson et al., 2015; Allen and Singh, 2016; McGowan et al., 2017). Assessing static individual locations (i.e., using habitat selection models and resource selection functions; Johnson, 1980; Kie et al., 2010) and measuring dynamic movement behavior (i.e., how and why organisms change locations and the consequences of that movement; movement ecology; Nathan et al., 2008; Mandel et al., 2011) are prerequisites for building models that accurately predict animal response to, and risks generated by, encounters with anthropogenic infrastructure. In effect, understanding the intimate, species-specific details of resource selection provides insight into how quality and alteration of habitat influences wildlife spatial occurrence and behavior (Sawyer et al., 2009). Likewise, understanding movement relative to humans or anthropogenic obstacles allows quantification of potential behavioral and physiological costs, and projection of associated demographic risks (Miller et al., 2014; Reid et al., 2015). Finally, integrating physiological data delivered by bio-logging together with habitat selection and movement information provides insight into how the environment constrains animal behavioral and demographic response to anthropogenic influences (Shepard et al., 2011; Mosser et al., 2014).

In spite of the applied relevance of understanding animal movement and the long history of animal tracking for applied purposes, applied studies are not prominent in the movement ecology literature. This may be because of ethical concerns associated with tracking rare species (Cooke et al., 2017). However, that is not a universal sentiment and, in some countries rare species may be preferentially tracked [e.g., California condor *Gymnogyps californianus* (Sheppard et al., 2015) and gray wolf *Canis lupus* (Bergman et al., 2006) in North America]. Therefore, the goal of this review is to evaluate the realized contribution to conservation science of terrestrial (i.e. non marine), tracking-based animal movement ecology, and to identify barriers that may hinder expansion of that contribution.

Our review begins by briefly covering the history of applied terrestrial animal tracking and bio-logging, and the current sensor technologies and environmental databases used in the field. This history is important because it is highly applied, in contrast to the modern basic emphasis of movement ecology. Likewise, describing sensor technology is important because doing so highlights constraints that may influence the applied potential of work done using these tools. Some of these issues are covered in greater detail in other reviews (Robinson et al., 2010; Tomkiewicz et al., 2010; Kays et al., 2015; Williams et al., 2020), and so we only briefly touch on these topics. However, no one manuscript summarizes all of these components together, and so their inclusion here is important in setting the stage for the concepts we present. Subsequently we use series of literature searches to evaluate, and then summarize, the realized prevalence of research that applies movement ecology principles to solve conservation problems specific to terrestrial ecosystems. This section illustrates the connections and discontinuities between movement ecology and conservation. The final section builds on the findings from the prior two to identify challenges that limit the applied relevance of the field of movement ecology and to propose pathways to expand that applied relevance.

ANIMAL TRACKING AND BIO-LOGGING: APPLIED HISTORY AND TECHNOLOGY REVIEW

There is a long history of humans tracking animal movement for specific game management goals. Prehistoric communities of hunters-gatherers tracked and anticipated animal movements (Epp, 1988; Shaffer and Gardner, 1997) to enhance access to food (Kornfeld et al., 1999; Benedict, 2005). The first radio-based animal tracking systems were developed in the 1950s and 1960s (LeMunyan et al., 1959; Cochran and Lord, 1963). Although a predominant use of these early systems was to provide track information for wildlife management (Silv, 2012), a few also provided biotelemetry data, for example related to activity, respiration, temperature, cardiovascular, gastroenterological, and neurophysiological function (Lord et al., 1962; Kimmich, 1980). The technology to track animals in a truly remote manner was first applied in the 1960s and 1970s (Craighead et al., 1971, 1972), and was expanded with the development of the ARGOS satellite system in the 1980s. Again, these early remote tracking systems were most frequently used in applied settings.

Communication Protocols

Development of newer communication protocols has accelerated access to a suite of remotely collected sensor data, supplied in large volumes, that has moved animal tracking away from its applied roots. For example, mobile telephony [Global System for Mobile communication (GSM) or Code Division Multiple Access (CDMA)] has been used to transmit high precision Global Positioning Satellite (GPS) locations and other data collected on mammals (Bunnefeld et al., 2011) and birds (Lanzone et al., 2012). There are also tags from which data can be downloaded via other radio connections such as ZigBee (Bouten et al., 2013) or UHF (http://www.e-obs.de/index.html). Finally, when devices must be tiny, dataloggers that fall off (Sapir et al., 2014) or that require recapture and manual removal (Bridge et al., 2013) can provide locational information or monitor physiology and movements (Bevan et al., 1997; Boyd et al., 1999; Mandel et al., 2008; Bächler et al., 2010). Likewise, networks of VHF or other radios (Clements et al., 2005; Campbell et al., 2012; https://motus.org/) can track "pinging" devices attached to animals.

Sensors

There is a rapidly growing suite of miniaturized digital sensors available as off-the-shelf hardware components that can provide detailed information on animals. Although the newest of these sensors have been used primarily to advance basic ecological understanding, they have the potential for extensive use in applied ecology. Likewise, understanding these sensors and their details provides some potential insight into reasons for the limited conservation application of movement ecology principles.

More than 30 types of sensors are commercially available to technology developers and manufacturers (**Table 1**). Several of these—GPS, accelerometers—are already used with high frequency for bio-logging and sometimes for applied ecology. A second group, including heart rate, blood pressure, and camera sensors, are occasionally used in ecological studies and almost never in applied ecology. A third group, including proximity, current, force, and flex sensors, have potential applications to ecological research but have, to our knowledge, only rarely or never been used for either basic or applied bio-logging. The subset of these devices that are not used to address applied problems are especially important to consider here because their integration in conjunction with principles of movement ecology has the potential to stimulate new growth in applied ecology.

Data Management

A common step in processing sensor data gathered via animal tracking or bio-logging data is to associate them with external data describing the environment animals occupy. GIS and web-based tools have been developed to make these associations (Kemp et al., 2011; Mandel et al., 2011). In this way, terrestrial sensor data have been linked to a wide suite of data on land use and land cover, elevation, topography, weather, the built environment, and other features (Hebblewhite and Haydon, 2010; **Table 2**). The original development of the tools to statistically evaluate these linkages was often for applied purposes (e.g., Johnson, 1980). However, those applied tools are typically used with a subset of available external data types (the upper, unshaded, rows of **Table 2**), and less frequently used with newer datasets that are sometimes used to answer basic movement ecology questions (the lower, shaded, rows of **Table 2**); we return to this issue later in our review.

TABLE 1 | Types of sensors available from commercial manufacturers that have been or that could be integrated into on-board animal bio-logging devices in terrestrial systems.

Sensor type	Actual or potential uses	Citations
Accelerometer—1-axis and 3-axis	Movement, behavior	Mosser et al., 2014
GPS	Location, speed, direction, geofencing	–
Light sensors—IR, visible and UV	Geolocation, context for behavior	Bridge et al., 2013
Temperature[a]	Context for behavior, ecol. interactions and physiology	Mandel et al., 2008; Arlettaz et al., 2015
Camera (photo or video)	Behavior, ecological interactions	Moll et al., 2007
Identification sensors[b]	Behavior	Bonter and Bridge, 2011; Aplin et al., 2012
Inertial measurement unit sensors[c]	Movement, behavior	Reynolds et al., 2014
Magnetometers	Movement, behavior	Guo et al., 2009; Chakravarty et al., 2019; Williams et al., 2015
Microphones (sound)	Behavior, ecol. interactions	Cvikel et al., 2015
Physiological[d]	Physiology, behavior	Arlettaz et al., 2000, 2015; Mandel et al., 2008
Air speed (Pitot tubes)	Air speed measurement	Reynolds et al., 2014
Biometric (fingerprint, retinal)	–	N/A
Current and capacitive	–	N/A
Dead reckoning	Animal movement	Wilson et al., 1991
Flex and force	Movement, behavior	N/A
Gyroscopes—2-axis and 3-axis	Movement, behavior	N/A
Gas/pollution sensors[e]	Respiration, toxicology	N/A
Humidity	Context for behavior	N/A
Proximity (radio and acoustic)	Social behavior, ecol. interactions	Prange et al., 2006; Hamede et al., 2009
Solar and nuclear radiation	Context for behavior, toxicology	N/A

Sensors are listed alphabetically within groups, with the top group (shaded in gray) used most frequently in both applied and movement ecological studies and the last group (also shaded in gray) used least frequently. Implicit in use of most of these sensors is association with some kind of clock, either onboard (e.g., a "real-time-clock") or external (e.g., using GPS time). Also provided are potential uses for sensors and a small number of representative citations that either describe the sensor or use data they produce. An "NA" indicates that use of this sensor is rarely explored in the movement ecology or applied ecology literature we surveyed. We do not provide a citation for use of GPS, as this technology is used in so many studies. Tables with fewer sensors but other citations are provided in Moll et al. (2007), Baratachi et al. (2013), Krause et al. (2013).
[a] Can include thermistors, thermocouples, and thermometers, and ambient or body temperature.
[b] Includes active and passive, such as RFID, tokens, and card readers.
[c] Combinations of accelerometers, gyroscopes, and sometimes magnetometers, usually to assess movement.
[d] A wide range including heart rate, blood pressure, pulse, muscle activity, respiration rate, body and periphery temperature, etc.
[e] Measuring a wide variety of substances, including H, CO_2, CH_4, NO, −OH, volatile organic compounds (VOCs), liquid petroleum, particulates (by size), etc.

TABLE 2 | External data sets regularly associated with animal tracking or bio-logging data, some of the typical parameters in those datasets that are associated with terrestrial animal movement data, and the typical spatial and temporal scales at which the data are collected.

External data type	Typical parameters[a]	Typical scales	
		Spatial[b]	Temporal
Digital Elevation Models (DEM)	Ground elevation, topography, roughness, etc.	1 m−1 km	Static
Geological data	Soil or substrate type	10 m−regional	Static
Land use and land cover maps	Vegetative cover, land use, imagery, features	30 m−1 km	Annual/seasonal
Political data	Administrative boundaries	Variable	Variable
Population density	Human population density (continuous/categorical)	Variable	Annual
Primary productivity data	NDVI, NPP, and their oceanic equivalents	≥250 m	Seasonal/weekly
Socio-economic data	GDP, etc.	Country or regional	Annual
Air quality	Particulates, toxins,	Regional	Variable
Astronomical data	Sunrise, sunset, solar activity, moon phase, magnetic	Location-specific	–
Global climate indices	ENSO, NAO, SOI, drought	Continental-scale	Annual/seasonal
Hydrology and water data	Interpolated or derived data of many types	Large-scale	–
Modeled weather data	Interpolated or derived data of many types	30+ km	3–24 h
Measured weather data	Location-specific data of many types	Location-specific	Variable

Data types are listed alphabetically within groups, with the top (unshaded) group more frequently associated with applied ecology than the second (shaded) group. The variety of scales in the last two columns serves to illustrate the "scale mismatch problem" discussed in the main text.
[a]*Can be either measured or modeled.*
[b]*Spatial scales vary widely both by the type of data produced and its spatial extent. In many cases, global maps have coarse grained data but regional maps have finer-grained scales.*

LITERATURE REVIEW: APPLICATIONS OF ANIMAL TRACKING AND BIO-LOGGING TO APPLIED ECOLOGY

Within the field of terrestrial wildlife management, there has been no shortage of studies of animal home range and habitat associations, movements, connectivity, and biogeography (Kie et al., 2010; Urios et al., 2015; Reiners et al., 2017). These form the foundation of modern applications of animal tracking and bio-logging science. That said, it has been suggested that modern movement ecology principles are not strongly integrated into conservation biology (Wilson et al., 2015; Allen and Singh, 2016; McGowan et al., 2017). A recent keyword-based review (Fraser et al., 2018) supports this casual observation. That review noted that many studies discuss the potential relevance to conservation of movement studies, but that a key paper framing the discipline of movement ecology (Nathan et al., 2008) did not mention conservation.

Literature Searches—Methods

To assess this observation, we conducted a series of literature searches to evaluate the realized prevalence of research that applies movement ecology principles to solve specific terrestrial conservation problems. Because different academic search engines may generate different types of results, we conducted 5 different searches using two search engines [GoogleScholar (GS) and Web of Science (WS)]. In our searches, we used four different dyads of search terms, pairing the term "movement ecology" with the terms "wildlife management" (GS + WS), "conservation biology" (WS), "species conservation" (WS), and "conservation" (WS). In our search engine surveys, we limited time frames to the period starting in 2008, when the field of movement ecology

was defined (Nathan et al., 2008). Finally, we also evaluated all the articles published to date in the journal "Movement Ecology" (the 184 articles from 1:1 through 7:28).

In our interpretation of search results, we differentiated between research with ecological goals that has the potential to provide information for use in management, and research whose goals was to address specific conservation problems. Our approach builds on recent keyword-based searches that consider larger numbers of papers in less detail (Fraser et al., 2018). For example, we considered a study of home range or habitat associations of a species to be one that provides information with the potential for use in management. Although these papers represent important advances, they were not relevant to the goals of our literature review and we categorized them, together with those that generated theoretical advances, as "Descriptive." However, we considered a study of change in the home range or habitat associations of that species in response to oil and gas development to be addressing a specific conservation problem. We categorized such papers as "Relevant" to this analysis. Other categories of papers we considered were those that were Perspectives, Viewpoints, Frameworks, or "calls to arms" ("Calls"), those that described new tools for data collection or analysis ("Tool"), review papers ("Review"), and those that were not applicable to any of these categories ("NA," includes editorials, corrections, or papers not about movement ecology). The results of our searches are predominantly focused on terrestrial studies, but because we knew of no effective mechanism to separate terrestrial and marine studies, our results do contain some marine research papers. We did not filter those papers from our search results.

It should be noted that although we were stringent in considering which papers fit into the "Relevant" category, many papers fit into more than one of the other categories. For

instance, some manuscripts reviewed background and proposed, and sometimes even used, new or modified tools. As such, these manuscripts reasonably could have been categorized as "Review," "Descriptive," or "Tools." We were less stringent in assigning papers to these non-relevant categories and, thus, it may not be appropriate to use our summaries of categorization of papers for goals other than those we present here.

Literature Searches—Results

Searching GoogleScholar for the words "movement ecology" yielded about 10,300 results; searching for the words "wildlife management" yielded about 781,000 results. However, searching for the two together, and limiting our search period to the period starting in 2008 yielded about 1,900 results. We reviewed the first 200 of these (when sorted by Google's "relevance"; **Table 3**, **Table S1**). Only 14% of these papers could reasonably be classified as research in which elements of movement ecology are used to solve specific conservation problem. An additional 7% of studies were "calls to arms," some of which discuss the need for animal movement studies to have more applied relevance. The remainder of those first 200 papers were not relevant to this review.

We performed four other searches using Web of Science. Searching for the terms "movement ecology" and "wildlife management" returned eight papers, of which one was relevant (**Table 3**, **Table S2**). Searching for the terms "movement ecology" and "conservation biology" returned nine papers, one of which was relevant (**Table 3**,**Table S2**). Searching for the terms "movement ecology" and "species conservation" returned eight papers, two of which were relevant (**Table 3**, **Table S2**). Finally, searching for the terms "movement ecology" and the general term "conservation" returned 202 papers, of which only 14% were relevant (**Table 3**, **Table S3**). Interestingly, the number of these

papers has been increasing over time (**Figure 1**), and 16 of these 29 articles (55%) were published in the last 2 years.

Finally, we reviewed all 184 articles published in the journal "Movement Ecology" since its creation (**Table 3**, **Table S4**). Conservation relevance is not part of the journal aims and scope and so, not surprisingly, we categorized the vast majority of papers as "descriptive" of biology or theory. We categorized only seven papers (4%) as those that used movement ecology principles or tools to solve specific conservation problems. Four of these seven were published in the last 2 years. That said, several of the descriptive papers (at a minimum, #26, 37, 78, and 114, in bold font in **Table S4**) had the data that would have allowed the authors to tell an applied conservation story. One other paper (#179, also in bold) was a review that drew linkages between movement ecology and biodiversity conservation.

Literature Searches—Summary

Although our literature search illustrated the paucity with which modern movement ecology approaches are used to generate solutions to specific conservation problems, it also highlighted several examples of this being done. Here, to illustrate those examples, we summarize the major themes in these and related publications.

Wildlife management problems have been addressed in a movement ecology framework by overlaying tracking data on data layers describing anthropogenic activity. For example, one paper noted in our literature search maps animal movement in the context of proposed oil and gas development (Sawyer et al., 2009). In other studies, presence data based on snow tracks were used to build spatially explicit models of wildlife abundance and overlay them on maps of projected human recreational activity (Braunisch et al., 2011) and telemetry data illustrated how raptors changed home range size in response to human recreation (Perona et al., 2019). Similarly, models of avian flight behavior

TABLE 3 | Results from six literature searches to assess the degree to which modern movement ecology principles are integrated into conservation biology.

Search term	Search engine	Total returned	Relevant	Descriptive	Tools	Calls	Review	NA
Movement ecology & wildlife management	GS	200	28	70	54	14	25	9
			14%	35%	27%	7%	13%	5%
Movement ecology & wildlife management	WoS	8	1	1	2	2	2	
			13%	13%	25%	25%	25%	0%
Movement ecology & conservation biology	WoS	9	1	2	1	5	0	0
			11%	22%	11%	56%	0%	0%
Movement ecology & species conservation	WoS	8	2	5	0	1	0	0
			25%	63%	0%	13%	0%	0%
Movement ecology & conservation	WoS	202	29	107	23	13	22	8
			14%	53%	11%	6%	11%	4%
Movement ecology journal	All	184	7	111	43	4	12	7
			4%	60%	23%	2%	7%	4%
Totals		**611**	**66**	**302**	**117**	**39**	**58**	**29**
			11%	**49%**	**19%**	**6%**	**9%**	**5%**

Five of the literature searches were based on the search terms and search engines described in the table. The sixth was a review of all manuscripts published in the journal "Movement Ecology." Search engines are GoogleScholar (GS) and Web of Science (WoS). We considered the first 200 articles, as sorted by "relevance," returned by GoogleScholar. Descriptions of the different categories of papers we defined are provided in the main text.
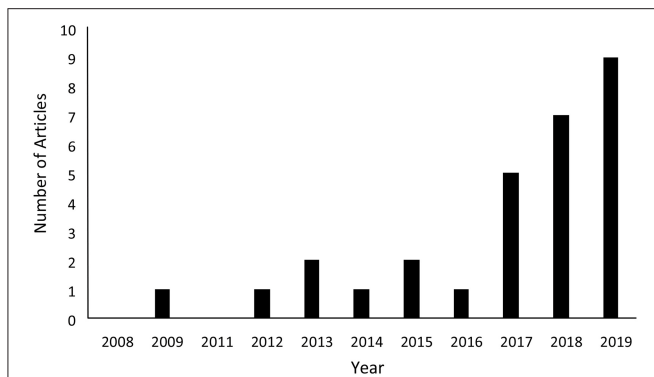
FIGURE 1 | Number of papers published in which movement ecology principles were used to solve specific conservation problems. These data are based on returns from a search of Web of Science for the terms "movement ecology" and "conservation." The search returned 202 papers, of which 16 were categorized as those in which movement ecology principles were used to solve specific conservation problems.

have been linked to projections of wind turbine locations to predict risk to birds from blade-strike (Miller et al., 2014; Reid et al., 2015). In fact, the majority of the relevant studies we found in our searches and in the journal evaluated animal movement in the context of data layers describing habitat alterations, roads, resource extraction or anthropogenic influences (**Tables S1–S4**). One of the salient features of these papers is that many authors seem to struggle with issues related to the scale, accuracy and precision of these external data layers; we return to this issue later in our review.

Human-wildlife conflict issues also have been addressed with real-time alerts generated by tracking technologies commonly used in movement ecology. For example, alerts were created when California condors (Sheppard et al., 2015) and African elephants (*Loxodonta africana*; Wall et al., 2014) were near to human-driven threats (wind turbines and subsistence farms, respectively). These alerts can lead to actions to reduce risk (by shutting down wind turbines) or to change the animal's trajectory (aversive conditioning to keep the elephant out of a farm). In the case of the elephants, there was additional wildlife health benefit because alerts were generated when elephants altered or stopped movements in ways that indicated illness or death. In another applied study, real-time tracking of gulls was used to identify illegal waste dumping (Navarro et al., 2016). However, in spite of their novelty and utility as an applied tool, real-time alerts have technological constraints and are only relevant to the individual or groups of animals being tracked. As such, although alerts can be useful in solving an individual-specific management problem, they are rarely relevant to broad population-level conservation solutions.

Movement ecology approaches have been used in a few other applied settings. For example, statistical modeling of remotely gathered bio-logging data can provide new insight about the environment an animal experiences. In this vein, analysis of data from soaring birds has been used as a tool to infer information about wind velocity and scale that may contribute to high-resolution weather observations (Treep et al.,

2016; Weinzierl et al., 2016). Likewise, data from GPS sensors or accelerometry, together or separately, can be interpreted to characterize animal behaviors (e.g., Wilson et al., 2006; Shepard et al., 2011; Nathan et al., 2012; Katzner et al., 2015; Sur et al., 2017) that can then be modeled as a function of either energy expenditure or response to disturbance (Wilson et al., 2015). In contrast to real-time alerts, integration of bio-logging data into these types of statistical models is applicable to populations and therefore has greater, often unrealized, potential for broad applied ecological relevance.

Finally, a recurring theme in our review was the presence of a fairly large number of papers pointing out the relevance to conservation biology of principles developed via movement ecology (i.e., "call to arms"). These pieces illustrate a broader recognition that there is value to using principles of movement ecology for conservation purposes. That said, the fact that such papers still are being published suggests that there is room for improvement in this regard.

DISCUSSION: CONSTRAINTS THAT LIMIT APPLICATION OF MOVEMENT ECOLOGY TO CONSERVATION BIOLOGY

Movement ecology aims to triangulate among the organism's internal state, its capacity to move, and the external factors it experiences (Nathan et al., 2008). Our review highlights both some of the ways this triangulation has been used in applied settings but also how technological and other constraints may influence applied interpretation of movement data. Evaluating those constraints highlights potential reasons why applied studies are not prominent in the movement ecology literature and this process identifies potential solutions to that problem.

Constraints Due to Data Scale, Accuracy, and Precision

Literature review suggests that making linkages between animal movement and the environment is prone to bias imposed by variation in the scale, accuracy, and precision of environmental data types. These biases manifest themselves in at least three different and highly relevant ways. The first of these is the problem of mismatches in scale between different sources of data used in movement research (i.e., a "scale mismatch problem"; see **Table 2**; Neumann et al., 2015; Remelgado et al., 2018). For example, although GPS data often are accurate to a spatial scale of meters or centimeters and a temporal scale of seconds, land cover data are at time scales of seasons or years and spatial scales of 10s or 100s of meters. Likewise, weather data are modeled over temporal scales of hours and spatial scales of tens of kilometers (e.g., Mandel et al., 2011). This constrains analyses to inference at the scale of the coarsest dataset. However, behavior often is the result of decisions at finer scales, creating challenges in identifying drivers of animal behavior.

A second bias can be imposed by compounding of measurement errors in data sets commonly used in movement ecology (i.e., an "error compounding problem"). For example, when estimating an animal's location in 3D, GPS measurement

error combines with error and averaging within an elevation model (Péron et al., 2017; Poessel et al., 2018). As a consequence, small errors of measurement in GPS data from a bird flying 100 m above ground and 5 m from a cliff may cause the animal to appear to be in the cliff and, therefore, below ground. Such infrequent errors may be of limited consequence to the process of detecting ecological patterns in data, but they may be substantially more relevant in an applied situation where rare events (e.g., collisions of birds with wind turbine blades or airplanes) can dictate policy. Furthermore, although their presence can be evaluated with modern ecological statistics, minimizing, rather than characterizing, errors is of key importance to managers.

A third bias may be imposed by the paucity of data describing ecologically relevant resources (e.g., distribution of food, nests, or den sites; a "data paucity problem"). This is akin to the knowledge gap problem identified in previous reviews (Fraser et al., 2018). Without such ecologically relevant data, interpretation relies on inference from proxies rather than direct measurement. As an example, mapping potential breeding areas for cavity nesting birds might be best evaluated by measuring snag density. This is difficult though and, instead, potential nesting areas are usually identified by inference, using land cover class or tree species richness as a proxy for snag density (van der Hoek et al., 2017).

Addressing all three of these problems would have relevance to both fundamental and applied ecology. However, because so many management problems are scale- and measurement-specific, solving these issues may be especially relevant to applied ecology. With this in mind, one way to give the field of movement ecology more applied relevance may be through integration of data from less frequently used on-board or intrinsic sensors that can describe and map the environment the animal experiences (e.g., Treep et al., 2016). Integrating cameras, weather sensors and GPS data could provide dramatic new insights into micro-habitat selection and its consequences for conservation-dependent wildlife. Similarly, in wildlife disease studies, samples collected from an animal's environment (e.g., toxins in potential food) are linked to those collected from the animal itself (e.g., toxins in blood). Here again, rarely-used on-board sensors that sample toxins or disease in the animal and in the environment or the food an animal ate (Loyd et al., 2013; Lavelle et al., 2015; McGregor et al., 2015) could make explicit, and more valuable, the linkages between the location, experience, and the internal state of an animal.

All of these solutions though share a common theme. In each case, they illustrate the value of onboard sensors to measure the actual environment the animal experiences, contributing to potential resolution of the data mismatch, error compounding, and data paucity problems. Such an approach would reduce reliance on coarse-scale environmental data layers that may limit application of movement ecology principles to conservation settings.

Constraints Due to Data Availability, Integration, Validation, and Transmission

It was evident in our review that miniaturization of new generations of sensors has created reams of data that yield both opportunity and overload. The first ARGOS telemetry systems used a single sensor to measure location. Modern devices use a suite of sensors to measure repeatedly the location, the environment, and the animal's condition, actions, and physiology. Integration of these data from multiple sensors, although rarely achieved, allows users to refine understanding not only of animal movement but also of error in any one sensor. These refinements make data more accurate and precise and, thus, more relevant to both fundamental and applied ecology.

Developing the conceptual and quantitative tools to integrate, validate, analyze, and interpret these data is non-trivial. As a consequence, it is not unusual for users of sensor data in basic ecological studies to classify behaviors without externally validating their classification algorithms (e.g., Bishop et al., 2015). Although such an approach may be acceptable for basic ecology, it is not well-suited to the applied arena. Consider, for example, the sociological consequences of even a low rate of false positives or false negatives associated with real-time alerts for crop-raiding elephants (Wall et al., 2014). Therefore, two important steps in bridging the gap between basic and applied animal movement science are (a) developing methodological tools to integrate, analyze and interpret data from multiple sensors (for example, drawing from tools used to evaluate human mobility data; Thums et al., 2018), and (b) moving to consistent use of supervised classification and validation of remotely gathered biotelemetry data (e.g., Nathan et al., 2012).

Perhaps the greatest technological limitation to data collection via remotely-sensed animal bio-logging is the narrow bandwidth pipe connecting the animal in the field to the computing servers that host the data. Such constraints are especially relevant to applied ecology because conservation-dependent terrestrial species are only sometimes well-suited to intensive study. Thus, massive amounts of accelerometry data from griffon vultures in Europe and the Middle East can be sent over VHF systems, in part because these birds are colonial and regularly return to a set of nest cliffs (Nathan et al., 2012). In contrast, it would be far more difficult to collect such data from ecologically similar but non-colonial California condors that often occupy more remote and roadless areas (Poessel et al., 2018). This limitation explains why accelerometry and animal-borne video studies are often performed on wildlife that are faithfully colonial or easily recaptured, or on captive or domestic animals (Moll et al., 2007; Loyd et al., 2013; McGregor et al., 2015; den Uijl et al., 2017; Hernández-Pliego et al., 2017; Hicks et al., 2017; le Roux et al., 2017).

In certain areas the use of mobile phone telemetry can greatly expand the volume and speed of data transfer from bio-logging devices to scientists. That said, even 4G and LTE systems often are insufficient to transfer the large quantities of data collected at many measurements per second. This is likely why wildlife accelerometry that uses GSM systems is, to date, largely experimental (Yuan et al., 2010; Gor et al., 2017; Sur et al., 2017). Likewise, for those animals that live outside mobile phone coverage, the only option to recover large volumes of data is animal recapture and removal of data loggers. A potential solution to this problem are hybrid solutions that send GPS data via satellite but other data via other systems (e.g., GSM, ZigBee, VHF, or satellite internet services). Eventual deployment of 5G mobile phone systems also has the potential to speed up data transfer rates to address this issue.

Constraints and Conservation

The constraints we highlight here are all influential for movement ecology in general, and not exclusively for solving conservation problems. In fact, the early research into animal movement was more strongly influenced by these constraints than is modern movement ecology, yet it was still highly applied. Similarly, rapid advances have been made linking movement ecology and conservation management in the marine environment, despite greater data constraints than in terrestrial settings.

Since these constraints didn't influence historical or marine studies, it is therefore not easy to understand why the constraints we identify in literature may limit applied relevance of movement ecology to terrestrial conservation management. One possible explanation is that, in the subset of marine ecological and early animal movement studies that are relevant to conservation, measurements are collected and models built at relatively large spatial and temporal scales (e.g., hours and kilometers, see **Tables 1**, **2**; Reisinger et al., 2018). As such, the coarse scales of movement match the coarse scale of environmental datasets, and are thus relatively uninfluenced by error rates, and data transmission and management constraints. In contrast, terrestrial movement ecology collects measurements and build models at precise spatial and temporal scales (e.g., meters and seconds, see **Tables 1**, **2**; Kays et al., 2015). In those situations, the constraints we note here have a greater influence both on the ability to conduct the work, and also on the conservation relevance of the data.

CONCLUSIONS

Our review highlights the fact that principles of movement ecology are sometimes used to solve specific conservation problems. However, there is immense potential for expansion in this regard and that potential is starting to be realized, as illustrated by the increase in papers in this area in the past 2 years. There are constraints that may limit the continued expansion in this area. Some of these constraints include those highlighted by others, such as the availability of data or results, improved dialogue between scientists and practitioners, and development of frameworks for incorporating movement ecology into conservation (Fraser et al., 2018). Others we identify here are linked to issues of the transmission and validation of massive amounts of telemetry data, others to the scale, accuracy, precision, error rates, availability and integration of external data layers that are used to infer drivers of behavior. Nonetheless, solutions or work-arounds are already being developed to overcome many of these social and technological constraints. As these solutions come on-line, there will be new opportunities for movement ecologists to meet the urgent and growing need for evidence-based conservation. It is our hope that, by highlighting these issues, this review and commentary will spur growth in applied movement ecology studies.

AUTHOR CONTRIBUTIONS

The concept for this manuscript was developed as a result of discussions between the two authors. TK led writing. Both authors participated in revising and editing the document.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2019.00519/full#supplementary-material

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