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Movement in 3D: Novel Opportunities for Understanding Animal Behaviour and Space Use

Robert J. Lennox^{1,2,3}  | Timo Adam⁴ | Milan Riha⁵ | Natasha Klappstein³ | Christopher T. Monk⁶ | Knut Wiik Vollset² | Larissa T. Beumer^{7,8}

¹Norwegian Institute for Nature Research, Trondheim, Norway | ²NORCE Norwegian Research Centre Laboratory for Freshwater Ecology and Inland Fisheries, Bergen, Norway | ³Ocean Tracking Network, Department of Biology, Dalhousie University, Halifax, Nova Scotia, Canada | ⁴Bielefeld University, Bielefeld, Germany | ⁵Biology Centre of the Czech Academy of Sciences, Institute of Hydrobiology, České Budějovice, Czech Republic | ⁶GEOMAR Helmholtz Centre for Ocean Research Kiel, Kiel, Germany | ⁷Senckenberg Biodiversity and Climate Research Centre, Frankfurt am Main, Germany | ⁸The University Centre in Svalbard, Longyearbyen, Svalbard, Norway

Correspondence: Robert J. Lennox (lennox@dal.ca)

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ABSTRACT

Animals move in three spatial dimensions, but many animal movement tools have only focused on the use of 2D coordinates for modelling space use, habitat selection, behavioural classification, social interactions and movement. Here, we submit that many common movement ecology analyses can and should be extended to consider all three spatial dimensions to make more robust inferences about ecological processes. We provide an overview of how home range analysis, network analysis and social network analysis, hidden Markov models, resource selection and step selection functions and hierarchical linear and additive models are used for studying animal movement in two dimensions. Then, we explain how the third dimension, *z*, can be used within these existing frameworks to consider how depth and altitude affect key ecological inferences drawn from animal tracking data. Our position builds on empirical and theoretical work about how three-dimensional methods can contribute to stronger inferences in movement ecology. Key limitations to operationalisation of this framework include calibration of uncertainty in pressure sensors used to measure depth and altitude, visualisation and rendering of three-dimensional data to make them interpretable and understandable to end-users and generally more conventional and accepted methods for using three dimensions when conducting standard animal movement analyses.

1 | Introduction

Accurate quantification and classification of animal movement phenotypes is crucial to understanding ecosystem functioning and proper management (Morales et al. 2010; Spiegel et al. 2017; Brodie et al. 2018). Technological advancements

in geolocation using global positioning systems (GPS), environmental estimators (e.g., light-based geolocation) and high-frequency transmissions to remote stations (e.g., radio receivers, acoustic receivers, passive integrated transponder antennas, motes and satellites) have revolutionised ecological sciences and provided new perspectives for studying

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animals and their interactions with the environment and humans (Hussey et al. 2015; Kays et al. 2011; Lennox et al. 2017; Nathan et al. 2022).

Tracking the two-dimensional movement of animals as they cross plains, grasslands or the seabed yields critical information about movement corridors and habitat use of walking animals (Kays et al. 2011). For applied questions, this is often particularly useful because humans operate predominantly in two dimensions (Gonzalez, Hidalgo, and Barabasi 2008). Consequently, conceptualisation of many habitat features and modelling of animal spatial and movement ecology are often summarised by longitudinal and latitudinal planes (Montgomery, Ortiz-Calo, and Heit 2020). Management zones are not generally differentiated vertically; therefore, protected areas or harvesting regulations do not change dynamically with altitude or depth but scale from sea-level on a map through the full vertical dimension in many cases. However, there is extensive use of vertical habitat by animals that fly, swim, dig or climb. Specific challenges associated with such habitat use, such as vertical gradients in physical and chemical habitats, make this dimensionality ecologically important (Adachi et al. 2017; Wright et al. 2017). While vertical habitat is generally taken into account within studies aiming to describe the habitat use of flying and swimming animals, it is typically considered separately from the latitudinal/longitudinal measurements rather than integrated in three dimensions (3D; Guzzo et al. 2016; Mulder et al. 2018; Říha et al. 2021).

The animal tracking community is aware of the challenges of working in three dimensions and the development of tools is ongoing to improve researchers' ability to consider vertical space use when modelling animal behaviour (Deng et al. 2011; Vivancos, Closs, and Tentelier 2016; Lee et al. 2017; Wright et al. 2017; Venegas-Li et al. 2018; Klein et al. 2019; Montgomery, Ortiz-Calo, and Heit 2020; Lato et al. 2022). For instance, pressure-sensing biologgers and transmitters can measure the depth or altitude at the high temporal and spatial resolution, often with better accuracy than latitude and longitude can be estimated from detection data (Whoriskey et al. 2019; Lato et al. 2022). Although there is accelerating potential for telemetry data to be analysed and presented in three dimensions, a toolbox for three-dimensional analytical methods is currently lacking, rendering available three-dimensional data an unexploited resource (Ahmed, Bailey, and Bonsall 2022). In this paper, we suggest ways in which the untapped potential of three-dimensional methods for studying animal movement is hindering progress in fundamental and applied biology, especially for swimming and flying species. We review key methods in analytical movement ecology with respect to their potential for integrating three-dimensional data, highlight promising new developments and discuss needed methodological improvements. Finally, we outline new avenues for both fundamental and applied research that may emerge with the development of three-dimensional tools in movement ecology.

2 | Dimensionality of Animal Movement

Animals move in three dimensions, but capturing the dimensionality of these movements can be challenging. Horizontal

positions are available from electronic tags that connect to global navigation satellite systems (GNSS), estimate position from the environment (i.e., light-based geolocation) or transmit identification signals to base stations at known locations. Positions can be stored onboard tags from GPS fixes, estimated from other data stored on the tag (i.e., light-based geolocation) or estimated from transmissions via multilateration (Baktoft et al. 2017). It is possible to use camera tracking to estimate locations in three-dimensional space from positions resolved by particle tracking or other laboratory-based methods. For example, Neuswanger et al. (2022) used camera tracking of juvenile salmonids to resolve 3D positions and calculate territoriality and intraspecific competition in a hypervolume of water. Yet, to date, most tracking is conducted using telemetry, as described above, along two horizontal planes resolved from GPS or reverse-GPS fixes of the animal in field or mesocosm studies (Nathan et al. 2022).

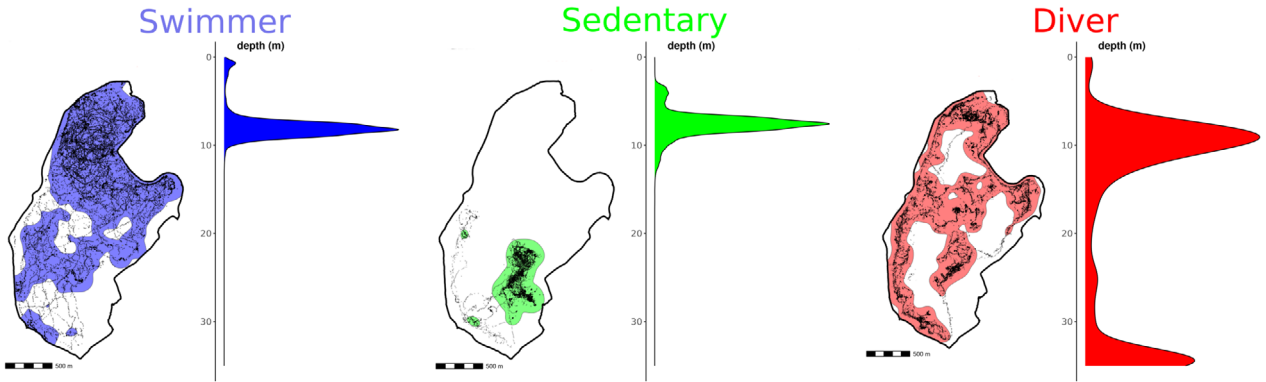
Animal tracking devices provide the option to record or transmit data from pressure sensors, opening a third dimension that can be used to better understand the exact position of an animal on terrain, in the air or in water. Knowledge about the position of an animal in this third dimension is non-trivial for the purposes of understanding habitat use, social association, behaviour and most other physicochemical associations of an animal to its environment. For example, animals may be relatively stationary in two dimensions but travel vertically in ways that are energetically costly (Box 1). Most aquatic species exhibit vertical patterns in activity to exploit the 3D structure of their environment in a way that has long been adopted into modelling approaches and to answer specific hypotheses such as habitat compression (Vedor et al. 2021) and collision risks with turbines (Scacco et al. 2023). Flying or descending in the water column also has energetic implications for animals and their three-dimensional movements can help to exploit spatial variability in costs of transport (Masello et al. 2021; Scacco et al. 2023). Many species even display routine diel vertical migrations (Mehner 2012; Brierley 2014). Coastal and reef species take refuge in the substrate and have a dynamic three-dimensional habitat (Udyawer, Simpfendorfer, and Heupel 2015). Light, temperature and oxygen can all vary greatly at different depths or altitudes. Physiological performance of animals will respond to these vertical gradients in environmental quality, especially oxygen in thin air (Hawkes et al. 2017) and in the deep ocean or lakes. Consequently, animals' movements from sea level to depth or altitude can affect their physiology and vulnerability to stressors including temperature stress as well as potential barriers such as buildings/windmills or fishing nets with fixed depths/heights. Arboreal animals that climb trees (Harel et al. 2022) and species that use complex terrains such as montane mammals (Heit et al. 2023) may also use 3D habitat in complex ways that can benefit from pressure sensors or altimeters that help analysts infer the spatial position of the animal in its habitat (Box 2).

An important consideration in the dimensionality of animal movement for animals that move in three dimensions is that the costs of transport may differ horizontally and vertically. Gravity in air and in water ensures that the physical costs of moving vertically are likely to exceed the costs of horizontal transport.

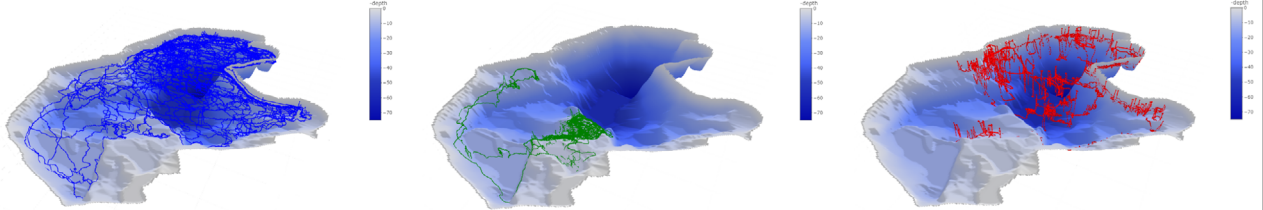
BOX 1 |

Comparison of two-dimensional and three-dimensional analyses of movement data from three tagged northern pike (*Esox lucius*) in a lake in Czechia. The positions of the animals were resolved from multilateration of acoustic tags within a grid of acoustic receivers in the lake. The three pike are named based on their general behaviour, swimmer, sedentary and diver. Although two-dimensional area use suggests the swimmer has the largest territory (a), three-dimensional trajectories provide a different picture, because the diver has the largest 3D home range (b, c, d). The inset table of home range overlap shows the percentage of the home range area (2D) or volume (3D) of an individual 'x' (rows) that is overlapped by an individual 'y' (columns). For example, in 2D, 49% of the 'sedentary' HR overlaps with the 'swimmer' HR, but only 8% of the 'swimmer' HR is overlapped with the 'sedentary' HR.

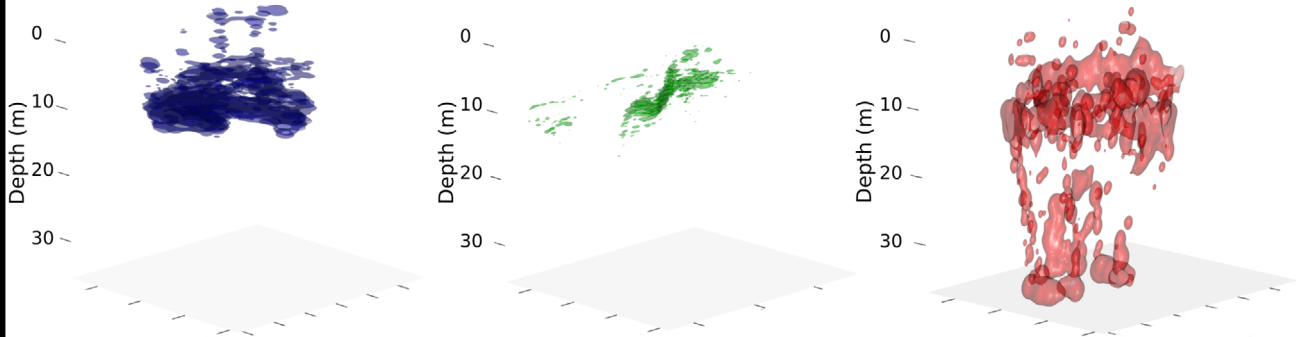
a) 2D locations, home range and depth used



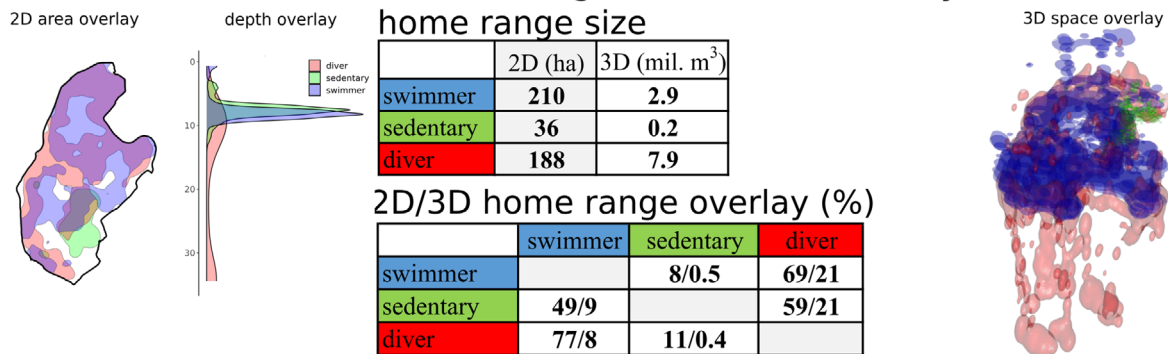
b) 3D trajectories (one week only)



c) 3D home range



d) 2D/3D individual home range size and overlay



BOX 2 | Examples of 3 three-dimensional habitat use by animals and potential biases in common movement models. All images provided by R.JL.

Leopards (*Panthera pardus*) will use vertical structure in the habitat. Calculating the costs of transport within this habitat based on two-dimensional steps will underestimate total activity and energy budgets of the animals.



The unicorn fish *Naso unicornis* swims in three dimensions in the water around this French Polynesian atoll. Positioning these fish with acoustic transmitters without depth sensors to calculate movement step lengths would likely bias inferences about the animal's habitat selection.

This flamingo (*Phoenicopterus roseus*) flies above conspecifics on a marshland in the Mediterranean. Although the flying individual overlaps substantially in two dimensions with conspecifics, a pressure sensor indicates that it is spatially distinct and not co-located, significantly affecting interpretations about sociality.



Hedgehogs will dig burrows in the ground to seek refuge using subterranean habitat, they can live a three-dimensional life. Understanding how the hedgehog uses the full dimensionality of its available habitat is important to investigate the space use and habitat requirements and will influence how behavioural analysis tools like hidden Markov models will interpret the animal's daily movements.

As evidence of this, buoyancy control mechanisms have evolved in many aquatic species to account for the costs of vertical movement in water (Strand, Jørgensen, and Huse 2005). Many birds have evolved behaviours that exploit thermal updrafts that reduce the costs of vertical transport in air against gravity (Bohrer et al. 2012). For terrestrial animals, walking or slithering up slopes or climbing trees is also more costly than moving on flat ground (Halsey 2016). Although the three dimensions are all isotropic in space, the different costs of movement in the vertical

plane may need to be considered anisotropic for the purposes of modelling.

3 | Applications

To be effective, future management applications will necessarily need to refine their approaches to consider animals' three-dimensional space use. For instance, Khosravifard

et al. (2020) showed that three-dimensional kernel methods were more effective for determining the collision risk of griffon vultures (*Gyps fulvus*) with wind turbines than the two-dimensional methods that had been used in previous risk assessments (see also Figure 1). Similarly, Kahane-Rapport et al. (2022) demonstrated that foraging depths of baleen whales tend to overlap in depth with microplastic aggregation zones, suggesting high potential impact on species such as blue whales (*Balaenoptera musculus*) and pointing to the need for depth data along with horizontal positions to correctly interpret risks encountered by animals in the environment as they use it, not necessarily just as we see it largely viewing the world from our two-dimensional platform.

Three-dimensional modelling can help to better protect animals from disturbance in their environment. Protected areas are presently two-dimensional boundaries but may eventually be refined to limit activities at certain depths or altitudes, requiring better models of habitat and species compositions in three dimensions. Brito-Morales et al. (2022) advocated for the use of depth data to create three-dimensional marine protected areas, which will rely on or motivate increased application of the three-dimensional tools that are available to support such ambitions. Commercial and recreational fisheries are already operating with intricate planning for positions of their gear in depth and good models of three-dimensional animal niches can help minimise bycatch, assist with invasive species control or minimise entrainment of animals in infrastructure like turbines. For example, studying the three-dimensional habitat of invasive sea lamprey can provide insight into the placement of traps (Rous 2014) and the three-dimensional positioning of salmon can help determine the optimal placement of diversion structures to help avoid entrainment in a dam (Silva et al. 2020). In the sky, Walter et al. (2012) combined GPS and altitude data from vultures to model bird collision risk around airfields. Three-dimensional models of animal movement can make the most of three-dimensional environmental data such as fluid dynamics models (Khan 2006), which can increase the resolution with which we can understand and manage species. However, measurement error inherent to both the tracking devices and the environmental models should be considered when

trying to evaluate very fine-scale responses of animals to their environment.

4 | Methods Extending Movement Ecology to Three Dimensions

4.1 | Movement Modelling

Animal locations are collected as a time series of spatial coordinates, either in two dimensions (x, y) or three dimensions (x, y, z). From these data, animal movement patterns can be described in terms of step lengths and turning angles (Codling, Plank, and Benhamou 2008; Benhamou 2019). These parameters can be captured via a correlated random walk (CRW) that models both speed and directional persistence of movement tracks. In two dimensions, CRWs can be formulated in terms of these step lengths and turning angles (i.e., based on their polar coordinates; Figure 1a). Step lengths are calculated as the Euclidean distance between successive observations,

$$L_t = \sqrt{(x_t - x_{t-1})^2 + (y_t - y_{t-1})^2}$$

and turning angles are calculated as the difference in bearings between successive steps.

However, for animals moving in three dimensions, the walk can be extended to simulate three-dimensional animal locations, which can be expressed in spherical coordinates: step length L_t , azimuthal (i.e., horizontal) bearing θ_t , and the polar (i.e., vertical) bearing ψ_t (Figure 1a). Step lengths are extended to measure the three-dimensional segments,

$$L_t = \sqrt{(x_t - x_{t-1})^2 + (y_t - y_{t-1})^2 + (z_t - z_{t-1})^2}$$

better representing the speed and energy consumption of moving animals (although note that energy costs in the third dimension may not be equivalent to costs in the horizontal dimensions). Further, three-dimensional turning angles are based on the

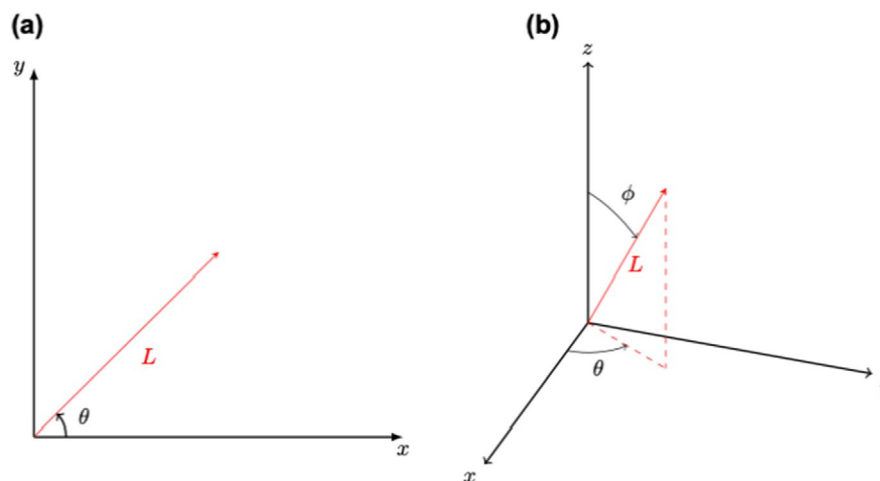


FIGURE 1 | Illustration of two-dimensional and three-dimensional coordinates, for the red vector. (a) Two-dimensional polar coordinates, where L is the Euclidean distance and θ is the bearing. (b) Three-dimensional spherical coordinates, where L is the Euclidean distance, θ is the azimuthal (i.e., horizontal) bearing, and ϕ is the polar (i.e., vertical) bearing.

change in both horizontal and vertical bearings and can be modelled with spherical distributions in a CRW (Ahmed et al. 2021; Pike and Burman 2023). CRWs based on step lengths and turning angles are very common in movement ecology, but note that it is also possible to model position-based CRWs (Jonsen, Mills Flemming, and Myers 2005; Whoriskey et al. 2019) and these are also extendable to three dimensions. Investigators should consider if and how the cost of transport in the third dimension differs from the cost in horizontal planes when applying these three-dimensional models.

CRWs form the basis of most modern movement models, including hidden Markov models (HMMs) for behaviour, energetics models, habitat selection functions and continuous-time approaches based on stochastic differential equations (SDEs). These models have important uses for quantifying animal behaviour, space use and accounting for missing or error-prone data (Johnson et al. 2008; Avgar et al. 2016; Morales et al. 2010). Therefore, three-dimensional CRWs that better quantify movement speed and tortuosity have important implications for ecological inference, although they have rarely been employed in animal movement ecology (but see Ahmed et al. 2021 for an application to insect trap counts). In the next section, we elaborate on several uses of spatial and movement-based models and explain how their extension to three dimensions can improve inference.

4.2 | Home Ranges/Space Use

Home range estimation aims to summarise the distribution of an animal, traditionally achieved by mapping a polygon around a series of 2D positions. Home range estimation from tracking data is an active field and various analytical approaches have been developed over the past decades. Commonly used approaches include the (autocorrelated) Kernel Density Estimator (Fleming et al. 2015), minimum convex polygons and local convex hulls (Kie et al. 2010; Silva et al. 2022; Kraft et al. 2023). Importantly, range estimators, which target the long-term, stationary space-use distribution of animals, are distinct from estimators of the occurrence distribution, such as Brownian bridge methods, which target movement paths and their uncertainty over a specific time interval (Alston et al. 2022).

Independent of the chosen estimator, home ranges of aquatic and aerial species are likely to be misrepresented by horizontal positioning not accounting for the third dimension (Khosravifard et al. 2020; Chandler et al. 2020). The accuracy of 2D home range calculations has been significantly enhanced through the integration of autocorrelation structures, movement models, simulations and the consideration of physical barriers (Calabrese, Fleming, and Gurarie 2016; Calenge 2006). This refinement has rendered 2D home range estimates more reliable and applicable, particularly when dealing with unevenly spaced tracking data (Calabrese, Fleming, and Gurarie 2016). Despite these advancements, the application of similar calculation procedures for 3D home range estimates remains limited, and there is a notable absence of user-friendly computational support in this regard. However, promising alternatives are available that extend the home range into three

dimensions (Keating and Cherry 2009; Tracey et al. 2014). Udyawer, Simpfendorfer, and Heupel (2015) demonstrated the potential of using three-dimensional data combining horizontal positions with data from pressure sensors to estimate a more accurate home range volume. Similarly, Aspillaga et al. (2019) provided a novel method of estimating fish space use in three dimensions to infer spawning behaviour. Finally, Ferraini et al. (2023) used 3D home ranges to develop an index of overlap among kestrels (*Falco naumanni*), highlighting that the identification of any overlap critically depended on accurate description of their flying altitude. In Box 2, we illustrate how different conclusions can be made about the space use of three northern pike (*Esox lucius*) moving in a lake when 2D and 3D space use estimates are compared. ‘True’ three-dimensional space use clearly illustrated a larger volume for one pike that had a smaller home range when calculated in two dimensions.

For estimating range from detection data (i.e., tagged animal is recorded at a radio or acoustic station), networks are often used instead of kernel or convex polygon-based methods (Ledee et al. 2015; Jacoby and Freeman 2016). Networks have the advantage of not requiring continuous position data for estimating space use. However, networks will underestimate space use where the detection array is smaller than the potential area that an individual can use. Networks are most commonly used for acoustic, radio and PIT telemetry (Kraft et al. 2023). Acoustic and radio transmitters commonly have, or can easily be complemented by, continuous depth sensors that can provide information on the third dimension beyond what is available from horizontal positioning systems. However, to establish such a three-dimensional network, depth would have to be binned, for example into ‘surface’, ‘mid-water column’ and ‘bottom’, because networks are inherently based on discrete rather than continuous observations. Method development for how to discretise space for three-dimensional networks and validations are needed in this area to understand the benefits of three-dimensional networks for calculating spatial summary statistics such as node degree and betweenness in discrete space.

4.3 | Resource and Habitat Selection

Understanding animals’ resource and habitat selection is a key question in wildlife ecology and of importance for informing management and conservation strategies (Fletcher, and Fortin (2018). Resource selection functions (RSFs) and step selection functions (SSFs) assess animals’ habitat preferences by contrasting the spatial features of observed locations to the surrounding habitat (via a sample of ‘random’ or ‘available’ points; Fieberg et al. 2021). However, RSFs and SSFs investigate different spatiotemporal scales (Johnson 1980; Michelot, Blackwell, and Matthiopoulos 2019). RSFs describe space use at larger scales, assume that animal locations are independent and generally sample random points at the home range scale (Manly et al. 2002). Therefore, they are less suited to autocorrelated tracking data (Alston et al. 2023). In contrast, SSFs consider habitat selection at the scale of the movement step and consist of both a habitat selection function and a movement kernel. The movement kernel can be estimated from the

empirical distribution of step lengths and turn angles (and then used to generate available locations) or estimated jointly with habitat selection (Rhodes et al. 2005; Forester, Kyung Im, and Rathouz 2009; Michelot et al. 2024). The latter approach (sometimes termed an integrated SSF; Avgar et al. 2016) has been shown to reduce bias in habitat selection parameters, when the movement kernel is correctly specified (Forester, Kyung Im, and Rathouz 2009), and allows for interactions between movement and habitat variables (Prokopenko, Boyce, and Avgar 2017). In recent years, many methodological extensions have been proposed for SSFs and RSFs, including individual-level and spatial random effects, time-varying dynamics and behavioural variation (Nicosia et al. 2017; Muff, Signer, and Fieberg 2020; McCabe et al. 2021; Arce Guillen et al. 2023; Dejeante, Valeix, and Chamaillé-Jammes 2024; Chatterjee et al. 2024; Klappstein et al. 2024). This has made them flexible and popular tools for assessing animal movement and space use, but little attention has been paid to these processes in three dimensions.

SSFs were developed in large part for terrestrial species that live in two spatial dimensions, and the movement kernel is generally defined as a two-dimensional CRW. However, SSFs have recently been used to study the migration routes of grey-faced buzzards (*Butastur indicus*; Nourani et al. 2018), hunting strategies of barn owls (*Tyto alba*; Séchaud et al. 2021), movement decisions of forest bird species (Aben et al. 2021), and habitat use of marine turtles in protected areas (Roberts et al. 2021). For the animals that use three dimensions, the potential of SSFs for characterising habitat selection has so far not been fully realised due to the lack of options to account for the vertical dimension. For many flying and swimming species, the physicochemistry of the 3D environment is critical, including thermal gradients, flow/wind at different depths/altitudes, salinity or oxygen content in the water, or the rugosity and resistance of the land. The cost of transport in the vertical dimension must also be considered, and investigators will need to consider this when specifying the movement kernel, perhaps via the inclusion of interaction terms (e.g., vertical bearing affects distance travelled). To account for the impact of the environment on movement, SSFs could be improved by modelling movement in three dimensions via three-dimensional CRWs, which would better capture the true movement process and potentially reduce bias (i.e., as shown for two-dimensional SSFs; Forester, Kyung Im, and Rathouz 2009). Three-dimensional modelling could also be used to better account for the energetics of movement, properly accounting for energetic differences between the horizontal and vertical dimensions, in energy-based step selection analyses (Klappstein et al. 2022). Similarly, RSFs can be extended to model space use in three dimensions, by considering a three-dimensional availability domain of the three-dimensional habitat in air or water. Therefore, these approaches could include three-dimensional covariates, which may be important in understanding how animals use space when the habitat is highly vertically structured, while retaining the flexibility to include two-dimensional variables, where ecologically relevant. Indeed, it is unlikely that habitats at ground level are influencing movement decisions for fish swimming, or birds/bats flying, above these areas. An approach that accounts for the three-dimensional habitat has the potential to reduce bias

by appropriately modelling movement and habitat structure at the scale the animal moves, if the challenges of measuring the environment in three dimensions can be overcome in both practical and computational terms.

4.4 | Inter- and Intraspecific Interactions

Animal tracking data are increasingly used to understand co-occurrence and interactions of animals by inferring proximity (Long et al. 2014; e.g. Haulsee et al. 2016). Any tag type can be used to infer proximity by establishing a distance threshold a priori and calculating rates of association, ideally compared to a null model of simulated encounter probabilities (Farine 2017). Associations among individuals can then be used to investigate sociality and inter-/intraspecific interactions. Interactions of guinea fowl (*Acryllium vulturinum*), for example, have been inferred from GNSS tracking data to draw networks and identify complex social dynamics in their societies (Papageorgiou et al. 2019). Alternative metrics of association or habitat partitioning may draw on home range methods or similar kernel-based measurements to evaluate overlap in space and time (Fieberg and Kochanny 2005). Space use metrics derived from kernel analysis (i.e., kernel-based methods such as kernel utilisation distribution) may be used to calculate overlap and test hypotheses about individual interactions such as competition. Importantly, co-occurrence does not necessarily imply interaction (Jacoby, Papastamatiou, and Freeman 2016), although it may be a strong predictor of dynamics (Farine 2015).

Crucially, inferring association for walking species that live in a two-dimensional plane is simpler than for species exploiting three-dimensional habitats where horizontal positioning can misrepresent association (Figure 1). MacArthur and MacArthur (1961) famously showed that avian species split habitat overlapping in horizontal space into three-dimensional niche partitioning, facilitating coexistence. Simpfendorfer et al. (2012) demonstrated that European eel (*Anguilla anguilla*) overlapped substantially in their 95% kernel utilisation distribution (KUD), but when considering their depth use, they were in fact overlapping very little. Similarly, Lee et al. (2017) showed that 3D KUDs were effective for identifying intraspecific overlap of Eastern blue groper (*Achoerodus viridis*) during the spawning season. For species using three-dimensional space, accounting for depth/altitude is necessary to accurately characterise inter- and intraspecific interactions and three-dimensional spatiotemporal niche partitioning. By identifying accurate space use and estimating interactions more accurately, it is possible to generate more robust inferences of social interaction and social networks.

4.5 | Behavioural Classification With HMMs

Various methods exist to extract behavioural information from tracking data (see Edelhoff, Signer, and Balkenhol 2016; Gurarie et al. 2016). HMMs are increasingly popular tools that provide a natural framework to infer behavioural modes (e.g., foraging and travelling) and their various drivers from position data (Langrock et al. 2012; McClintock et al. 2020).

HMMs are hierarchical time series models which assume that each observation arises from an unobserved or latent state. In movement ecology, these states are interpreted as behavioural modes, and are usually defined as state-dependent CRWs. For example, foraging is often associated with slower, more tortuous movement, compared to fast, directed travelling behaviour (Morales et al. 2010). The state-dependent CRWs are usually formulated in terms of step lengths and turning angles (Michelot, Langrock, and Patterson 2016; Michelot, and Blackwell (2019)) but can also be position-based models (Whoriskey et al. 2019). Step lengths between two tri-dimensional sets of coordinates may be more precise information about many species, revealing new behavioural types not possible to identify using two-dimensional step length measurements. For animals living in 3D space, step lengths will consistently be underestimated from 2D Euclidean distance calculations, and behavioural state classification will consequently be biased.

Recent studies have recognised the potential of integrating depth/altitude data into HMMs. Langrock et al. (2012) were early to suggest a hidden Markov modelling approach accounting for depth data of a diving whale to explicitly model movement and foraging behaviour in the water column. Heit et al. (2023) incorporated altitude data for *Puma concolor* and found better fitting HMMs using the third dimension (they call it 2D+ rather than 3D). Especially for marine mammals, this approach has subsequently proven useful in classifying behavioural states and link behavioural variation to environmental conditions (van Beest et al. 2018; Photopoulou et al. 2020). Similarly, for aerial species, Pritchard et al. (2022) used the 3D flight paths of hummingbirds to classify search and travel behaviours. Although it is becoming relatively common to include vertical observations (e.g., depth and altitude) as an additional HMM data stream (Langrock et al. 2012; McClintock and Michelot 2018; Adam et al. 2019), it is also possible to define each behavioural state as a fully three-dimensional CRW. This is a promising extension of the HMM approach to more accurately classify behaviours of animals that swim, fly or otherwise move across three axes.

4.6 | Hierarchical Models

Animal tracking data often violate assumptions of independence in many modelling approaches. Hierarchical models can be used to account for the autocorrelation in tracking data, via the inclusion of spatial, temporal or individual-level random effects (Pedersen et al. 2019). Hierarchical models may aim to model factors that affect the movement of animals in space and time by using the step as the sample unit, for example, directly measuring the step length or transforming steps to a rate (speed). Hypotheses that animal movement is affected by time of day, location in space, and individual variation (i.e., random effects) will likely yield different results when the steps are calculated with consideration of three-dimensional movement rather than assuming two-dimensional activity on a single plane, as implied by two-dimensional calculations of step length or speed.

Hierarchical models for telemetry data necessarily must consider spatial effects, frequently using stochastic partial differential equations or spatial smoothing to reveal hotspots and coldspots in spatial effects and manage autocorrelation inherent in time-series data with spatial dependency (Gutowsky et al. 2020). When individual positions are available in three axes, the spatial autocorrelation may not be adequately described by two-dimensional Gaussian Markov Random Fields or other smoothing solutions that do not consider the three-dimensional location of the animal. Three-dimensional smoothing of positions are possible in R packages such as *mgcv* (Wood 2017) to estimate spatial effects in three dimensions, but will be challenging to visualise and may require some effort to render. Nevertheless, the *mgcv* package provides a strong functionality with which to consider isotropic or anisotropic three-dimensional effects of space by specifying a smoother, for example, $s(x, y, z)$ or $te(x, y, z)$ for anisotropic smoothers. In the latter case, anisotropic smoothers are appropriate where the vertical dimension is not measured in the same units as the two horizontal planes; in the former isotropic case, a metric or imperial coordinate reference system (e.g. UTM) would be combined with a vertical measurement of depth or altitude in metres. Anisotropy may also be necessary for species that have relatively high costs of movement in the vertical plane.

5 | Prospectus

Most animals move in three dimensions, a feature of movement that we submit to be underdeveloped in many analytical frameworks for animal tracking data. Moreover, where a 3D framework is available, such as 3D kernel utilisation distributions for home range analysis (Keating and Cherry 2009), utilisation appears not to be fully realised in movement studies. The dimensionality of movement is particularly salient to most aquatic and aerial species whose vertical displacement can be measured by available tracking technology but is typically not accounted for in estimations of space use, behaviour, and habitat selection. We have provided an overview of key methods in animal movement ecology that we believe would be improved with the consideration of three-dimensional data. It is certain that better integration of depth data for aquatic species and altitude data for their airborne counterparts will refine our understanding of their ecology and will influence the way that aquatic and aerial movement data are interpreted. We have outlined applications where such improved ecological understanding can foster more effective management and conservation strategies.

One of the major challenges facing three-dimensional data in ecology is the computational cost for model fitting and visualisation. Adding an additional dimension will certainly increase the cost of model fitting and the time required for spatial models to provide estimates. Illustrating three-dimensional data in two dimensions is not intuitive, notwithstanding the intensive computational power required to render many of the more richly illustrated visualisations (Demšar et al. 2015). Specialised programs for rendering space in three dimensions have been developed for other applications, and we envision that these tools will become more accessible to ecologists to assist with visualisation and

presentation of information about animal movements in three dimensions. Software for illustrating data in three dimensions includes rayshader, a renderer in the R environment that can facilitate plotting voxels (i.e., three-dimensional pixels) from home ranges, for example (Morgan-Wall 2021). Other promising applications are immersive virtual or augmented reality visualisations that can create engaging communication tools but also open new avenues for understanding data and how animals use their environment in three-dimensional planes (Klein et al. 2019).

The primary limitation of three-dimensional methods is accounting for differences in the costs of vertical movement. Slopes and inclines in the terrestrial environment make the costs of moving altitudinally different from horizontal movements for walking species (Carnahan et al. 2021). For diving species like birds, the physical and physiological demands of diving are different from those of flying (or swimming); Gómez-Laich et al. (2013) demonstrated high energetic costs of diving for shags, for example. For many soaring birds, the cost of moving altitudinally is subsidised by their careful use of thermal updrafts (Shamoun-Baranes et al. 2016). Three-dimensional analytical tools that do not consider how gravity affects the costs of movement in the third dimension can risk underestimating the costs of movement in 3D. A second limitation is the sampling resolution of the devices. Biologgers that measure pressure may sample at 1–100 Hz whereas GPS locations may be available at greater intervals, creating a mismatch that requires some interpolation for modelling. Investigators should think carefully about the sampling resolution that they need to gather depth or altitude data for modelling movement in 3D.

Collecting 3D data from animals using biotelemetry and logging devices is one part of the equation to advance movement ecology into three dimensions (Hussey et al. 2015; Kays et al. 2011). However, an equally important aspect is to advance the dimensionality of environmental measurements. Methods for mapping land- and seascapes in three dimensions are advancing (Lepczyk et al. 2021). In aquatic environments, vertical profiling of temperature, salinity, and oxygen is routinely performed with conductivity, temperature, depth recorders (CTD) and may also include additional measurements such as total dissolved gas, nutrients, light availability, salinity or biological variables such as food. These environmental data collected at discrete sampling points can be smoothed using additive models or kriging to generate three-dimensional habitat voxels into which three-dimensional animal locations can be superimposed, for instance, to identify 3D habitat selection (Pedersen et al. 2019). In terrestrial environments with vertical structuring, such as forests, Light Detection and Ranging (LiDAR) systems have drastically improved our ability to map, for example, canopy habitat structure in 3D (Harel et al. 2022). Depending on the scale of interest, LiDAR sensors can be mounted on drones, planes or satellites, offering opportunities to characterise tree and forest structure, canopy height, and vegetation density from fine to coarse spatial scales (Asner et al. 2008; Dubayah et al. 2020; Lang et al. 2021). Ongoing advances in LiDAR technology and processing of LiDAR data consequently show great promise for accurate, high-resolution and large-scale mapping of terrestrial 3D habitats and thus for improving our understanding of animal behaviour and habitat use in 3D (or 2.5D; aka Harel et al. 2022).

Computer vision technology and mapping of three-dimensional airspace has been used for example to investigate hawk flight (Miñano et al. 2023).

Three-dimensional methods are clearly promising for swimming and flying species and can help reveal new aspects of their ecologies that have been challenging to detect otherwise (Neuswanger et al. 2022). Pressure sensors are frequently incorporated into tracking packages and there are therefore great opportunities to increase the use of these data by developing and applying extensions of commonly used models ranging from simple calculations of step length and speed to estimating home range dimensions, spatial and social networks, classifying behaviour, and estimating resource use of tagged animals. New developments may be possible in sensor technology that increases precision or resolution of these sensors. In many cases, the functionality to apply these advances is already available, and increased awareness and convention around the use of all three spatial dimensions will strengthen the science provided by electronic tagging and tracking tools. However, it is important to remember that the model quality will always depend on properly calibrated sensors, which may require further development or calibration for some applications (Veilleux et al. 2016; Lato et al. 2022). Because most species use a three-dimensional habitat, improved technology for recording locations/positions in 3D and more conventional use of tools for analysing these data in adequate dimensionality has great potential to contribute to ecological studies of animals, their environments, and conservation initiatives on land and in water.

6 | Conclusion

It is clear that many studies have started to include depth and altitude data in their analysis and new methods have started to emerge such as 3D home range estimators. Many of the suggested extensions in this paper are actionable but will require some development by statisticians and integration into functions for popular software like R to realise their potential. With large volumes of animal tracking data being archived in global databases like Movebank and Ocean Tracking Network, ensuring that horizontal locations are paired with depth and altitude data as much as possible should be prioritised to ensure that the most information possible can be exploited to model animal movement.

Author Contributions

Robert J. Lennox: conceptualization, investigation, writing – original draft, methodology, project administration, writing – review and editing. **Timo Adam:** conceptualization, investigation, funding acquisition, writing – original draft, writing – review and editing, validation, methodology. **Milan Riha:** conceptualization, investigation, funding acquisition, writing – original draft, methodology, validation, writing – review and editing, visualization. **Natasha Klappstein:** conceptualization, investigation, funding acquisition, writing – original draft, methodology, validation, writing – review and editing, visualization. **Christopher T. Monk:** investigation, conceptualization, funding acquisition, writing – original draft, methodology, writing – review and editing. **Knut Wiik Vollset:** conceptualization, investigation, funding acquisition, writing – original draft, writing – review and editing, methodology, validation. **Larissa T. Beumer:** conceptualization,

investigation, funding acquisition, writing – original draft, writing – review and editing, methodology, visualization, validation.

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Ethics Statement

The authors have nothing to report.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The authors have nothing to report.

References

- Aben, J., J. Signer, J. Heiskanen, P. Pellikka, and J. M. Travis. 2021. “What You See is Where You Go: Visibility Influences Movement Decisions of a Forest Bird Navigating a Three-Dimensional-Structured Matrix.” *Biology Letters* 17, no. 1: 20200478.
- Adachi, T., D. P. Costa, P. W. Robinson, et al. 2017. “Searching for Prey in a Three-Dimensional Environment: Hierarchical Movements Enhance Foraging Success in Northern Elephant Seals.” *Functional Ecology* 31, no. 2: 361–369.
- Adam, T., C. A. Griffiths, V. Leos-Barajas, et al. 2019. “Joint Modelling of Multi-Scale Animal Movement Data Using Hierarchical Hidden Markov Models.” *Methods in Ecology and Evolution* 10, no. 9: 1536–1550.
- Ahmed, D., J. Bailey, and M. Bonsall. 2022. “On Random Walk Models as a Baseline for Animal Movement in Three-Dimensional Space.” *Ecological Modelling* 475: 110169.
- Ahmed, D., S. Benhamou, M. Bonsall, and S. V. Petrovskii. 2021. “Three-Dimensional Random Walk Models of Individual Animal Movement and Their Application to Trap Counts Modelling.” *Journal of Theoretical Biology* 524: 110728.
- Alston, J. M., C. H. Fleming, R. Kays, et al. 2023. “Mitigating Pseudoreplication and Bias in Resource Selection Functions With Autocorrelation-Informed Weighting.” *Methods in Ecology and Evolution* 14, no. 2: 643–654.
- Alston, J. M., C. H. Fleming, M. J. Noonan, et al. 2022. “Clarifying Space Use Concepts in Ecology: Range vs. Occurrence Distributions.” *bioRxiv*, 2022-09. <https://doi.org/10.1101/2022.09.29.509951>.
- Arce Guillen, R., F. Lindgren, S. Muff, T. W. Glass, G. A. Breed, and U. E. Schlaegel. 2023. “Accounting for Unobserved Spatial Variation in Step Selection Analyses of Animal Movement via Spatial Random Effects.” *bioRxiv*, 2023-01. <https://doi.org/10.1101/2023.01.17.524368>.
- Asner, G. P., D. E. Knapp, T. Kennedy-Bowdoin, et al. 2008. “Invasive Species Detection in Hawaiian Rainforests Using Airborne Imaging Spectroscopy and Lidar.” *Remote Sensing of Environment* 112: 1942–1955. <https://doi.org/10.1016/j.rse.2007.11.016>.
- Aspillaga, E., K. Safi, B. Hereu, and F. Bartumeus. 2019. “Modelling the Three-Dimensional Space Use of Aquatic Animals Combining Topography and Eulerian Telemetry Data.” *Methods in Ecology and Evolution* 10, no. 9: 1551–1557.
- Avgar, T., J. R. Potts, M. A. Lewis, and M. S. Boyce. 2016. “Integrated Step Selection Analysis: Bridging the Gap Between Resource Selection and Animal Movement.” *Methods in Ecology and Evolution* 7, no. 5: 619–630.
- Baktoft, H., K. Ø. Gjelland, F. Økland, and U. H. Thygesen. 2017. “Positioning of Aquatic Animals Based on Time-Of-Arrival and Random Walk Models Using YAPS (Yet Another Positioning Solver).” *Scientific Reports* 7: 14294.
- Benhamou, S. 2019. “Mean Squared Displacement and Sinuosity of Three-Dimensional Random Search Movements.” *arXiv*. <http://arxiv.org/abs/1801.02435>.
- Bohrer, G., D. Brandes, J. T. Mandel, et al. 2012. “Estimating Updraft Velocity Components Over Large Spatial Scales: Contrasting Migration Strategies of Golden Eagles and Turkey Vultures.” *Ecology Letters* 15, no. 2: 96–103.
- Brierley, A. S. 2014. “Diel vertical migration.” *Current Biology* 24, no. 22: R1074–R1076.
- Brito-Morales, I., D. S. Schoeman, J. D. Everett, et al. 2022. “Towards Climate-Smart, Three-Dimensional Protected Areas for Biodiversity Conservation in the High Seas.” *Nature Climate Change* 12, no. 4: 402–407.
- Brodie, S., E. J. Lédée, M. R. Heupel, et al. 2018. “Continental-Scale Animal Tracking Reveals Functional Movement Classes Across Marine Taxa.” *Scientific Reports* 8, no. 1: 3717.
- Calabrese, J. M., C. H. Fleming, and E. Gurarie. 2016. “Ctmm: An R Package for Analyzing Animal Relocation Data as a Continuous-Time Stochastic Process.” *Methods in Ecology and Evolution* 7, no. 9: 1124–1132.
- Calenge, C. 2006. “The Package ‘adehabitat’ for the R Software: A Tool for the Analysis of Space and Habitat Use by Animals.” *Ecological Modelling* 197, no. 3-4: 516–519.
- Carnahan, A. M., F. T. van Manen, M. A. Haroldson, G. B. Stenhouse, and C. T. Robbins. 2021. “Quantifying Energetic Costs and Defining Energy Landscapes Experienced by Grizzly Bears.” *Journal of Experimental Biology* 224, no. 6: jeb241083.
- Chandler, C. J., B. E. Van Helden, P. G. Close, and P. C. Speldewinde. 2020. “2D or Not 2D? Three-Dimensional Home Range Analysis Better Represents Space Use by an Arboreal Mammal.” *Acta Oecologica* 105: 103576.
- Chatterjee, N., D. Wolfson, D. Kim, et al. 2024. “Modelling Individual Variability in Habitat Selection and Movement Using Integrated Step-Selection Analysis.” *Methods in Ecology and Evolution* 15: 1034–1047.
- Codling, E. A., M. J. Plank, and S. Benhamou. 2008. “Random Walk Models in Biology.” *Journal of the Royal Society, Interface* 5, no. 25: 5813–5834.
- Dejeante, R., M. Valeix, and S. Chamaillé-Jammes. 2024. “Time-Varying Habitat Selection Analysis: A Model and Applications for Studying Diel, Seasonal, and Post-Release Changes.” *Ecology* 105, no. 2: e4233.
- Demšar, U., K. Buchin, F. Cagnacci, et al. 2015. “Analysis and Visualisation of Movement: An Interdisciplinary Review.” *Movement Ecology* 3, no. 1: 1–24.
- Deng, Z. D., M. A. Weiland, T. Fu, et al. 2011. “A Cabled Acoustic Telemetry System for Detecting and Tracking Juvenile Salmon: Part 2. Three-Dimensional Tracking and Passage Outcomes.” *Sensors* 11, no. 6: 5661–5676.
- Dubayah, R., J. B. Blair, S. Goetz, et al. 2020. “The Global Ecosystem Dynamics Investigation: High-Resolution Laser Ranging of the earth’s

- Forests and Topography." *Science of Remote Sensing* 1: 100002. <https://doi.org/10.1016/j.srs.2020.100002>.
- Edelhoff, H., J. Signer, and N. Balkenhol. 2016. "Path Segmentation for Beginners: An Overview of Current Methods for Detecting Changes in Animal Movement Patterns." *Movement Ecology* 4, no. 1: 1–21.
- Farine, D. R. 2015. "Proximity as a Proxy for Interactions: Issues of Scale in Social Network Analysis." *Animal Behaviour* 104: e1–e5.
- Farine, D. R. 2017. "A Guide to Null Models for Animal Social Network Analysis." *Methods in Ecology and Evolution* 8, no. 10: 1309–1320.
- Ferraini, A., G. Giglio, S. C. Pellegrino, and M. Gustin. 2023. "Overlap and Segregation Among Multiple 3D Home Ranges: A Non-Pairwise Metric With Demonstrative Application to the Lesser Kestrel *Falco naumanni*." *Biology* 12, no. 1: 77.
- Fieberg, J., and C. O. Kochanny. 2005. "Quantifying Home-Range Overlap: The Importance of the Utilization Distribution." *Journal of Wildlife Management* 69, no. 4: 1346–1359.
- Fieberg, J., J. Signer, B. Smith, and T. Avgar. 2021. "A 'How to' Guide for Interpreting Parameters in Habitat-Selection Analyses." *Journal of Animal Ecology* 90, no. 5: 1027–1043.
- Fleming, C. H., W. F. Fagan, T. Mueller, K. A. Olson, P. Leimgruber, and J. M. Calabrese. 2015. "Rigorous Home Range Estimation With Movement Data: A New Autocorrelated Kernel Density Estimator." *Ecology* 96, no. 5: 1182–1188.
- Fletcher, R., and M. Fortin. 2018. *Spatial Ecology and Conservation Modeling*, 523. Cham: Springer International Publishing.
- Forester, J., H. Kyung Im, and P. Rathouz. 2009. "Accounting for Animal Movement in Estimation of Resource Selection Functions: Sampling and Data Analysis." *Ecology* 90, no. 12: 3554–3565.
- Gómez-Laich, A., R. P. Wilson, E. L. Shepard, and F. Quintana. 2013. "Energy Expenditure and Food Consumption of Foraging Imperial Cormorants in Patagonia, Argentina." *Marine Biology* 160, no. 7: 1697–1707.
- Gonzalez, M. C., C. A. Hidalgo, and A. L. Barabasi. 2008. "Understanding Individual Human Mobility Patterns." *Nature* 453, no. 7196: 779–782.
- Gurarie, E., C. Bracis, M. Delgado, T. D. Meckley, I. Kojola, and C. M. Wagner. 2016. "What Is the Animal Doing? Tools for Exploring Behavioural Structure in Animal Movements." *Journal of Animal Ecology* 85, no. 1: 69–84.
- Gutowsky, L. F., J. G. Romine, N. A. Heredia, et al. 2020. "Revealing Migration and Reproductive Habitat of Invasive Fish Under an Active Population Suppression Program." *Conservation Science and Practice* 2, no. 3: e119.
- Guzzo, M. M., P. J. Blanchfield, A. J. Chapelsky, and P. A. Cott. 2016. "Resource Partitioning Among Top-Level Piscivores in a Sub-Arctic Lake During Thermal Stratification." *Journal of Great Lakes Research* 42, no. 2: 276–285.
- Halsey, L. G. 2016. "Terrestrial Movement Energetics: Current Knowledge and Its Application to the Optimising Animal." *Journal of Experimental Biology* 219, no. 10: 1424–1431.
- Harel, R., S. Alavi, A. M. Ashbury, et al. 2022. "Life in 2.5 D: Animal Movement in the Trees." *Frontiers in Ecology and Evolution* 10: 801850.
- Haulsee, D. E., D. A. Fox, M. W. Breece, et al. 2016. "Social Network Analysis Reveals Potential Fission-Fusion Behavior in a Shark." *Scientific Reports* 6, no. 1: 1–9.
- Hawkes, L. A., N. Batbayar, P. J. Butler, et al. 2017. "Do Bar-Headed Geese Train for High Altitude Flights?" *Integrative and Comparative Biology* 57, no. 2: 240–251.
- Heit, D. R., C. C. Wilmers, W. Oritz-Calo, and R. A. Montgomery. 2023. "Incorporating Vertical Dimensionality Improves Biological Interpretation of Hidden Markov Model Outputs." *Oikos* 2023: e09820.
- Hussey, N. E., S. T. Kessel, K. Aarestrup, et al. 2015. "Aquatic Animal Telemetry: A Panoramic Window into the Underwater World." *Science* 348, no. 6240: 1255642.
- Jacoby, D. M., and R. Freeman. 2016. "Emerging Network-Based Tools in Movement Ecology." *Trends in Ecology & Evolution* 31, no. 4: 301–314.
- Jacoby, D. M., Y. P. Papastamatiou, and R. Freeman. 2016. "Inferring Animal Social Networks and Leadership: Applications for Passive Monitoring Arrays." *Journal of the Royal Society Interface* 13, no. 124: 20160676.
- Johnson, D. H. 1980. "The Comparison of Usage and Availability Measurements for Evaluating Resource Preferences." *Ecology* 61: 65–71.
- Johnson, D. S., J. M. London, M.-A. Lea, and J. W. Durban. 2008. "Continuous-Time Correlated Random Walk Model for Animal Telemetry Data." *Ecology* 89, no. 5: 1208–1215.
- Jonsen, I. D., J. Mills Flemming, and R. Myers. 2005. "Robust State-Space Modeling of Animal Movement Data." *Ecology* 86, no. 11: 2874–2880.
- Kahane-Rapport, S. R., M. F. Czapansky, J. A. Fahlbusch, et al. 2022. "Field Measurements Reveal Exposure Risk to Microplastic Ingestion by Filter-Feeding Megafauna." *Nature Communications* 13, no. 1: 6327.
- Kays, R., S. Tilak, M. Crofoot, et al. 2011. "Tracking Animal Location and Activity with an Automated Radio Telemetry System in a Tropical Rainforest." *Computer Journal* 54, no. 12: 1931–1948.
- Keating, K. A., and S. Cherry. 2009. "Modeling Utilization Distributions in Space and Time." *Ecology* 90, no. 7: 1971–1980.
- Khan, L. A. 2006. "A Three-Dimensional Computational Fluid Dynamics (CFD) Model Analysis of Free Surface Hydrodynamics and Fish Passage Energetics in a Vertical-Slot Fishway." *North American Journal of Fisheries Management* 26, no. 2: 255–267.
- Khosravifard, S., A. K. Skidmore, B. Naimi, V. Venus, A. R. Muñoz, and A. G. Toxopeus. 2020. "Identifying Birds' Collision Risk With Wind Turbines Using a Multidimensional Utilization Distribution Method." *Wildlife Society Bulletin* 44, no. 1: 191–199.
- Kie, J. G., J. Matthiopoulos, J. Fieberg, et al. 2010. "The Home-Range Concept: Are Traditional Estimators Still Relevant With Modern Telemetry Technology?" *Philosophical Transactions of the Royal Society, B: Biological Sciences* 365, no. 1550: 2221–2231.
- Klappstein, N. J., T. Michelot, J. Fieberg, E. J. Pedersen, C. Field, and F. J. Mills. 2024. "Step Selection Analysis With Non-linear and Random Effects in MgcV." *bioRxiv*. <https://doi.org/10.1101/2024.01.05.574363>.
- Klappstein, N. J., J. R. Potts, T. Michelot, et al. 2022. "Energy-Based Step Selection Analysis: Modelling the Energetic Basis of Animal Movement and Habitat Use." *Journal of Animal Ecology* 91: 946–957.
- Klein, K., B. Sommer, H. T. Nim, et al. 2019. "Fly With the Flock: Immersive Solutions for Animal Movement Visualization and Analytics." *Journal of the Royal Society Interface* 16, no. 153: 20180794.
- Kraft, S., M. Gandra, R. J. Lennox, J. Mourier, A. C. Winkler, and D. Abecasis. 2023. "Residency and Space Use Estimation Methods Based on Passive Acoustic Telemetry Data." *Movement Ecology* 11, no. 1: 12.
- Lang, N., N. Kalischek, J. Armston, K. Schindler, R. Dubayah, and J. D. Wegner. 2021. "Global Canopy Height Estimation With GEDI LIDAR Waveforms and Bayesian Deep Learning." *arXiv e-Prints*, arXiv:2103. <https://doi.org/10.48550/arXiv.2103.03975>.
- Langrock, R., R. King, J. Matthiopoulos, L. Thomas, D. Fortin, and J. M. Morales. 2012. "Flexible and Practical Modelling of Animal Telemetry Data: Hidden Markov Models and Extensions." *Ecology* 93, no. 11: 2336–2342.
- Lato, K. A., J. E. Stepanuk, E. I. Heywood, M. G. Conners, and L. H. Thorne. 2022. "Assessing the Accuracy of Altitude Estimates in Avian Biologging Devices." *PLoS One* 17, no. 10: e0276098.

- Ledee, E. J., M. R. Heupel, A. J. Tobin, D. M. Knip, and C. A. Simpfendorfer. 2015. "A Comparison Between Traditional Kernel-Based Methods and Network Analysis: An Example From Two Nearshore Shark Species." *Animal Behaviour* 103: 17–28.
- Lee, K. A., C. Huvaneers, T. Duong, and R. G. Harcourt. 2017. "The Ocean Has Depth: Two-Versus Three-Dimensional Space Use Estimators in a Demersal Reef Fish." *Marine Ecology Progress Series* 572: 223–241.
- Lennox, R. J., K. Aarestrup, S. J. Cooke, et al. 2017. "Envisioning the Future of Aquatic Animal Tracking: Technology, Science, and Application." *BioScience* 67, no. 10: 884–896.
- Lepczyk, C. A., L. M. Wedding, G. P. Asner, et al. 2021. "Advancing Landscape and Seascape Ecology From a 2D to a 3D Science." *Bioscience* 71, no. 6: 596–608.
- Long, J. A., T. A. Nelson, S. L. Webb, and K. L. Gee. 2014. "A Critical Examination of Indices of Dynamic Interaction for Wildlife Telemetry Studies." *Journal of Animal Ecology* 83, no. 5: 1216–1233.
- MacArthur, R. H., and J. W. MacArthur. 1961. "On Bird Species Diversity." *Ecology* 42, no. 3: 594–598.
- Manly, B., L. McDonald, D. Thomas, T. L. McDonald, and W. P. Erickson. 2002. *Resource Selection by Animals: Statistical Design and Analysis for Field Studies*. Berlin: Springer Science & Business Media.
- Masello, J. F., A. Barbosa, A. Kato, et al. 2021. "How Animals Distribute Themselves in Space: Energy Landscapes of Antarctic Avian Predators." *Movement Ecology* 9, no. 1: 24.
- McCabe, J. D., J. D. Clare, T. A. Miller, et al. 2021. "Resource Selection Functions Based on Hierarchical Generalized Additive Models Provide New Insights Into Individual Animal Variation and Species Distributions." *Ecography* 44, no. 12: 1756–1768.
- McClintock, B. T., and T. Michelot. 2018. "momentuHMM: R Package for Generalized Hidden Markov Models of Animal Movement." *Methods in Ecology and Evolution* 9, no. 6: 1518–1530.
- McClintock, B. T., R. Langrock, O. Gimenez, et al. 2020. "Uncovering Ecological State Dynamics with Hidden Markov Models." *Ecology Letters* 23, no. 12: 1878–1903.
- Mehner, T. 2012. "Diel Vertical Migration of Freshwater Fishes—Proximate Triggers, Ultimate Causes and Research Perspectives." *Freshwater Biology* 57, no. 7: 1342–1359.
- Michelot, T., R. Langrock, and T. A. Patterson. 2016. "moveHMM: An R Package for the Statistical Modelling of Animal Movement Data Using Hidden Markov Models." *Methods in Ecology and Evolution* 7, no. 11: 1308–1315.
- Michelot, T., P. G. Blackwell, and J. Matthiopoulos. 2019. "Linking Resource Selection and Step Selection Models for Habitat Preferences in Animals." *Ecology* 100, no. 1: e02452.
- Michelot, T., and P. G. Blackwell. 2019. "State-Switching Continuous-Time Correlated Random Walks." *Methods in Ecology and Evolution* 10, no. 5: 637–649.
- Michelot, T., N. J. Klappstein, J. R. Potts, & J. Fieberg, 2024. "Understanding step selection analysis through numerical integration." *Methods in Ecology and Evolution* 15: 24–35.
- Miñano, S., S. Golodetz, T. Cavallari, and G. K. Taylor. 2023. "Through Hawks' Eyes: Synthetically Reconstructing the Visual Field of a Bird in Flight." *International Journal of Computer Vision* 131, no. 6: 1497–1531.
- Montgomery, R. A., W. Ortiz-Calo, and D. R. Heit. 2020. "Integrating the Multi-Domains and Multi-Dimensional Nature of Animal Movement Into Ecological Modelling." *Ecological Modelling* 436: 109220.
- Morales, J. M., P. R. Moorcroft, J. Matthiopoulos, et al. 2010. "Building the Bridge Between Animal Movement and Population Dynamics." *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 365, no. 1550: 2289–2301.
- Morgan-Wall, T. 2021. "Rayshader: Create Maps and Visualize Data in 2D and 3D." R Package Version 0.24.10. <https://CRAN.R-project.org/package=rayshader>.
- Muff, S., J. Signer, and J. Fieberg. 2020. "Accounting for Individual-Specific Variation in Habitat Selection Studies: Efficient Estimation of Mixed-Effects Models Using Bayesian or Frequentist Computation." *Journal of Animal Ecology* 89, no. 1: 80–92.
- Mulder, I. M., C. J. Morris, J. B. Dempson, I. A. Fleming, and M. Power. 2018. "Overwinter Thermal Habitat Use in Lakes by Anadromous Arctic Char." *Canadian Journal of Fisheries and Aquatic Sciences* 75, no. 12: 2343–2353.
- Nathan, R., C. T. Monk, R. Arlinghaus, et al. 2022. "Big-Data Approaches Lead to an Increased Understanding of the Ecology of Animal Movement." *Science* 375, no. 6582: eabg1780.
- Neuswanger, J. R., A. E. Rosenberger, M. S. Wipfli, and N. F. Hughes. 2022. "Territories Within Groups: The Dynamic Competition of Drift-Feeding Juvenile Chinook Salmon in 3-Dimensional Space." *Canadian Journal of Fisheries and Aquatic Sciences* 80: 346–359.
- Nicosia, A., T. Duchesne, L.-P. Rivest, and D. Fortin. 2017. "A Multi-State Conditional Logistic Regression Model for the Analysis of Animal Movement." *Annals of Applied Statistics* 11, no. 3: 1537–1560.
- Nourani, E., K. Safi, N. M. Yamaguchi, and H. Higuchi. 2018. "Raptor Migration in an Oceanic Flyway: Wind and Geography Shape the Migratory Route of Grey-Faced Buzzards in East Asia." *Royal Society Open Science* 5, no. 3: 171555.
- Papageorgiou, D., C. Christensen, G. E. Gall, et al. 2019. "The Multilevel Society of a Small-Brained Bird." *Current Biology* 29, no. 21: R1120–R1121.
- Pedersen, E. J., D. L. Miller, G. L. Simpson, and N. Ross. 2019. "Hierarchical Generalized Additive Models in Ecology: An Introduction with mgcv." *PeerJ* 7: e6876.
- Photopoulou, T., K. Heerah, J. Pohle, and L. Boehme. 2020. "Sex-Specific Variation in the Use of Vertical Habitat by a Resident Antarctic Top Predator." *Proceedings of the Royal Society B* 287, no. 1937: 20201447.
- Pike, T. W., and O. H. P. Burman. 2023. "Simulating Individual Movement in Fish." *Scientific Reports* 13, no. 1: 14581.
- Pritchard, D. J., T. A. Hurly, T. Photopoulou, and S. D. Healy. 2022. "3D Flightpaths Reveal the Development of Spatial Memory in Wild Hummingbirds." *bioRxiv*. <https://doi.org/10.1101/2022.05.18.492296>.
- Prokopenko, C., M. S. Boyce, and T. Avgar. 2017. "Characterizing Wildlife Behavioural Responses to Roads Using Integrated Step Selection Analysis." *Journal of Applied Ecology* 54: 470–479.
- Rhodes, J. R., C. A. McAlpine, D. Lunney, and H. P. Possingham. 2005. "A Spatially Explicit Habitat Selection Model Incorporating Home Range Behavior." *Ecology* 86, no. 5: 1199–1205.
- Říha, M., K. O. Gjelland, V. Déd, et al. 2021. "Contrasting Structural Complexity Differentiate Hunting Strategy in an Ambush Apex Predator." *Scientific Reports* 11: 17472.
- Roberts, K. E., B. J. Smith, D. Burkholder, and K. M. Hart. 2021. "Evaluating the Use of Marine Protected Areas by Endangered Species: A Habitat Selection Approach." *Ecological Solutions and Evidence* 2, no. 1: e12035.
- Rous, A. 2014. "Behaviour and Space Use of Sea Lamprey Near Traps at a Hydroelectric Generating Station." Doctoral diss., University of Guelph.
- Scacco, M., E. Arrondo, J. A. Donazar, et al. 2023. "The Species-Specificity of Energy Landscapes for Soaring Birds, and Its Consequences for Transferring Suitability Models Across Species." *Landscape Ecology* 38, no. 1: 239–252.

- Séchaud, R., K. Schalcher, A. P. Machado, et al. 2021. "Behaviour-Specific Habitat Selection Patterns of Breeding Barn Owls." *Movement Ecology* 9, no. 1: 1–11.
- Shamoun-Baranes, J., W. Bouten, E. E. Van Loon, C. Meijer, and C. J. Camphuysen. 2016. "Flap or Soar? How a Flight Generalist Responds to Its Aerial Environment." *Philosophical Transactions of the Royal Society, B: Biological Sciences* 371, no. 1704: 20150395.
- Silva, A. T., K. M. Bærum, R. D. Hedger, et al. 2020. "The Effects of Hydrodynamics on the Three-Dimensional Downstream Migratory Movement of Atlantic Salmon." *Science of the Total Environment* 705: 135773.
- Silva, I., C. H. Fleming, M. J. Noonan, et al. 2022. "Autocorrelation-Informed Home Range Estimation: A Review and Practical Guide." *Methods in Ecology and Evolution* 13, no. 3: 534–544.
- Simpfendorfer, C. A., E. M. Olsen, M. R. Heupel, and E. Moland. 2012. "Three-Dimensional Kernel Utilization Distributions Improve Estimates of Space Use in Aquatic Animals." *Canadian Journal of Fisheries and Aquatic Sciences* 69, no. 3: 565–572.
- Spiegel, O., S. T. Leu, C. M. Bull, and A. Sih. 2017. "What's Your Move? Movement as a Link Between Personality and Spatial Dynamics in Animal Populations." *Ecology Letters* 20, no. 1: 3–18.
- Strand, E., C. Jørgensen, and G. Huse. 2005. "Modelling Buoyancy Regulation in Fishes With Swimbladders: Bioenergetics and Behaviour." *Ecological Modelling* 185, no. 2–4: 309–327.
- Tracey, J. A., J. Sheppard, J. Zhu, F. Wei, R. R. Swaisgood, and R. N. Fisher. 2014. "Movement-Based Estimation and Visualization of Space Use in 3D for Wildlife Ecology and Conservation." *PLoS One* 9, no. 7: e101205.
- Udyawer, V., C. A. Simpfendorfer, and M. R. Heupel. 2015. "Diel Patterns in Three-Dimensional Use of Space by Sea Snakes." *Animal Biotelemetry* 3, no. 1: 1–9.
- van Beest, F. M., J. Teilmann, R. Dietz, et al. 2018. "Environmental Drivers of Harbour Porpoise Fine-Scale Movements." *Marine Biology* 165: 1–13.
- Vedor, M., N. Queiroz, G. Mucientes, et al. 2021. "Climate-Driven Deoxygenation Elevates Fishing Vulnerability for the ocean's Widest Ranging Shark." *eLife* 10: e62508.
- Veilleux, M. A., N. W. Lapointe, D. M. Webber, et al. 2016. "Pressure Sensor Calibrations of Acoustic Telemetry Transmitters." *Animal Biotelemetry* 4: 1–8.
- Venegas-Li, R., N. Levin, H. Possingham, and S. Kark. 2018. "3D Spatial Conservation Prioritisation: Accounting for Depth in Marine Environments." *Methods in Ecology and Evolution* 9, no. 3: 773–784.
- Vivancos, A., G. Closs, and C. Tentelier. 2016. "Are 2D Space-Use Analyses Adapted to Animals Living in 3D Environments? A Case Study on a Fish Shoal." *Behavioral Ecology* 28, no. 2: 485–493.
- Walter, W. D., J. W. Fischer, J. S. Humphrey, et al. 2012. "Using Three-Dimensional Flight Patterns at Airfields to Identify Hotspots for Avian–Aircraft Collisions." *Applied Geography* 35, no. 1-2: 53–59.
- Whoriskey, K., E. G. Martins, M. Auger-Méthé, et al. 2019. "Current and Emerging Statistical Techniques for Aquatic Telemetry Data: A Guide to Analysing Spatially Discrete Animal Detections." *Methods in Ecology and Evolution* 10, no. 7: 935–948.
- Wood, S. N. 2017. *Generalized Additive Models: An Introduction with R*. 2nd ed. Chapman and Hall/CRC.
- Wright, B. M., J. K. Ford, G. M. Ellis, et al. 2017. "Fine-Scale Foraging Movements by Fish-Eating Killer Whales (*Orcinus orca*) Relate to the Vertical Distributions and Escape Responses of Salmonid Prey (*Oncorhynchus* spp.)." *Movement Ecology* 5, no. 1: 3.