ANIMAL SOCIAL NETWORKS

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## Analysis of temporal patterns in animal movement networks

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## Abstract

- 1. Understanding how animal movements change across space and time is a fundamental question in ecology. While classical analyses of trajectories give insightful descriptors of spatial patterns, a satisfying method for assessing the temporal succession of such patterns is lacking.
- 2. Network analyses are increasingly used to capture properties of complex animal trajectories in simple graphical metrics. Here, building on this approach, we introduce a method that incorporates time into movement network analyses based on temporal sequences of network motifs.
- 3. We illustrate our method using four example trajectories (bumblebee, black kite, roe deer, wolf) collected with different technologies (harmonic radar, platform terminal transmitter, global positioning system). First, we transformed each trajectory into a spatial network by defining the animal's coordinates as nodes and movements in between as edges. Second, we extracted temporal sequences of network motifs from each movement network and compared the resulting behavioural profiles to topological features of the original trajectory. Finally, we compared each sequence of motifs with simulated Brownian and Lévy random motions to statistically determine differences between trajectories and classical movement models.
- 4. Our analysis of the temporal sequences of network motifs in individual movement networks revealed successions of spatial patterns corresponding to changes in behavioural modes that can be attributed to specific spatio-temporal events of each animal trajectory. Future applications of our method to multi-layered movement and social network analysis yield considerable promises for extending the study of complex movement patterns at the population level.

#### KEYWORDS

animal trajectories, Argos, GPS tracking, harmonic radar, motifs time series, movement ecology, movement networks, spatial networks

## 1 | INTRODUCTION

Over the past recent years, the study of animal movements has experienced a rapid growth thanks to the development of new technologies to automatically collect long-term individual data on wild animals (Flack, Nagy, Fiedler, Couzin, & Wikelski, 2018; Strandburg-Peshkin, Farine, Couzin, & Crofoot, 2015; Tomkiewicz, Fuller, Kie, & Bates, 2010). The acquisition of high resolution data has also required the development of new statistical tools to describe and analyse movements. At the most basic level, it is possible to visualize the sequence of locations visited by the animal by joining those locations with a line, that is, the animal trajectory. Speed, step length (distance between successive locations), residency (the time an individual remains at a specific location before moving) and turning angle (change of direction between successive steps) are some of the main parameters that can be extracted from such a trajectory (Dodge, Weibel, & Lautenschütz, 2008; Patterson, Thomas, Wilcox, Ovaskainen, & Matthiopoulos, 2008). These parameters tend to be correlated with specific behavioural states (Edelhoff, Signer, & Balkenhol, 2016) and can be grouped into patterns dependent of environmental constraints and spatial variability. So far, however, this approach has yielded little information about the temporal dimension of animal trajectories (Jacoby & Freeman, 2016). For many animals, movements can show dramatic changes with time as a result of motivation, experience, social interactions or modifications of the environment (Swingland & Greenwood, 1983). Identifying these changes in complex movement datasets can thus bring critical insights into the fundamental ecology of animals.

Recent attempts to develop a unified spatio-temporal analytical framework of movement data have shown the existence of a relationship between temporal autocorrelations of movement parameters (i.e. step length) and spatial distribution of critical resources (Wittemyer, Polansky, Douglas-Hamilton, & Getz, 2008). Others have proposed to analyse the sequence of habitats encountered by an animal to extract behavioural changes in a trajectory (De Groeve et al., 2016; van Toor, Newman, Takekawa, Wegmann, & Safi, 2016). Behavioural change point analysis of movement parameters is a powerful tool to estimate the time at which an animal changes its movement patterns and how this corresponds to behavioural states such as resting, foraging or moving (Gurarie, Andrews, & Laidre, 2009; Teimouri, Indahl, Sickel, & Tveite, 2018). Multiple unsupervised statistical methods have also been used to reduce complex animal trajectories into human understandable format such as the circular standard deviation (Potts et al., 2018), the t-stochastic neighbouring embedding (t-SNE) algorithm (Bartumeus et al., 2016), the recursive multi-frequency segmentation (Ahearn & Dodge, 2018), or the Fourier and wavelet analysis (Polansky, Wittemyer, Cross, Tambling, & Getz, 2010). Despite satisfying the quantitative aspects of spatio-temporal analysis of animal movement data, these methods often require advanced mathematical knowledge and lack intuitive tools to help data visualization and interpretation by ecologists.

Network analysis may constitute a simpler, yet powerful, approach for such analyses (Bastille-Rousseau, Douglas-Hamilton, Blake, Northrup, & Wittemyer, 2018; Jacoby & Freeman, 2016; Pasquaretta, Jeanson, Andalo, Chittka, & Lihoreau, 2017; Pasquaretta et al., 2019). For example, Bastille-Rousseau et al. (2018) transposed global positioning system (GPS) locations obtained from three different species (African elephants, giant Galapagos tortoises, Mule deer) into networks. In such networks, nodes represent spatial locations visited by the animals and edges animal movements between these locations. The analysis of node-level network metrics demonstrated that locations with high betweenness centrality scores (frequency

at which a node acts as bridge along the shortest paths passing by two other nodes) was indicative of bridges between migration areas for tortoises and corridors between foraging sites for elephants (Bastille-Rousseau et al., 2018). Network analysis of spatial data can thus bring important information for studying associations of complex behavioural patterns and spatial characteristics. So far, however, this method relies on a static representation of animal space use and does not consider the temporal nature of movements (Bastille-Rousseau et al., 2018; Jacoby & Freeman, 2016).

Here, we built on this approach to analyse temporal patterns in animal movement networks. Our method consists in transforming trajectories into movement networks and analysing the temporal succession of motif patterns (i.e. three-node subgraphs, Wasserman & Faust, 1994) in these networks. To illustrate the validity of the method, we analysed example datasets of insects (bumblebee), birds (black kite) and mammals (roe deer, wolf) monitored with different technologies and at different spatio-temporal scales. We argue that this method, easily accessible to ecologists, can favour comparative analyses and bring new insights into the movement ecology of a wide range of species.

## 2 | MATERIALS AND METHODS

#### 2.1 | Movement datasets

We tested our method on animal trajectories obtained from two original datasets (bumblebee, black kite) provided in Dryad (https:// doi.org/10.5061/dryad.47d7wm390), and two published datasets (roe deer, wolf) publicly available on the MoveBank data repository (Wikelski & Kays, 2020). The trajectories were selected to illustrate how the analysis of spatio-temporal behavioural patterns in movement networks can apply to different types of raw data (harmonic radar, GPS), to animal species with different locomotion modes (flying, walking), at different spatial scales (region, across countries) and in different behavioural contexts (search, migration, roaming).

### 2.1.1 | Bumblebee search trajectory

We used a harmonic radar to obtain a search trajectory of a bumblebee worker on 15 April 2018 (1 recording every 3.3 s, 364 data points, Figure S1a). We set up a commercial colony of *Bombus terrestris* (Biobest NV) in a flat dry rice farm land in Sevilla (Spain; Figure S2). We trained multiple bumblebees to forage on three artificial flowers (i.e. blue platform with 40% (v/v) sucrose solution, see details in Lihoreau et al., 2012) positioned 2 m in front of the nest box. Once a regular forager was identified (bumblebee performing several consecutive foraging bouts), we closed the colony entrance and randomly moved the three artificial flowers away in the field. The focal bumblebee was equipped with a transponder (16 mm vertical dipole) upon leaving the nest box and tracked with the harmonic radar until it returned to the colony (Riley et al., 1996). The radar was placed 350 m away from the colony nest box (Figure S3) and returned the two-dimensional coordinates of the tagged bumblebee within a range of 700 m.

#### 2.1.2 | Black kite long-range migration trajectory

We used GPS to track an adult female black kite *Milvus migrans* moving across Spain from 28 May 2019 to 19 August 2019 (1 recording every 6 hr, 332 data points, Figure S1b). The bird was caught after an injury and maintained 5 weeks in an aviary for rehabilitation. We equipped the bird with a platform terminal transmitter (PTT) backpacked (Xerius Tracking) and released it in Toulouse (France), where it first moved within a limited area before migrating on its way to Morocco.

## 2.1.3 | Roe deer short-range migration trajectory

This dataset was obtained from the EURODEER collaborative project (E. Mach Foundation; http://sites.google.com/site/eurodeerpr oject; Cagnacci et al., 2011). It consists of one GPS trajectory of an adult male roe deer *Capreolus capreolus* collected from 23 October 2005 to 28 October 2006 (1 recording every 4 hr, 1,827 data points; Figure S1c). The roe deer was tracked in the area of Trentino Alto Adige (Italy). Behavioural patterns in this trajectory are dominated by short range migratory movements representing the yearly leaveand-back movements between two winter and summer sites. To compare this trajectory with the other example trajectories, we reduced the number of data points to 457 by resampling the trajectory every 16 hr.

## 2.1.4 | Wolf roaming trajectory

This dataset was obtained from a study of the Przewalskii horse reintroduction project of the International Takhi Group (Kaczensky, Ganbaatar, Enksaikhaan, & Walzer, 2006). It consists of one GPS trajectory of an adult male wolf *Canis lupus* collected from 05 March 2004 to 18 September 2005 (1 recording every 8 hr, 1,455 data points in total). The wolf was tracked in the mountains of the Goby Desert (Mongolia). Behavioural patterns in this trajectory are dominated by territorial movements around the mountains and one main roaming period (Figure S1d). To compare this trajectory with the other example trajectories, we reduced the number of data points to 485 by resampling the trajectory each 24 hr.

### 2.2 | Method overview

We analysed all the trajectories following four major steps. First, we transformed the raw spatial coordinates into movement networks built using different spatial resolutions (grid sizes). Second, we extracted the temporal sequence of network motifs obtained from these different networks and compared them to define an optimal grid size for further analyses. Third, we used the selected temporal sequence of network motifs to highlight spatio-temporal locations showing complex behaviours in the original trajectory. Fourth, we extracted the non-random temporal transitions between consecutive motifs in the experimental datasets and compared them with the non-random transitions of simulated data from classical movement models. The complete R code is available in Dryad (https://doi.org/10.5061/dryad.47d7wm390) with description in Text S1.

# 2.2.1 | Transform spatial coordinates into a temporal movement network

The first step consisted in transforming the raw movement data into a format that can be automatically analysed with network metrics. To do so, we rasterized the animal coordinates on a spatial grid. Because different grid resolutions affect the topological structure of the resulting network (Bastille-Rousseau et al., 2018), we built a range of networks with different grid resolutions.

Building a movement network from an animal trajectory has the risk of oversimplifying the information depending on grid resolution (Figure 1). Effects vary from large grid size, where the entire trajectory can be summarized into movement loops starting and ending at a single location, to small grid size, where each location of the raw trajectory corresponds to different grid cell. The optimal grid resolution capturing biologically relevant behavioural patterns is expected to lay somewhere in the middle. Previous studies have used the median of the step length distribution as grid size, based on the fact that this value leads to robust results under the assumption of Brownian movements (Bastille-Rousseau et al., 2018). However, many animal trajectories show more complex patterns. To address this issue, for each trajectory we tested nine grid resolutions. Each grid resolution corresponded to one specific quantile of the step length distribution of the trajectory (i.e. p = .1, .2, .3, .4, .5, .6, .7, .8, .9). The animal coordinates were thus transformed into nodes and movements between them into directed edges (see Figure 1b). We attributed the same node identity to each coordinate falling into the same grid cell. Empty cells were considered as non-visited cells at this stage. We then transformed the spatial network into a temporal edge list by associating a time to each movement of the sequence.

# 2.2.2 | Extract temporal sequence of network motifs from movement networks

Treating animal trajectories as behavioural sequences provides a description of topological movement structures and can reveal the processes by which these patterns appear and are maintained in the sequences (De Groeve et al., 2016). For each trajectory, we extracted temporal sequences of motif patterns between three



**FIGURE 1** Transformation of an animal movement data into a temporal movement network: the problem of grid resolution. A hypothetical trajectory is transformed using three different cell sizes: large, medium and small. (a) Original trajectory embedded in each grid resolution. Orange dots represent the coordinates of the animal. (b) Resulting movement network built by assigning a single node identity to each of the coordinates that fall into the same cell. The trajectory is transformed into a movement network in which spatial coordinates are nodes (orange dots) and movements between them are directed edges (light blue arrows). Directed edges associated to a specific time produce a temporal movement network. Shannon diversity index used to select the optimal grid size given the data (see adjustment of grid resolution paragraph below)

nodes from the edge list of each movement network. In the context of movement networks, these sequences refer to subgraphs that describe spatio-temporal movements (Pasquaretta et al., 2017) and can be used to understand non-random successions of patterns in a complex behavioural sequence (Patel, Keogh, Lin, & Lonardi, 2002).

Among the 13 possible different motifs between three nodes, five are irrelevant for movement data (Figure S4, see details in Wasserman & Faust, 1994). Four of the eight remaining motifs belong to the family of 'loosely connected motifs', that is, subgraphs missing one edge between two out of three nodes (Juszczyszyn, 2014; Figure 2a). The four other motifs belong to the family of 'closely connected motifs', that is, subgraphs with edges between all nodes. In the context of movement data, the loosely connected motif M3 indicates movements across locations without any revisit to any location. All other motifs indicate more complex movement patterns characterized by at least one revisit to a location.

Temporal sequences of network motifs can be extracted by dividing the edge list into specific motif windows including at least three different connected nodes (Paranjape, Benson, & Leskovec, 2017). Here we built sliding windows containing a maximum of three nodes, allowing us to create a temporal sequence of successive motifs based on the utilization of three consecutive locations. To do so, we started from the first node of the network and iteratively analysed the entire sequence to create subsequences of three nodes. Each node in this subsequence can be visited only once (e.g. M3) or several times (e.g. M13). Once the first subsequence was created, we applied the same iterative algorithm to find all the successive motifs using the last node of the previous subgraph as starting point for the next one (Figure 2b).

## 2.2.3 | Adjustment of grid resolution

We applied the Dynamic Time Warping (DTW) algorithm (Sakoe & Chiba, 1978) to compare temporal sequences of motifs built with different grid resolutions and select the most suitable grid resolution given the data. The DTW compares two, or more, time series and returns the number of steps needed to transform one reference time series into another. Each step corresponds to the minimum number of changes needed to transform one query series into its reference series (see details in Giorgino, 2009).

We used this approach to create matrices of similarity between motif time series. From these data, we finally selected the most suitable motif time series characterized by: (a) the largest number of different motifs (abundance) and (b) the most equal proportion of each motif (evenness). To do so, we created a list of temporal sequences of network motifs obtained from different

#### Motif patterns (a)

#### loosely connected motifs



FIGURE 2 Possible three-node motifs in movement networks and extraction of their temporal sequence. (a) Eight out of 13 possible motifs were retained. These included four loosely connected motifs (M3, M4, M5, M6), that is, subgraphs missing one edge between two out of three nodes, and four closely connected motifs (M8, M10, M12, M13), that is, subgraphs with at least one edge between each node. (b) Hypothetical directed movement network (left) represented as a node sequence (right). Horizontal red bars refer to the subsequence of three nodes used to extract each motif

grid resolutions (i.e. *p* = .2, .3, .4, .5, .6, .7, .8, .9) and calculated a similarity matrix using the DTW distance between them with the function 'dist' of the R package STATS (R Core Team, 2018). We applied the Shannon diversity index (Shannon, 1948), using the R package VEGAN (Oksanen et al., 2018), to select the optimal time series. Specifically, we used as optimal grid size the step length corresponding to the highest value of Shannon diversity index (to illustrate the robustness of the method, results from the second highest value are presented in Text S2). With this procedure, we ensured an objective way to select the best grid resolution value returning the time series with the largest number of motifs which proportions were also more equally represented. For each dataset, we identified the best grid resolution to analyse complex movement patterns using sequences of behavioural patterns instead of the trajectory parameters themselves (e.g. median step length, mean turning angle). We evaluated whether the proportion of motifs differed across datasets with a chi-square ( $\chi^2$ ) test, applied to a table with rows and columns corresponding to motif counts and animals, using the 'chisq.test' function in R.

## 2.2.4 | Visualization of temporal behavioural patterns

To illustrate that our method can be used to identify spatio-temporal behavioural patterns from complex animal trajectories, we represented the evolution of motifs through time. Here, we focused only on the seven motifs identified as indicative of complex movements: characterized by at least one revisit to a node. We extracted the geographic locations involved in the construction of these motifs and represented them in the network to describe spatio-temporal patterns of complex behaviours. Loops (movements starting and ending at the same location) are structurally removed when analysing network motifs (Wasserman & Faust, 1994). To account for such behavioural patterns, we first extracted the number of loops observed inside each motif and we later applied a generalized linear model (GLM) for count data (Poisson error distribution) to estimate the relationship between motif complexity and the number of loops performed using the glm function of the R package STATS (R Core Team, 2018). We also tested different temporal windows by resampling the roe deer and wolf dataset (see Text S3).

## 2.2.5 | Evaluation of temporal motifs with a null model

The evaluation of motif counts of a static network is typically presented in terms of difference from a null model (Milo et al., 2002). The null model is usually a randomized version of the empirical network constrained by some of the network characteristics such as the degree sequence (node randomization) or the strength of the relationship between nodes (edge randomization) or both (Farine & Whitehead, 2015). If the count of a specific motif significantly exceeds that of the null model, the motif is considered to be structurally significant. However, if the null model is far from having realistic features, the differences observed (even if statistically significant) do not tell anything insightful about the nature of each motif (Artzy-Randrup, Fleishman, Ben-Tal, & Stone, 2004).

In temporal directed networks, where a temporal correlation between successive motifs can be expected, an effective way to



**FIGURE 3** Examples of simulated random movements. Brownian motion is characterized by a stationary behaviour throughout the entire trajectory whereas Lévy walk shows an alternance of local stationarity and ballistic movements

compare the experimental sequence with a randomized sequence is by time-shuffling, that is randomly sample motifs in a sequence and change their temporal position. The focus is then made on the structure of the motif sequence itself and on the probability of temporal co-occurrence (conditional probability) of specific motif associations. Here we used the conditional probabilities between each pair of motif to reveal the existence of non-random transitions between specific behavioural patterns. We first calculated the probability matrix to move from each motif to the next (8 × 8 matrix) and compared this matrix with 100 probability matrices obtained from time-shuffled time series. For each pair of temporal patterns, we calculated the 95% confidence intervals (CIs) and compared the probabilities from the original motifs time series to the corresponding probabilities obtained from time-shuffled motif time series. We used a onetail analysis and consider probabilities falling outside of the upper 95% CI as significant. The obtained resulting binary matrix thus assigns 1 to all the positive non-random conditional probabilities and 0 to the others.

## 2.2.6 | Comparing non-random probabilities with Brownian motion and Lévy walk

Brownian motion and Lévy walks are two main theoretical random movement patterns used to describe trajectories observed in nature (Turchin, 1998; Figure 3). Pure Brownian random walks have been introduced to describe animal search strategies when no information is available. Brownian motions are determined by successive steps in random directions whose step lengths and turning angles are randomly drawn from a normal distribution (Bartumeus, Catalan, Fulco, Lyra, & Viswanathan, 2002). Lévy walks are defined by movement patterns following a powerlaw distribution (Reynolds, 2018; Shlesinger & Klafter, 1986; Viswanathan et al., 1996). To estimate the degree by which the four original trajectories differed from Brownian and Lévy random movements, we compared the binary matrices of transition between motifs obtained for each of the four animal trajectories with 100 probability matrices obtained from both simulated Brownian and Lévy trajectories by calculating the Jaccard index of similarity using the function *birewire.similarity* in the R package 'BIREWIRE' (Gobbi, Iorio, Albanese, Jurman, & Saez-Rodriguez, 2017). We thus obtained four distributions of Jaccard indices (one for each dataset) and compared them using *t*-statistic. We adjusted the  $\alpha$  value using the sequential Bonferroni correction (Rice, 1989).

## 3 | RESULTS

## 3.1 | Identification of optimal grid size

The crucial step in transforming an animal trajectory into a movement network involves the selection of an optimal grid resolution that is small enough to obtain a suitable number of nodes to create a network, and large enough to provide insightful details on the animal movement patterns. For each dataset, we extracted the step length values of the nine quantiles of the step length distribution of the trajectory, and removed any quantiles with step length value close to zero (i.e. values lower than  $10^{-6}$ ). We obtained seven possible quantile values for the black kite, and nine quantile values for the bumblebee, the roe deer and the wolf (Table S1). We used these quantile values as cell size to build spatial grids and generate movement networks. From these networks, we extracted temporal sequences of network motifs and compared them using the DTW distance to select the optimal grid resolution given the data. We then applied the Shannon diversity index to select the motif time series for each dataset as candidate sequence for subsequent analyses. The Shannon diversity index retained the motif time series 5, 5, 7 and 8, corresponding to a cell size of step length value 11.209 (i.e. quantile 0.5) for the bumblebee, 0.0075 (i.e. quantile 0.7) for the black kite, 0.0037 (i.e. quantile 0.7) for the roe deer and 0.2642 (i.e. quantile 0.8) for the wolf (Figure 4; see Table S1 for the values of all quantiles). Thus, the optimal grid size selected for the temporal analyses of network motifs varied across the four datasets.

**FIGURE 4** Motif time series selection. The Shannon diversity index was applied to motif time series for each dataset: (a) bumblebee, (b) black kite, (c) roe deer, (d) wolf. The highest Shannon diversity index value, used to select the most suitable motif time series for each dataset, is highlighted in red

FIGURE 5 Proportion of network motifs in each dataset. For each species (a) bumblebee, (b) black kite, (c) roe deer, (d) wolf, the proportion of motifs has been divided into two main categories: a motif describing a unidirectional movement (orange) and seven motifs describing more complex bidirectional patterns (blue)



## 3.2 | Analysis of behavioural patterns

The proportion of motifs was different across the four datasets ( $\chi^2 = 56.77$ , df = 21, p < .001). The dominant motif was the motif M3 (Figure 5) that characterizes unidirectional movements across three nodes without revisits. This motif has different biological meanings depending on the species under consideration. In the black kite and the roe deer, a succession of M3 motifs is characteristic of migratory movement patterns. In the wolf, however, this temporal pattern is characteristic of movements towards familiar locations in a home range, such as hunting areas. In the bumblebee, the succession of M3 motif is indicative of search flights.

The seven other motifs characterize bidirectional movements with at least one revisit to the same node, indicating a temporal reuse of specific areas. The different proportions of such motifs in the movements may have different biological meanings in the different species and, once identified, are open to study.

To further explore and interpret the succession of temporal motifs, we constructed simplified trajectories highlighting the spatial locations of the simple (unidirectional) motif and the more complex (bidirectional) motifs in the original data. Because motif analysis does not allow to include loops (self-edges), we also constructed simplified trajectories highlighting the spatial locations of each loop (Figure 6). The number of loops on the same location increased with the complexity of network motifs indicating that for all four trajectories, more complex behavioural patterns represent areas of temporal interest in animals (GLM for count databumblebee: estimate = 0.243, SE = 0.058, z = 4.175, p < .001; black kite: estimate = 0.203, SE = 0.025, z = 8.252, p < .001; roe deer: estimate = 0.122, SE = 0.019, z = 6.296, p < .001; wolf: estimate = 0.275, SE = 0.014, z = 19.698, p < .001). In the bumblebee trajectory, bidirectional motifs occurred when the individual was in the nest area and near flowers, indicating an association between complex behavioural patterns and familiar locations,



**FIGURE 6** Spatio-temporal sequence of behavioural patterns. *Evolution of motifs*: temporal sequence of network motifs for each dataset. Blue: bidirectional motifs (M4, M5, M6, M8, M12, M13). Red: unidirectional motif (M3). *Complex motifs*: temporal motifs mapped on original trajectories. Blue gradient encodes the temporal sequence of the more complex bidirectional motifs. *Loops*: movements starting and ending at the same location mapped on original trajectories. Blue gradient encodes the temporal sequence of the nest and the artificial flowers (F1–F3) while loops are disproportionally observed around the nest location. (b) Black kite data: bidirectional motifs are observed before migration and at stopover locations along the migration route and loop behaviours tend to correspond to those locations. (c) Roe deer data: bidirectional motifs are observed in both winter and summer territories while loops evidence some specific sub-areas of repeated intensive use. (d) Wolf data: bidirectional motifs are observed only for the summer territory of the wolf (Kaczensky et al., 2006)

while loops tended to be concentrated around the nest only, a behavioural pattern reminiscent of orientation flights (Osborne et al., 2013; Figure 6a). In the black kite trajectory, more complex bidirectional motifs occurred in areas around the release point and few locations after the start of the migration and they also correspond to single locations of intensive use (loops; Figure 6b). **TABLE 1** Students t-statistics between distributions of 100Jaccard indices calculated from the comparison of each binary non-<br/>random motif conditional probabilities with 100 simulated matrices<br/>obtained from a Brownian and a Lévy random movement model

Brownian motion	Lévy walk
Bumblebee—Black kite	Bumblebee—Black kite
(t = 5.97; <i>p</i> < .001)	(t = 6.68; p < .001)
Bumblebee—Roe deer	Bumblebee—Roe deer
(t = 2.59; p = .009) ns	(t = 8.97; p < .001)
Bumblebee—Wolf	Bumblebee–Wolf
( <i>t</i> = 9.31; <i>p</i> < .001)	(t = 5.24; p < .001)
Wolf—Black kite	Wolf—Black kite
(t = −2.58; p = .009) ns	(t = −1.14; p = .255) ns
Roe deer—Black kite	Roe deer—Black kite
(t = 3.75; <i>p</i> < .001)	(t = 1.40; p = .162) ns
Roe deer–Wolf	Roe deer—Wolf (t = 2.55;
(t = 7.32; p < .001)	p = .010) ns

*Note*: We applied a Bonferroni correction for six multiple comparisons (new reference  $\alpha$  = 0.008).

In the roe deer trajectory, complex motifs occurred intensely in two different areas while loops gathered around specific smaller areas (Figure 6c). In the wolf trajectory, complex bidirectional motifs were observed in two spatially differentiated areas, while loops were only observed in one of them (Figure 6d).

## 3.2.1 | Comparison with Brownian and Lévy walks

We studied the degree by which the four experimental datasets differed from Brownian and Lévy random movements. We calculated probability matrices of temporal co-occurrence (conditional probability) of specific motif associations from original trajectories and from simulated ones. We extracted the Jaccard index of similarity between each original matrix and 100 Brownian motions and 100 Lévy walks thus obtaining two distributions of 100 values for each trajectory. We compared the obtained distributions between them using a t-test with Bonferroni correction. Between each pair of distributions, the one having higher mean resembles more to the selected theoretical model than the other one. The trajectories of the bumblebee and the roe deer tend to be equally similar to Brownian motion and to differ from both the black kite and wolf trajectories (Table 1, Brownian motion). The bumblebee trajectory resembles more to a Lévy random walk than the other trajectories (Table 1, Lévy walk).

## 4 | DISCUSSION

Network analyses are powerful tools to statistically describe and compare the spatial structures of animal movements (Jacoby & Freeman, 2016). So far, however, these approaches do not take into account the temporal dimension of movements, which is essential to interpret complex behavioural patterns and their dynamics (ontogeny, repetition, changes). Here we introduced a method to automatically extract motif patterns from animal tracking data and analyse their succession over time.

Our approach builds on the utilization of movement networks to analyse patterns of space use by animals (Bastille-Rousseau et al., 2018; Jacoby & Freeman, 2016; Pasquaretta et al., 2017). Starting from the proposition of Bastille-Rousseau et al. (2018) to isolate areas of intensive use from static spatial network representations of animal movements, we propose to keep trace of temporal information and create behavioural time series embedded in space. Our method is simple to operate and thus expected to be embraced by a large community of ecologists. First the animal trajectory is transformed into a spatial movement network in which nodes are geographic locations and edges are movements between these locations. Next, the step length distribution of the trajectory is used to calculate multiple movement networks, extract their motif time series and compare them to estimate the optimal grid size providing the most diverse sequence of motifs. This selection is used to objectively determine the most suitable resolution for the spatio-temporal analysis of animal trajectories given the data. The temporal exploration of movement trajectories from four case studies demonstrates that our approach is functional and insightful. The analysis of movement patterns matched very well with our knowledge of the ecological context in which the data were recorded, allowing us to identify simple behavioural patterns associated with search routines and migration (unidirectional motifs), and more complex patterns (bidirectional motifs) correlated with the exploitation of familiar areas (migration sites, home range), revisits to specific locations (nest, flowers), resting phases during migrations (stopovers, sparse area of temporary use).

In the bumblebee dataset, complex motifs occurred when the individual was near to biologically relevant locations (nest and flowers). These results are consistent with the well-described observations that bumblebees searching for nectar resources often return to their nest and previously discovered flowers (Lihoreau et al., 2012; Osborne et al., 2013), possibly to explore new areas from known reference spatial locations (Lihoreau, Ings, Chittka, & Reynolds, 2016). Additionally, the loop analysis revealed a strong tendency of the bumblebee to remain around the nest before flying longer distances. This finding is in accordance with previous works demonstrating that bumblebees use learning flights, in the form of loops around the nest, to learn and memorize the location of the nest in the environment (Osborne et al., 2013). In the black kite dataset, complex movement patterns and loops overlap almost perfectly, which likely indicates the existence of stopover sites along the migratory route of the bird. The spatio-temporal analysis of the roe deer dataset highlighted the existence of two successive migratory events during which similar use of spatially distinct home ranges occurs. Interestingly, loops were concentrated around specific areas which might correspond to areas of core usage (i.e. 50% of the time is spent in these specific areas) of the home range of the animal during both summer and winter seasons. The wolf dataset presents complex bidirectional motifs across a summer and a winter territory (Kaczensky et al., 2006). Sparse areas of temporary use are also revealed along the trajectory suggesting possible resting areas during the roaming process. In this case, interestingly, loop behaviours were only observed in the summer territory, suggesting the possible existence of valuable resources in this area.

Comparing the four trajectories with simulated random movement indicated that some trajectories resemble more to a Brownian motion or Lévy walk than others. The bumblebee trajectory, for example, resembles more to a Lévy walk than the other trajectories, thus confirming previous studies suggesting the existence of Lévy flights as optimal search strategy in bumblebees (Lihoreau et al., 2016; Reynolds, 2008; Reynolds, Smith, Reynolds, Carreck, & Osborne, 2007). The black kite and the wolf trajectories appeared different from both Brownian and Lévy motions thus suggesting the possibility to study these movements using more complex behavioural models. Indeed, Brownian motion often underestimates long range movements while pure Lévy walk often overestimates them (Vallaeys, Tyson, Lane, Deleersnijder, & Hanert, 2017). More realistic motions might also be tested in the future (e.g. correlated random walks; Bovet & Benhamou, 1988) to compare trajectories between them and against specific hypothesis.

Future quantitative analyses using multiple trajectories from more individuals will be essential to develop fruitful research on the movement ecology of species. Studies of animal movement are generally based on high resolution data from a few individuals, partly because obtaining long-term data in the field is not an easy task. However, with the fast development of automated tracking systems, analyses of rich movement datasets based on large numbers of trajectories from many individuals are becoming possible (Cagnacci, Boitani, Powell, & Boyce, 2010). Our automated analysis has the main advantages of capturing the temporal properties of complex movement patterns into synthetic and standardized network metrics that facilitate comparative analyses. The metrics obtained are comparable through time for the same individual (e.g. if we are interested in learning and memory) or across individuals (e.g. to assess inter-individual variability in a population, between populations or between species). This approach may therefore facilitate the development of a truly comparative movement ecology based on statistics on standard network metrics.

Our utilization of network metrics could be adjusted depending on the type of data collected and the question addressed. Interestingly, it is possible to study motifs with more than three nodes to compare multiple spatio-temporal level of behavioural complexity that might not emerge from the study of low order motifs. For instance, a four-node sequence such as A-B-C-D-A provides a description of a large area of interest for an animal while the threenode equivalent A-B-C plus C-D-A only provides description of two unidirectional movements between locations without any evidence of spatio-temporal clusters. Note however, the limitation of computational capabilities tend to restrict operational motif size for this type of analysis and debate on how to extract subgraphs with more than three nodes is still open (Agasse-Duval & Lawford, 2018; Ning, Liu, Yu, & Xia, 2017; Williams, Wang, Williams, & Yu, 2014).

Importantly, our method enables to compare the spatio-temporal structure of behavioural patterns to known theoretical movement models. In the future, a functional motif analysis could be implemented to highlight cluster of functional roles (McDonnell, Yaveroğlu, Schmerl, Iannella, & Ward, 2014). Functional motifs could help describe potential changes in behavioural patterns. The utilization of network motifs to analyse animal movements offers a detailed representation of behavioural patterns which is certainly complementary to more classical descriptors of animal movements (e.g. step length, turning angle) and other methods used to obtain behavioural modes (e.g. t-SNE). For instance, the t-SNE method is a procedure to cluster spatial data based on their similarity in various quantitative traits (e.g. straightness, net displacement, mean velocity, see Bartumeus et al., 2016). It enables to describe animal movements as behavioural patterns thus transforming a raw animal trajectory into smaller spatial segments representing diverse behavioural modes. The t-SNE method relies on the interpretation of these behavioural modes. Our spatio-temporal network method, by associating motifs to the specific segments obtained from the t-SNE, could be used to improve their interpretation by the use of direct visualization. Analysis of large movement datasets with our method will also provide the opportunity to develop time series analyses of network motifs using Markov chains. This approach would be a powerful means to move from describing and comparing to predicting temporal sequences of animal movements.

As illustrated above, another major advantage of our method is that it is broadly applicable and can suit different types of movement data collected with different technologies (GPS, PTT, harmonic radar), at different spatial scales (local territories, countries) and temporal scales (minutes, years), on animals with different locomotion modes (walking, flying) and in different ecological contexts (exploration, exploitation, migration). In principle, temporal analyses of spatial network can be used to study virtually all types of animal movement data in which individual animals are regularly re-located. If trajectories are incomplete, for instance because the signal of the animal is lost for some period of time, linear interpolation can be used to fill gaps (Strandburg-Peshkin et al., 2015; Strandburg-Peshkin, Farine, Crofoot, & Couzin, 2017). For any species, however, the main limiting factor is the length of the trajectory (i.e. number of data points). If the trajectory has too few data points, there is a high risk that simplification into a movement network does not provide enough motifs to allow for an insightful exploration of the data.

We have shown that network analyses can be used to investigate the temporal dimension of animal movements and get insights into how the animals interact with their ecological environment (exploitation of known resources, migration routes, stopover sites, territories and roaming areas). Since most animals (including those studied here) frequently interact with social partners or competitors, a major challenge for future studies is to analyse the temporal behavioural movement patterns of interacting animals. Important steps have been made to develop new methods to extract social network from animal trajectories and future directions have been pointed towards using social telemetry data to identify preferred habitats for entire



**FIGURE 7** Spatio-temporal sequence of loops of female and male wolves. (a) Male versus female visualization. Red: locations in which the male did no loop. Blue: locations where the male did at least one loop. Green: locations where the female was observed. (b) Female versus male visualization. Green: locations in which the female did no loop. Blue: locations where the female did at least one loop. Red: locations where the male was observed. Blue gradient encodes the temporal sequence of the loops in both graphs. Locations with the same gradient of blue were collected on the same day

groups (Robitaille, Webber, & Vander Wal, 2019). Our method can help analyse these data by allowing the characterization of complex behavioural patterns of space use by multiple interacting individuals. For example, a preliminary analysis of the trajectories of two wolves (male and female) inhabiting the same area of the Mongolia desert shows that the looping behaviours of both animals occur in separate zones. Specifically, the male repeatedly used locations surrounding the female's territory and performed the highest density of loops in an area facing the area where the female exhibited the highest density of loops (blue locations in Figure 7).

From this type of data, it is possible to construct temporal proximity matrices between individuals and apply classic social network approaches to study interactions among individuals (not showed here). The temporal dimension of our networks can thus inform about non-random associations between behavioural patterns expressed by the individuals. For instance, specific sequences of complex motifs (M8, M10, M12, M13) or loops may reveal behavioural patterns characteristic of mating, territory formation and maintenance or dispersal following social interactions. More generally, our work is part of a rapidly growing research domain aiming at developing multi-layered network methods to study social, spatial and temporal dimensions of animal movement (Finn, Silk, Porter, & Pinter-Wollman, 2019; Mourier, Ledee, & Jacoby, 2019; Silk, Finn, Porter, & Pinter-Wollman, 2018). By including motifs as an attribute of each node in each layer, it will be possible to integrate the temporal, social and spatial dimensions of movements into a single analytical framework and open new promising grounds for extending the analysis of complex movement patterns at the population level.

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### AUTHORS' CONTRIBUTIONS

C.P. and M.L. conceived the ideas and designed the methodology. C.P., T.D., T.G.-M. and M.L. collected the bumblebee data. V.P.D. provided the black kite data. C.P. analysed the data. C.P. and M.L. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## DATA AVAILABILITY STATEMENT

We implemented our method in R. We provide the codes and the bumblebee and black kite datasets in Dryad Digital Repository https://doi.org/10.5061/dryad.47d7wm390 (Pasquaretta et al., 2015). The roe deer dataset was obtained from MOVEBANK (Wikelski & Kays, 2020). Animal Identifier: Sandro (M06), from Cagnacci et al. (2011) (https://www.movebank.org/). The wolf dataset was obtained from MOVEBANK (Wikelski & Kays, 2020), Animal identifier: Zimzik, from Kaczensky et al. (2006) (https://www.movebank.org/).

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#### REFERENCES

- Agasse-Duval, M., & Lawford, S. (2018). Subgraphs and motifs in a dynamic airline network. arXiv preprint arXiv:1807.02585.
- Ahearn, S. C., & Dodge, S. (2018). Recursive multifrequency segmentation of movement trajectories (ReMuS). *Methods in Ecology and Evolution*, 9, 1075–1087. https://doi.org/10.1111/2041-210X.12958
- Artzy-Randrup, Y., Fleishman, S. J., Ben-Tal, N., & Stone, L. (2004). Comment on "Network motifs: Simple building blocks of complex networks" and

"Superfamilies of evolved and designed networks". *Science*, 305(5687), 1107–1107. https://doi.org/10.1126/science.1099334

- Bartumeus, F., Campos, D., Ryu, W. S., Lloret Cabot, R., Méndez, V., & Catalan, J. (2016). Foraging success under uncertainty: Search tradeoffs and optimal space use. *Ecology Letters*, 19, 1299–1313. https://doi. org/10.1111/ele.12660
- Bartumeus, F., Catalan, J., Fulco, U. L., Lyra, M. L., & Viswanathan, G. M. (2002). Optimizing the encounter rate in biological interactions: Lévy versus Brownian strategies. *Physical Review Letters*, 88, 097901. https://doi.org/10.1103/PhysRevLett.88.097901
- Bastille-Rousseau, G., Douglas-Hamilton, I., Blake, S., Northrup, J. M., & Wittemyer, G. (2018). Applying network theory to animal movements to identify properties of landscape space use. *Ecological Applications*, 28, 854–864. https://doi.org/10.1002/eap.1697
- Bovet, P., & Benhamou, S. (1988). Spatial analysis of animals' movements using a correlated random walk model. *Journal of Theoretical Biology*, 131, 419–433. https://doi.org/10.1016/S0022-5193(88)80038-9
- Cagnacci, F., Boitani, L., Powell, R. A., & Boyce, M. S. (2010). Animal ecology meets GPS-based radiotelemetry: A perfect storm of opportunities and challenges. *Philosophical Transaction of the Royal Society B*, 365, 2157–2162.
- Cagnacci, F., Focardi, S., Heurich, M., Stache, A., Hewison, A. J. M., Morellet, N., ... Urbano, F. (2011). Partial migration in roe deer: Migratory and resident tactics are end points of a behavioural gradient determined by ecological factors. *Oikos*, 120, 1790–1802. https:// doi.org/10.1111/j.1600-0706.2011.19441.x
- De Groeve, J., Van de Weghe, N., Ranc, N., Neutens, T., Ometto, L., Rota-Stabelli, O., & Cagnacci, F. (2016). Extracting spatio-temporal patterns in animal trajectories: An ecological application of sequence analysis methods. *Methods in Ecology and Evolution*, 7, 369–379. https:// doi.org/10.1111/2041-210X.12453
- Dodge, S., Weibel, R., & Lautenschütz, A. K. (2008). Towards a taxonomy of movement patterns. *Information Visualization*, 7, 240–252. https:// doi.org/10.1057/PALGRAVE.IVS.9500182
- Edelhoff, H., Signer, J., & Balkenhol, N. (2016). Path segmentation for beginners: An overview of current methods for detecting changes in animal movement patterns. *Movement Ecology*, 4(1), 21. https://doi. org/10.1186/s40462-016-0086-5
- Farine, D. R., & Whitehead, H. (2015). Constructing, conducting and interpreting animal social network analysis. *Journal of Animal Ecology*, 84(5), 1144–1163. https://doi.org/10.1111/1365-2656.12418
- Finn, K. R., Silk, M. J., Porter, M. A., & Pinter-Wollman, N. (2019). The use of multilayer network analysis in animal behaviour. *Animal Behaviour*, 149, 7–22. https://doi.org/10.1016/j.anbehav.2018.12.016
- Flack, A., Nagy, M., Fiedler, W., Couzin, I. D., & Wikelski, M. (2018). From local collective behavior to global migratory patterns in white storks. *Science*, 360, 911–914.
- Giorgino, T. (2009). Computing and visualizing dynamic time warping alignments in R: The dtw package. *Journal of Statistical Software*, 31(7), 1–24.
- Gobbi, A., Iorio, F., Albanese, D., Jurman, G., & Saez-Rodriguez, J. (2017). BiRewire: High-performing routines for the randomization of a bipartite graph (or a binary event matrix), undirected and directed signed graph preserving degree distribution (or marginal totals). R package version 3.18.0. Retrieved from http://www.ebi.ac.uk/~iorio/BiRewire
- Gurarie, E., Andrews, R. D., & Laidre, K. L. (2009). A novel method for identifying behavioural changes in animal movement data. *Ecology Letters*, 12, 395–408. https://doi.org/10.1111/j.1461-0248.2009.01293.x
- Jacoby, D. M., & Freeman, R. (2016). Emerging network-based tools in movement ecology. *Trends in Ecology & Evolution*, 31, 301–314. https:// doi.org/10.1016/j.tree.2016.01.011
- Juszczyszyn, K. (2014). Motif analysis. In R. Alhajj & J. Rokne (Eds.), Encyclopedia of social network analysis and mining (pp. 983–989). New York, NY: Springer.
- Kaczensky, P., Ganbaatar, O., Enksaikhaan, N., & Walzer, C. (2006). Wolves in Great Gobi B SPAGPS tracking study 2003–2005 dataset. Movebank Data Repository. Retrieved from www.movebank.org.

- Lihoreau, M., Ings, T. C., Chittka, L., & Reynolds, A. M. (2016). Signatures of a globally optimal searching strategy in the three-dimensional foraging flights of bumblebees. *Scientific Reports*, *6*, 30401. https://doi. org/10.1038/srep30401
- Lihoreau, M., Raine, N. E., Reynolds, A. M., Stelzer, R. J., Lim, K. S., Smith, A. D., ... Chittka, L. (2012). Radar tracking and motion-sensitive cameras on flowers reveal the development of pollinator multi-destination routes over large spatial scales. *PLoS Biology*, 10, e1001392. https://doi.org/10.1371/journal.pbio.1001392
- McDonnell, M. D., Yaveroğlu, Ö. N., Schmerl, B. A., Iannella, N., & Ward, L. M. (2014). Motif-role-fingerprints: The building-blocks of motifs, clustering-coefficients and transitivities in directed networks. *PLoS ONE*, 9, e114503. https://doi.org/10.1371/journal.pone.0114503
- Milo, R., Shen-Orr, S., Itzkovitz, S., Kashtan, N., Chklovskii, D., & Alon, U. (2002). Network motifs: Simple building blocks of complex networks. *Science*, 298(5594), 824–827. https://doi.org/10.1126/scien ce.298.5594.824
- Mourier, J., Ledee, E. J., & Jacoby, D. M. (2019). A multilayer perspective for inferring spatial and social functioning in animal movement networks. *bioRxiv*, 749085.
- Ning, Z., Liu, L., Yu, S., & Xia, F. (2017, November). Detection of four-node motif in complex networks. In *International conference on complex net*works and their applications (pp. 453–462). Cham, Switzerland: Springer.
- Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., ...Stevens, M. H. H. (2018). vegan: Community Ecology Package. R version 3.4.4. Retrieved from https://CRAN.R-project.org/package=vegan
- Osborne, J. L., Smith, A., Clark, S. J., Reynolds, D. R., Barron, M. C., Lim, K. S., & Reynolds, A. M. (2013). The ontogeny of bumblebee flight trajectories: From naïve explorers to experienced foragers. *PLoS ONE*, *8*, e78681. https://doi.org/10.1371/journal.pone.0078681
- Paranjape, A., Benson, A. R., & Leskovec, J. (2017). Motifs in temporal networks. In Proceedings of 10th ACM international conference on web search and data mining (pp. 601–610). https://doi.org/10.1145/30186 61.3018731
- Pasquaretta, C., Dubois, T., Gomez-Moracho, T., Le Loc'h, G., Delepoulle, V. P., Heeb, P., & Lihoreau, L. (2020). Data from: Analysis of temporal patterns in animal movement networks, v2. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.47d7wm390
- Pasquaretta, C., Jeanson, R., Andalo, C., Chittka, L., & Lihoreau, M. (2017). Analysing plant-pollinator interactions with spatial movement networks. *Ecological Entomology*, 42(1), 4–17. https://doi. org/10.1111/een.12446
- Pasquaretta, C., Jeanson, R., Pansanel, J., Raine, N. E., Chittka, L., & Lihoreau, M. (2019). A spatial network analysis of resource partitioning between bumblebees foraging on artificial flowers in a flight cage. *Movement Ecology*, 7(1), 4. https://doi.org/10.1186/ s40462-019-0150-z
- Patel, P., Keogh, E., Lin, J., & Lonardi, S. (2002, December). Mining motifs in massive time series databases. In *Proceedings of the 2002 IEEE international conference on data mining* (pp. 370–377). IEEE, Maebashi, Japan.
- Patterson, T. A., Thomas, L., Wilcox, C., Ovaskainen, O., & Matthiopoulos, J. (2008). State-space models of individual animal movement. *Trends* in Ecology & Evolution, 23(2), 87–94. https://doi.org/10.1016/j. tree.2007.10.009
- Polansky, L., Wittemyer, G., Cross, P. C., Tambling, C. J., & Getz, W. M. (2010). From moonlight to movement and synchronized randomness: Fourier and wavelet analyses of animal location time series data. *Ecology*, 91, 1506–1518. https://doi.org/10.1890/08-2159.1
- Potts, J. R., Börger, L., Scantlebury, D. M., Bennett, N. C., Alagaili, A., & Wilson, R. P. (2018). Finding turning-points in ultra-high-resolution animal movement data. *Methods in Ecology and Evolution*, *9*, 2091– 2101. https://doi.org/10.1111/2041-210X.13056
- R Core Team. (2018). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

- Reynolds, A. M. (2008). Optimal random Lévy-loop searching: New insights into the searching behaviours of central-place foragers. *EPL (Europhysics Letters)*, 82, 20001. https://doi.org/10.1209/0295-5075/82/20001
- Reynolds, A. M. (2018). Current status and future directions of Lévy walk research. *Biology Open*, 7(1), bio030106. https://doi.org/10.1242/ bio.030106
- Reynolds, A. M., Smith, A. D., Reynolds, D. R., Carreck, N. L., & Osborne, J. L. (2007). Honeybees perform optimal scale-free searching flights when attempting to locate a food source. *Journal of Experimental Biology*, 210, 3763–3770. https://doi.org/10.1242/jeb.009563
- Rice, W. R. (1989). Analyzing tables of statistical tests. *Evolution*, 43, 223–225. https://doi.org/10.1111/j.1558-5646.1989.tb04220.x
- Riley, J. R., Smith, A. D., Reynolds, D. R., Edwards, A. S., Osborne, J. L., Williams, I. H., ... Poppy, G. M. (1996). Tracking bees with harmonic radar. *Nature*, 379(6560), 29–30. https://doi.org/10.1038/379029b0
- Robitaille, A. L., Webber, Q. M., & Vander Wal, E. (2019). Conducting social network analysis with animal telemetry data: Applications and methods using spatsoc. *Methods in Ecology and Evolution*, 10, 1203–1211. https://doi.org/10.1111/2041-210X.13215
- Sakoe, H., & Chiba, S. (1978). Dynamic programming algorithm optimization for spoken word recognition. *IEEE Transactions on Acoustics*, *Speech, and Signal Processing*, 26(1), 43–49. https://doi.org/10.1109/ TASSP.1978.1163055
- Shannon, C. E. (1948). A mathematical theory of communication. Bell System Technical Journal, 27, 379–423. https://doi.org/10.1002/j.1538-7305.1948.tb01338.x
- Shlesinger, M. F., & Klafter, J. (1986). Lévy walks versus Lévy flights. In H. E. Stanley & N. Ostrowsky (Eds.), On growth and form (pp. 279–283). Dordrecht, The Netherlands: Springer.
- Silk, M. J., Finn, K. R., Porter, M. A., & Pinter-Wollman, N. (2018). Can multilayer networks advance animal behavior research? *Trends in Ecology* & *Evolution*, 33, 376–378. https://doi.org/10.1016/j.tree.2018.03.008
- Strandburg-Peshkin, A., Farine, D. R., Couzin, I. D., & Crofoot, M. C. (2015). Shared decision-making drives collective movement in wild baboons. *Science*, 348, 1358–1361.
- Strandburg-Peshkin, A., Farine, D. R., Crofoot, M. C., & Couzin, I. D. (2017). Habitat and social factors shape individual decisions and emergent group structure during baboon collective movement. *Elife*, 6, e19505. https://doi.org/10.7554/eLife.19505
- Swingland, I. R., & Greenwood, P. J. (1983). *Ecology of animal movement*. Oxford, UK: Clarendon Press.
- Teimouri, M., Indahl, U., Sickel, H., & Tveite, H. (2018). Deriving animal movement behaviors using movement parameters extracted from location data. *ISPRS International Journal of Geo-Information*, 7(2), 78. https://doi.org/10.3390/ijgi7020078

- Tomkiewicz, S. M., Fuller, M. R., Kie, J. G., & Bates, K. K. (2010). Global positioning system and associated technologies in animal behaviour and ecological research. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365, 2163–2176.
- Turchin, P. (1998). *Quantitative analysis of movement*. Sunderland, MA: Sinauer Associates.
- Vallaeys, V., Tyson, R. C., Lane, W. D., Deleersnijder, E., & Hanert, E. (2017). A Lévy-flight diffusion model to predict transgenic pollen dispersal. *Journal of the Royal Society Interface*, 14, 20160889. https:// doi.org/10.1098/rsif.2016.0889
- van Toor, M. L., Newman, S. H., Takekawa, J. Y., Wegmann, M., & Safi, K. (2016). Temporal segmentation of animal trajectories informed by habitat use. *Ecosphere*, 7, e01498. https://doi.org/10.1002/ecs2.1498
- Viswanathan, G. M., Afanasyev, V., Buldyrev, S. V., Murphy, E. J., Prince, P. A., & Stanley, H. E. (1996). Lévy flight search patterns of wandering albatrosses. *Nature*, 381, 413. https://doi.org/10.1038/381413a0
- Wasserman, S., & Faust, K. (1994). Social network analysis: Methods and applications (Vol. 8). Cambridge, UK: Cambridge University Press.
- Wikelski, M., & Kays, R. (2020). Movebank: Archive, analysis and sharing of animal movement data. World Wide Web Electronic Publication. Retrieved from http://www.movebank.org
- Williams, V. V., Wang, J. R., Williams, R., & Yu, H. (2014, December). Finding four-node subgraphs in triangle time. In *Proceedings of the twenty-sixth annual ACM-SIAM symposium on discrete algorithms* (pp. 1671–1680). Society for Industrial and Applied Mathematics.
- Wittemyer, G., Polansky, L., Douglas-Hamilton, I., & Getz, W. M. (2008). Disentangling the effects of forage, social rank, and risk on movement autocorrelation of elephants using Fourier and wavelet analyses. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 19108–19113. https://doi.org/10.1073/pnas.08017 44105

#### SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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