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View Point

On random walk models as a baseline for animal movement in three-dimensional space

Danish A. Ahmed[a,*], Joseph D. Bailey[b], Michael B. Bonsall[c]

[a] Center for Applied Mathematics and Bioinformatics, Department of Mathematics and Natural Sciences, Gulf University for Science and Technology, Kuwait
[b] Department of Mathematical Sciences, University of Essex, Colchester, UK
[c] Mathematical Ecology Research Group, Department of Zoology, University of Oxford, UK

A B S T R A C T

Discrete-time random walks (RWs) have proven to be a powerful modelling tool in ecology, particularly utilised for the study of animal movement at an individual level. There are several descriptors for the analysis of movement paths, but ecologists routinely use two simple metrics: the mean squared displacement and the sinuosity index (which measures movement tortuosity). The mathematical expressions for these metrics are already well known in 2D, and recently their 3D equivalents have been derived. Alongside this, cutting-edge developments in tagging and sensor technology have facilitated the recording of more accurate and refined long-term 3D movement data. Motivated by the multitudinous studies that have successfully used 2D RW models as a baseline against observed movement data, our viewpoint is that an extension to 3D is evidently due, with prospects of further insights in 3D animal space use in several ecological contexts.

1. Viewpoint article

Why, how, where and when animals move are fundamental questions in movement ecology. A better understanding of animal movement patterns can help explain movement behaviour at a range of spatiotemporal scales, from local scale foraging and home range exploration to large scale migration (Nathan et al., 2008). This has immediate consequences for numerous problems arising in spatial ecology, with focus on biodiversity (Jeltsch et al., 2013), nature management and conservation (Allen and Singh, 2016; Fraser et al., 2018), biological invasions (Shigesada and Kawasaki, 1997), and pest monitoring (Petrovskii et al., 2014). Discrete-time Random Walks (RWs) provide a useful modelling framework for individual movement by mapping an animal's continuous movement path as a time-series of distinct locations (Turchin 1998, Grimm and Railsback, 2005). The movement trajectory can then be modelled given the probability distributions of move lengths and turning angles, which can be obtained directly from observed movement data by statistical distribution fitting. This methodology has been applied for a wide variety of animals, such as: marine predators (e.g., sharks, tuna, billfish and ocean sunfish, Humphries et al., 2010), mammals (e.g., brushtail possums, hunter–gatherers, African bull elephants, Asian black bears, Postlethwaite and Dennis, 2013; Raichlen et al., 2014; Bailey and Codling, 2021; Ando et al., 2022), avian species (e.g., Egyptian vultures, López-López et al., 2013) and insects (e.g., butterflies, beetles, Marsh and Jones, 1988; Bailey et al., 2021). Moreover, the step length and turning angle distributions which describe the observed movement data most accurately can be identified by assessing the absolute goodness-of-fit of a set of candidate distributions using maximum likelihood methods (Plank et al., 2013).

The earliest RW models for animal movement were based on purely random motion (Simple Random Walk, SRW) (Lin and Segel, 1974; Okubo 1980), and later extended to the more realistic Correlated Random Walk (CRW). CRWs allow for a short-term localised directional persistence in the movement path accounting for an individual being likely to move in a similar direction as their previous step, with a relatively low probability of exercising abrupt turns (Kareiva and Shigesada, 1983; Bovet and Benhamou, 1988). CRWs have been used to describe and analyse the movement of various species, from smaller, simpler organisms such as microalga (Garcia et al., 2011) and insects (Byers, 2001) to larger animals, including both terrestrial (elk; Fortin et al., 2005) and marine (sperm whales; Whitehead et al. 2008). The Biased Random Walk (BRW) features a preference towards a certain direction at each step and, unlike the CRW, retains no knowledge of the previous movement direction. This long-term directional bias can be towards a global direction (often referred to as a 'point at infinity'), or a fixed point in space, in which case the orientation of the preferred direction will depend upon the spatial location of the individual at each step (Marsh and Jones, 1988; Codling et al., 2008). Examples of applications, BRWs have been used to model the trajectories of swimming microorganisms (Hill and Hader, 1997), and to model the movement of insects in the presence of baited traps (Alqubori and Petrovskii, 2022), where an external stimulus (e.g., pheromone, light or colour) invokes an attraction to the trap locations (Epsky et al., 2008). A mixture of both short- and long-term biases induced by balancing persistence and external navigation components result in the Biased and Correlated Random Walk (BCRW) (Benhamou and Bovet, 1992), which has been used, for exam-

* Corresponding author.
E-mail address: Ahmed.D@gust.edu.kw (D.A. Ahmed).

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ple, to study the navigational efficiency of animals (Bailey et al., 2018), including butterflies (Schultz and Crone, 2001), salmon (Morrice et al., 2020) and seals (McClintock et al., 2012). Whilst more complex RWs have been developed for increased realism, to date these null RWs remain as the most dominant conceptual frameworks, partly due to their relative simplicity and efficacy, which in turn has allowed for the development of advanced statistical modelling and analytical techniques that are widely used in animal movement research such as hidden Markov models (Langrock et al., 2012), state-space models (Patterson et al., 2008) and data-driven agent based models (Butts et al., 2022).

The mathematical properties of RWs in 2D are well known in the context of the movement of animals, micro-organisms and cells (Berg, 1983; Codling et al., 2008; Wadkin et al., 2018). Exact formulae of key metrics for the analysis of movement patterns such as the mean squared displacement (MSD, which measures the spatial spread of a population), and path sinuosity (which quantifies the amount of turning in an individual's movement path i.e., tortuosity) have been derived in 2D, and its equivalent in 3D is recently documented (Benhamou 2018; Ahmed et al., 2021). For instance, Sadjadi et al. (2015) first computed the MSD for the 3D balanced CRW in the context of anomalous transport of self-propelled particles using Fourier transforms, and later Benhamou (2018) derived the same mathematical expression motivated by the 3D random search movement of animals using a probabilistic approach. In terms of simulating a movement path in 3D, the distribution of move lengths can be inferred by distribution fitting to a histogram of step length data (as in the 2D case) and fitting a spherical distribution (e.g., a Fisher distribution, Mardia and Jupp, 2000) to 3D directional data – the methods for which are well established (Fisher et al., 1987; Leong and Carlile, 1998).

Due to technological limitations, animal movement was historically recorded in 2D, with 3D data usually projected into 2D space to allow for easier analysis. This risks losing important behavioural information as a degree of freedom is removed from the movement analysis (Tracey et al., 2014). However, many animals exercise movement in a clear vertical direction, such as volant and aquatic animals (Cooper et al., 2014; Aspillaga et al., 2019), as well as less obvious terrestrial animals who can move through different altitudes (e.g., giant panda, Tracey et al., 2014), albeit in this case the movement can be more constrained due to increased energy costs whilst traversing steep terrains (Dunford et al., 2020). In line with this, recent technological advancements have facilitated the recording of high-resolution long-term 3D movement data (Katzner and Arlettaz, 2020): GPS trackers are typically used to measure longitude and latitude but can also record elevation (albeit with lesser accuracy, Cagnacci et al., 2010); digital biotelemetry devices can track animals by recording 3D location data expressed precisely as Cartesian coordinates (Tracey et al., 2014); accelerometers and magnetometers can quantify the orientations of the surge, sway and heave axes with respect to gravity and the geomagnetic field (Williams et al., 2017); gyrometers provide direct measures of rotations (yaw, pitch and roll) (Noda et al., 2012; Gunner et al.,2020); bio-loggers are used to infer horizontal and vertical movement of marine animals across time and space (Williams et al., 2020); and video-based 3D photogrammetry is used for automated tracking of animals (Sellers and Hirasaki, 2014). These, along with a substantial increase in data availability and quality, has led to a rapid increase in the number of animal movement studies in 3D space, with a mixture of tools proposed to analyse 3D space use (e.g., see Demšar and Long, 2019) – however, none are based on the traditional null RWs.

Much progress in understanding important ecological processes such as population dynamics, navigational strategies, encounter rates and foraging theory, have developed due to the use of 2D RW models (Bartumeus et al, 2005; Barton et al., 2009; Gurarie and Ovaskainen, 2011; Viswanathan et al., 2011; Bailey et al., 2018). Yet it is unclear whether the same conclusions can be simply extended to three dimensions without similar rigorous analyses of the null 3D RW models compared against recorded movement. This is highlighted by recent findings that the cognitive processes when exploring a 3D volumetric space compared to a 2D planar space, can be inherently different and are yet to be fully understood (Grieves et al., 2021; Ginosar et al., 2021). There are many examples where 2D RW models have been useful in real world applications e.g., integrated pest management strategies (Petrovskii et al., 2014), diagnosing illnesses in farm animals (Vazquez Diosdado et al., 2018), managing fish stocks (Boyd et al., 2020) etc., and it can be expected that analysing movements in 3D can yield similar wide-ranging applications. More broadly, accounting for movement in a vertical direction has clear ecological implications, for instance; a better understanding of animal habitat use, spatial differentiation, size of home ranges, encounter rates with stationary non-revisitable targets, and resource use at different altitudes. As an example, some recent progress has been made to simulate the movement of insects in 3D space using 3D RWs, and to analyse the capture efficiency of voluminous traps based on the interplay between different movement types and trap geometry (Ahmed et al., 2021).

On synthesis, our viewpoint is that, alongside the usage of more complex movement models and the development of new tools for the analysis of space use in movement ecology, these null RW models warrant testing as a baseline against observed movement data for animals that exhibit strong vertical space use, so that important movement behaviour is neither discounted nor missed.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

No data was used for the research described in the article.

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