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Journal of Zoological Research
http://ojs.bilpublishing.com/index.php/jzr

REVIEW

Advances in Terrestrial Mammal Movement Ecology: An Overview

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ARTICLE INFO

Article history
Received: 26 February 2020
Accepted: 31 March 2020
Published Online: 30 April 2020

Keywords:
Heterogeneous landscape
Habitat selection
Migration
State-Space Model
Tracking technology

ABSTRACT

As a research field which is blooming quickly in recent years, movement ecology has been a worldwide concern and interest. However, movement ecology is so comprehensive and complicated that many articles only focus on few aspects or species. As tracking technologies and methods of movement data analysis develop, the abundance of movement data becomes available for demonstrating more scientific facts about animal movement. This article is aimed to summarize the advances of terrestrial mammal movement ecology in the past years to show its critical and potential research fields, as well as trying to ascertain direction of these advances.

1. Introduction

Movement ecology is defined as a kind of ecology which focuses on the relationship between organism movement and environment (biotic and abiotic). Research on terrestrial mammal movement ecology can cover many themes and aspects [1]. For example, based on an individual's movement data, the researcher can know about when and where animals moved, activity patterns and conclude motion capacities. Beyond this, given the movement path and home range of animals, accompanied with environment factors and food patch information, researchers can demonstrate habitat selection of animals [2]. With new technology of animal sensors, individual physiological states and behaviours can be recorded [2], enabling the researcher to understand further what drives animal movement. If the tracking of an animal lasts its whole life, the researcher can draw the life-movement and behaviour map of individuals, which can represent the life history of this individual[3]. This special sequence is simillar to a DNA strand [3], it may become an ID of this species, or even this individual. If the individual samples are enough and data is fitted, even social relationships of a group can be explored[4]. Population ecology can also be supported by movement data, reflecting population distribution and competition. Movement of prey and predator is also connected in population movement ecology. For some species, long-term and large spatial scale tracking may reveal the relationships between animal migration and global climate change.

Nowadays, movement ecology is becoming more and more generalized and concerning at many objects wildly,

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DOI: https://doi.org/10.30564/jzr.v1i2.1717

from dispersal of seed to migration of blue whine. As the development of tracking technology, it is no doubt that the number of research papers about movement ecology is increasing in recent years. Holyoak et al. (2008) figured out that at least 2,6000 papers referd to movement ecology in 1997-2006. He selected 1,000 articles randomly and found that 12% of them aiming at mammal movement ecology, which was just lower than plants and birds (both of them are 19%) [5]. It suggest that mammal, whose majority is terrestrial mammal, is an important taxa in movement ecology research.

We searched papers as terms such as "migration", "dispersal", "movement pattern", "home range", "activity" and filter them with the limit of "terrestrial mammals" to summarize the papers about terrestrial mammal movement ecology. We found that probably 1,800 papers about terrestrial mammal movement ecology were published during 2017-2020. To descript the history of movement terrestrial mammal ecology, we also reviewed previous papers.

In China, rare species such as Giant Panda (*Ailuropoda melanoleuca*) and Golden Monkey (*Rhinopithecus* spp.) have had their movement patterns and habitat use explored [6,7]. Ungulates are also a hot taxonomic class in China and North America [8]. Some smaller wild animals are little focused because their sampling is very challenging [9]. Some larger animals like Black bear (*Ursus thibetanus*) and African elephants (*Loxodonta*) have been tracked with Global Positioning System (GPS) collars to achieve their movement trace [10,11]. Many feline animals like Amur tiger (*Panthera tigris altaica*), Cheetah (*Acinonyx jubatus*), lynx (*Lynx lynx*), Jaguar (*Panthera onca*) and African Lion (*Panthera leo*) also has been tracked[12-16]. Rodents like Mice (*Muridae*) and Squirrel (*Sciuridae*) are also important target species[17]. Many research themes has been explored compared to other species but internal state and navigation capacity of individuals during their movement are seldomly mentioned.

This article is aimed to focus on the terrestrial mammals as object species of movement ecology, find the access to get and analyse movement data and summarize the critical and potential research fields of terrestrial mammal movement ecology to try to find the trend and missing parts in terrestrial mammal movement ecology.

2. Method and Themes of Research

2.1 Tracking Technology

Tracking technology is the supporting of the development of terrestrial mammal movement ecology. The original method of animal tracking is observing animals in the field or checking the animal traces such as footprints on the snow ground. This method is very precise but will take much time and bring many difficulties to researchers. This kind of movement data is generally short-term data [18].

Nowadays, researchers often use Very-High-Frequency (VHF) telemetry or GPS to track terrestrial mammals. VHF is also known as radio tracking, whereby researchers can deploy VHF transmitters onto animals and carry the corresponding VHF receiver to the field to locate animals periodically and draw the location map depending on the dirction of observation [19]. However, GPS technology is the most commonly used tracking technology at the present time. The devices can be built as collars, ear tags or some other gadgets. After deploying the devices, they send location data to satellites in a particular frequency and researchers can retrieve data from specific websites or software [20]. Differ from bird or fish tracking , tracking of terrestrial animals usually needs shorter fix interval and higher precision because there are much canopy on the ground. This requir bigger battery and more advanced positioning device than other species.

Additionally, there are other state of the art technologies which record animal internal state and behaviour, and even the environmental factors can be recorded along the animal's pathway at the same time [21]. Such a technological revolution must bring more opportunities and possibilities to terrestrial mammal movement research.

2.2 Research Themes

Individual movement is fundamental in terrestrial mammal movement ecology. Nathan et al. (2008) proposed the paradigm of individual movement ecology, which contains four frameworks (internal state, motion capacity, navigation capacity and external factors) which can affect an animal's movement path [3]. He also listed five links between them as the movement ecology research direction. The following research themes mentioned in this paper will be fitted to these frameworks to facilitate future research.

2.2.1 Movement Pattern and Locomotion

Movement pattern and locomotion is the most common theme in individual movement ecology, and has been broadly explored in previous times. This theme focuses on the motion capacity. Movement pattern can be demonstrated by activity quantity and active time, which can reflect which time period this individual prefers to move. Motion capacity can be measured by day range [22] and home range [23] and is affected by the physiological condition and life period of individuals or environment factors.

DOI: https://doi.org/10.30564/jzr.v1i2.1717

Home range is a common metric which is necessary for various studies [24] and seasonal home range is becoming a new focus [25,26].

Behaviour during the movement is a critical component of individual movement because they reflect the goal of animal movement. This theme mainly focuses on internal factors and external factors. When individuals stay, are they foraging or bedding? When individuals move, are they walking toward a food patch or seeking mating? Although animal behaviours can be partly deduced from their movement data, there will be error due to the environmental change and the observation [27]. Besides getting actual behaviour data to support movement analyses, State-Space Model (SSM) and Hidden Markov Model (HMM) are excellent tools to integrate individual hypothetical behaviours and movement [28].

2.2.2 Habitat Selection and Landscape use

Using movement data to explore habitat selection of animals is very popular in individual movement ecology studies. Internal state and external factors of individuals are more concerned in this field. Resource Select Function (RSF) is the usual method to study habitat selection. However, it ignore the nature of continuously movement data and has difficility in making "avaliable point" to match movement data. The appearance of Step Select Function (SSF) solved this problem and it is becoming the most common tool in habitat selection study with movement data. The integration of more metrics of SSF is making it more powerful [29].

Concerning external factors and animal movement paths, the landscape of the animal movement is a environmental factor that cannot be ignored. Landscape structure is proven to affect animal movement, which can be found in movement behaviour, home range change, dispersal progress and so on. The distribution, shape and area of different kinds of patches and the existence of corridors is all relevant and increases the variance [30,31]. Shepard et al. (2013) transform the landscape to energy cost distribution, indicating that energy landscapes shape animal movement [32]. Landscape connectivity is under focus in recent times [33]. For some rare species such as Amur tigers whose habitat fragmentation is obvious, corridor research is also important. Additionally, artificial landscapes of human activities are expanding and becoming part of animal habitat. Animal movement in artificial landscapes is also a focus of movement ecologists.

Spatiotemporal scales represent the minimum space and time unit within movement research. For example, the time interval of GPS data could be the temporal scale, and step, movement phase or movement path could be the spatial scale. The most suitable spatiotemporal scales in research differ across species, even differ within same species research. For example, multiple movement modes were observed in large herbivores by different spatiotemporal scales [34]. Accuracy of habitat selection of Giant panda is also different among different scales [35]. Sometimes different scales can bring new views of research and lead to new findings.

2.2.3 Migration, Dispersal and Homing

Navigation capacity of individual movement is often focused on the migration and dispersal phenomenon research. Certainly, external factors like heterogeneity of landscape also affects the result of migration and dispersal. In terrestrial mammals, elephants (*Elephas maximus*) [36] and some ungulates in Africa and North America are known for their long-distance migration [37,38]. Why do animals migrate and how can they navigate during their trip are the critical problems in this field. When a new group arrives at a new habitat, their distribution process is defined as dispersal. There is a hypothesis which assumes that animal movement is "random walk" in a homogeneous environment [39]; analyses of animal movement in heterogeneous environments are based on this hypothesis [40].

Memory and homing behaviour are themes related to internal states and navigation of individuals. Animal memory is always a problem researchers are interested in [41]. How can animals remember the location of the feeding points, water resources and their nests? It is sure that navigation and memory capacity contributes to it, but the environmental factors must drive their movement. Homing behaviour is a kind of memory which has been widely studied [42]. Revisitation of specific locations is a another kind of memory and has been used to prove animal habitat preference [43].

2.2.4 Population Movement and Intra-species Relationship

Sometimes, individuals' movement can reflect spatial organization of populations, but must be considered at suitable scales and with enough samples. In some conditions, individual behaviours can be extrapolated to population spacing patterns [44]. Even population dynamics can be derived from reproduction behaviour and mating related movement. Movement ecology is expected to connect with population ecology more widely.

Besides fundamental population ecology like population distribution and population size dynamics, gene flow is another theme of population movement ecology. Based

  DOI: https://doi.org/10.30564/jzr.v1i2.1717

on the spatial distribution and movement information of populations, combined with genetic samples of individuals, the change of population distribution and gene-flow can be revealed [10]. Certainly, progress of dispersal and mating is always accompanied with gene flow, which should be concerned in this field.

Tracking individuals of a group or family, researchers can find the social relationship between individuals by their interactive behaviours. These research directions often choose domestic animals as samples because their society information is known previously [45]. For terrestrial mammals, it gives great access to explore parenting behavior, battle behaviour for mating priority and obeying behaviour to higher-level individuals.

Intraspecific and interspecific relationships are also a focus of population movement ecology. Movement data provides a new access to explore competition between individuals in the same group and the pressures between prey and predator. Many metrics can measure competition between individuals, such as overlap of home range of individuals [46]. The predation pressure between prey and predator can be reflected by avoidance by prey and chasing behaviour of predator. Eriksen et al. (2011) compared moose and wolves (*Canis lupus*) activity patterns but found no correlation between them [47]. This indicates that co-analysing of prey and predator movement data may be not easy. Tracking critical movement behaviour of the target animals and keeping prey and predator in the same small research area may make such ecological pressures clearer to us [48].

2.2.5 Applications of Movement Ecology

There are some applications of movement ecology which can offer great ecological benefits. For example, the spread of infectious disease among animals is a concerned problem nowadays. Besides the information of the pathogen and ways of transmission, animal population distribution and movement is also necessary to build the transmission model[49]. But sometimes movement data cannot surrogate epidemiological indicators. Podgórski et al. (2018) found that no movement metric of wild boar contributed to swine fever outbreak in Europe [50].

Monitoring movement paths for rare species and candidate reintroduction animals is very supportive to their conservation. Movement monitoring can inform animal physiological state, and home range area can visually depict and demarcate high-quality habitat to guide and make convenient the implementation of in-situ protection. Movement monitoring of rare species also benefits education and publicity in animal conservation activities.

Making use of animal movement monitoring data to protect crops and control pest animals is a great application in agriculture. For example, a case study of American research used camera trap and GPS tracking of wild boar mark the breakpoints of farmland, and thus, were able to protect crops from invading wild boar. Jarolímek et al. (2014) tried to develop a similar platform whereby farmers and hunters can know about the movement of wild boar for hunting and protection against crop damage [51].

Climate change is a concerning topic nowadays that can be revealed by movement ecology. For some terrestrial mammals like Elk, their long-distance migration change may reflect the changing climate [37]. For some environmentally sensitive animals like Moose (*Alces alces*) who have the adaptive fitness to cold climates, their behaviour or habitat selection change may also be the sign of climate change[38]. Thus, we suggest that studying the effects of climate change is a potential direction of movement ecology.

2.3 Analysis of Movement Data

To solve specific movement ecology problem, researchers developed many metrics and modles to fit movement data. Day range and home range are normal metrics in terrestrail movement ecology. Day range can be measured by culcalate daily travel distance and can be modeled. There are many methods to calculate home range, including Minimum Convex Polygon (MCP), Kernel Density Estimation (KDE) and Brownie Bridge Movement Model (BBMM). MCP is a kind of geometry method. Due to the lack of distribution density estimation, MCP is rarely used nowadays. KDE is the most commonly used method to calculate home range now and has much reformation and expansion to fit most situations [52]. BBMM is suitable for drawing corridors between patches and has been more considered to estimate home range area [53].

To study habitat selection with movement data, the most popular and suitable method is Step Select Function (SSF). SSF are powerful models to study habitat selection during animal movement. A defined random steps from two distributions established from observation of step lengths and turning angles of monitored individuals. Compared to Resource Selection Functions (RSF), used steps are contrasted with a limited domain of random steps that characterize what is 'available' to the animal during its movement through the environment[54]. Researchers often use Conditional logistic regression as modeling approach to these "actual steps" and "random steps" [55]. At different spatial scales, Path Select Function (PathSF) is also suitable. Zeller et al. (2015) use PathSF to calculate landscape resistance surfaces of of pumas (*Puma concolor*) and found that PathSF is more suitable than SSF for this spe-

 DOI: https://doi.org/10.30564/jzr.v1i2.1717

cies [56].

State-Space Model (SSM) and Hidden Markov Model (HMM) are excellent tools to integrate individual hypothetical behaviours and movement. In movement ecology, SSM is a kind of model which can predict animal state in the future from the previous location and behaviour [57]. Forester et al. (2007) utilize SSM to quantify how elk (*Elaphurus davidianus*) respond both to local conditions and to their internal state in heterogeneous landscapes at different spatial scales [58]. HMM is a diversity process which can link the chain of movement and behaviour to environmental factors [59,60] and has been broadly used in movement ecology, like SSM. Movement and behaviour will be more steadily combined in future research.

3. Research Prospects

This article summarized the papers about terrestrial mammal movement ecology published rencently to find the main themes and object species of this research field. Generally, research themes of terrestrial mammal movement ecology are as follows: Movement pattern and locomotion, habitat selection and landscape use, migration, dispersal and homing and polpulation movement ecology. Despite of some small-size mammals, many terrestrial mammals are concerned in this field. As the development of tracking technology, there are more access to detailed information about animal movement. Terrestrial mammal movement ecology will keep on going basing on these technologies.

Compared to other species, terrestrial mammal share a big part in movement ecology. Maybe it's because the convenience of tracking of most terrestrial mammals or the amount of classes of terrestrial mammals, many research themes has been explored. However, we can't ignore that complexity and difficulity of terrestrial mammal movement research. It's a challenge to determine the internal state and behaviour of terrestrial mammal during their movement on heterogeneous landscape. In the same time, there are too many factors to impact animal movement path. This is the critical and difficult part of terrestrial mammal movement research. Secondly, because there are many shelters on the ground, movement data can be not accurate and have missing point, which bring troubles in movement data analysis. Researchers can choose more precise devices to track animals.

There are some trends and gaps in current terrestrial mammal movement research. According to the paradigm of movement ecology, most research only focuses on motion capacity and external factors; navigation capacity and the internal state are rarely studied. Maybe this is due to the associated difficulty of monitoring physiological state and navigation capacity. As animal behaviour and physiological state monitoring technologies develop, internal state will likely be more considered to demonstrate what drives animals to move [61]. Navigation mechanisms are studied to explain how animals locate and move with some directions. Accompanied with the finding of environment markers such as magnetic fields and the help of nerve and brain science, the researcher can get a deeper understanding of animal navigation [62].

On the other hand, some species are missed in current research. Some large-size terrestrial mammals are easier to track and are of more concern, but small-sized terrestrial mammals such as Mustelidae (*Mustelidae*), including mink (*Martes* spp.), badger (*Meles* spp.) and rodents (*Glires*) are harder to track and more ignored. Actually, small-sized terrestrial mammals also play important roles in ecological systems and their movement deserves more attention.

There are many potential research themes in terrestrial mammal movement ecology research. For animal individuals, movement and landscape are considered grand themes. With the expansion of human utilised land area, lots of artificial landscapes such as roads, farmland and residential areas will likely be highly influential on terrestrial mammal movement; habitat fragmentation caused by this cutting up of the natural landscape is also a problem to animal dispersal and distribution. Movement data is direct data to reflect animal movement affected by these landscape factors. The internal state factors during animal movement is also potential dirction of terrestrial mammal, even the personality can be inclued to factors to affect space use of terrestrial mammals [63].

For animal populations, combining movement data with gene samples to predict animal distribution changing and migration is very powerful. If an animal's reproduction and mortality information is collected, population numbers can also be predicted. Additionally, disease transmission and climate change are also potential fields to which movement data may be applied. Once supported by animal movement and contact information, disease transmission models will predictably be more accurate. Climate change must be felt by polar animals firstly; their adapted movement behaviours or changes of migration can inspire researchers to understand climate change.

Acknowledgments

This article is funded by National Natural Science Foundation of China (NSFC31872241), Fundamental Research Funds for the Central Universities (2572017PZ14), National Key Programme of Research and Development, Ministry of Science and Technology (2016YFC0503200),

DOI: https://doi.org/10.30564/jzr.v1i2.1717

Biodiversity Survey, Monitoring and Assessment Project of Ministry of Ecology and Environment, China (2019HB2096001006) and Heilongjiang Touyan Innovation Team Program for Forest Ecology and Conservation. The advice and revisions by Professor Guangshun Jiang have guided this article, and I further acknowledge the help of colleague Nathan J. Roberts for English editing, assistance and advice.

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