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1 Analysis of temporal patterns in animal movement
2 networks

3

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13

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15

16 Running headline: Temporal patterns in movement networks

17 **Abstract**

18 1. Understanding how animal movements change across space and time is a fundamental question
19 in ecology. While classical analyses of trajectories give insightful descriptors of spatial patterns, a
20 satisfying method for assessing the temporal succession of such patterns is lacking.

21

22 2. Network analyses are increasingly used to capture properties of complex animal trajectories in
23 simple graphical metrics. Here, building on this approach, we introduce a method that incorporates
24 time into movement network analyses based on temporal sequences of network motifs.

25

26 3. We illustrate our method using four example trajectories (bumblebee, black kite, roe deer, wolf)
27 collected with different technologies (harmonic radar, platform terminal transmitter, global
28 positioning system). First, we transformed each trajectory into a spatial network by defining the
29 animal's coordinates as nodes and movements in between as edges. Second, we extracted temporal
30 sequences of network motifs from each movement network and compare the resulting behavioural
31 profiles to topological features of the original trajectory. Finally, we compared each sequence of
32 motifs with simulated Brownian and Lévy random motions to statistically determine differences
33 between trajectories and classical movement models.

34

35 4. Our analysis of the temporal sequences of network motifs in individual movement networks
36 revealed successions of spatial patterns corresponding to changes in behavioural modes that can be
37 attributed to specific spatio-temporal events of each animal trajectory. Future applications of our
38 method to multi-layered movement and social network analysis yield considerable promises for
39 extending the study of complex movement patterns at the population level.

40

41 **KEYWORDS:** animal trajectories, Argos, GPS-tracking, harmonic radar, motifs time-series,
42 movement ecology, spatial networks

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49 **1. Introduction**

50

51 Over the past recent years, the study of animal movements has experienced a rapid growth thanks to
52 the development of new technologies to automatically collect long-term individual data on wild
53 animals (Tomkiewicz et al., 2010; Strandburg-Peshkin et al., 2015; Flack et al., 2018). The
54 acquisition of high resolution data has also required the development of new statistical tools to
55 describe and analyse movements. At the most basic level, it is possible to visualize the sequence of
56 locations visited by the animal by joining those locations with a line, i.e. the animal trajectory.
57 Speed, step length (distance between successive locations), residency (the time an individual
58 remains at a specific location before moving), and turning angle (change of direction between
59 successive steps) are some of the main parameters that can be extracted from such a trajectory
60 (Patterson et al., 2008; Dodge et al., 2008). These parameters tend to be correlated with specific
61 behavioural states (Edelhoff et al., 2016) and can be grouped into patterns dependent of
62 environmental constraints and spatial variability. So far, however, this approach has yielded little
63 information about the temporal dimension of animal trajectories (Jacoby & Freeman, 2016). For
64 many animals, movements can show dramatic changes with time as a result of motivation,
65 experience, social interactions or modifications of the environment (Swingland & Greenwood,
66 1983). Identifying these changes in complex movement datasets can thus bring critical insights into
67 the fundamental ecology of animals.

68 Recent attempts to develop a unified spatio-temporal analytical framework of
69 movement data have shown the existence of a relationship between temporal autocorrelations of
70 movement parameters (i.e. step length) and spatial distribution of critical resources (Wittemyer et
71 al., 2008). Others have proposed to analyse the sequence of habitats encountered by an animal to
72 extract behavioural changes in a trajectory (van Toor et al., 2016; de Groot et al., 2016).
73 Behavioural change point analysis (BCPA) of movement parameters is a powerful tool to estimate
74 the time at which an animal changes its movement patterns and how this corresponds to behavioural
75 states such as resting, foraging or moving (Gurarie et al., 2009; Teimouri et al., 2018). Multiple
76 unsupervised statistical methods have also been used to reduce complex animal trajectories into
77 human understandable format such as the circular standard deviation (Potts et al., 2018), the t-
78 stochastic neighbouring embedding (t-SNE) algorithm (Bartumeus et al., 2016), the recursive multi-
79 frequency segmentation (ReMuS) (Ahearn & Dodge, 2018), or the Fourier and wavelet analysis
80 (Polansky et al., 2010). Despite satisfying the quantitative aspects of spatio-temporal analysis of

81 animal movement data, these methods often require advanced mathematical knowledge and lack
82 intuitive tools to help data visualization and interpretation by ecologists.

83 Network analysis may constitute a simpler, yet powerful, approach for such analyses
84 (Jacoby & Freeman, 2016; Bastille-Rousseau et al., 2018; Pasquaretta et al., 2017; Pasquaretta et
85 al., 2019). For example, Bastille-Rousseau et al. (2018) transposed global positioning system (GPS)
86 locations obtained from three different species (African elephants, giant Galapagos tortoises, Mule
87 deer) into networks. In such networks, nodes represent spatial locations visited by the animals and
88 edges animal movements between these locations. The analysis of node-level network metrics
89 demonstrated that locations with high betweenness centrality scores (frequency at which a node acts
90 as bridge along the shortest paths passing by two other nodes) was indicative of bridges between
91 migration areas for tortoises and corridors between foraging sites for elephants (Bastille-Rousseau
92 et al., 2018). Network analysis of spatial data can thus bring important information for studying
93 associations of complex behavioural patterns and spatial characteristics. So far, however, this
94 method relies on a static representation of animal space use and does not consider the temporal
95 nature of movements (Jacoby & Freeman, 2016; Bastille-Rousseau et al., 2018).

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

104

105 **2. Materials and Methods**

106 **2.1 Movement datasets**

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

114 *Bumblebee search trajectory*

115 We used a harmonic radar to obtain a search trajectory of a bumblebee worker on 15/04/2018 (1
116 recording every 3.3s, 364 data points, Fig. S1A). We set up a commercial colony of *Bombus*
117 *terrestris* (Biobest NV, Westerlo, Belgium) in a flat dry rice farm land in Sevilla (Spain) (Fig. S2).
118 We trained multiple bumblebees to forage on three artificial flowers (i.e. blue platform with 40%
119 (v/v) sucrose solution, see details in Lihoreau et al., 2012) positioned two meters in front of the nest
120 box. Once a regular forager was identified (bumblebee performing several consecutive foraging
121 bouts), we closed the colony entrance and randomly moved the three artificial flowers away in the
122 field. The focal bumblebee was equipped with a transponder (16 mm vertical dipole) upon leaving
123 the nest box and tracked with the harmonic radar until it returned to the colony (Riley et al., 1996).
124 The radar was placed 350 meters away from the colony nest box (Fig. S3) and returned the 2D
125 coordinates of the tagged bumblebee within a range of 700 m.

126

127 *Black kite long-range migration trajectory*

128 We used GPS to track an adult female black kite (*Milvus migrans*) moving across Spain from
129 28/05/2019 to 19/08/2019 (1 recording every 6h, 332 data points, Fig. S1B). The bird was caught
130 after an injury and maintained five weeks in an aviary for rehabilitation. We equipped the bird with
131 a Platform Terminal Transmitter (PTT) back-packed (Xerius Tracking, France) and released it in
132 Toulouse (France), where it first moved within a limited area before migrating on its way to
133 Morocco.

134

135 *Roe deer short-range migration trajectory*

136 This dataset was obtained from the EURODEER collaborative project (E. Mach Foundation,
137 Trento, Italy; <http://sites.google.com/site/eurodeerproject>) (Cagnacci et al., 2011). It consists of one
138 GPS trajectory of an adult male roe deer (*Capreolus capreolus*) collected from 23/10/2005 to
139 28/10/2006 (1 recording every 4 h, 1827 data points; Fig. S1C). The roe deer was tracked in the
140 area of Trentino Alto Adige (Italy). Behavioural patterns in this trajectory are dominated by short
141 range migratory movements representing the yearly leave-and-back movements between two winter
142 and summer sites. To compare this trajectory with the other example trajectories, we reduced the
143 number of data points to 457 by resampling the trajectory every 16h.

144

145 *Wolf roaming trajectory*

146 This dataset was obtained from a study of the Przewalskii horse reintroduction project of the
147 International Takhi Group (ITG) (Kaczensky et al., 2006). It consists of one GPS trajectory of an

148 adult male wolf (*Canis lupus*) collected from 05/03/2004 to 18/09/2005 (1 recording every 8 h,
149 1455 data points in total). The wolf was tracked in the mountains of the Goby Desert (Mongolia).
150 Behavioural patterns in this trajectory are dominated by territorial movements around the mountains
151 and one main roaming period (Fig. S1D). To compare this trajectory with the other example
152 trajectories, we reduced the number of data points to 485 by resampling the trajectory each 24h.

153

154 **2.2 Method overview**

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

164

165 *Transform spatial coordinates into a temporal movement network*

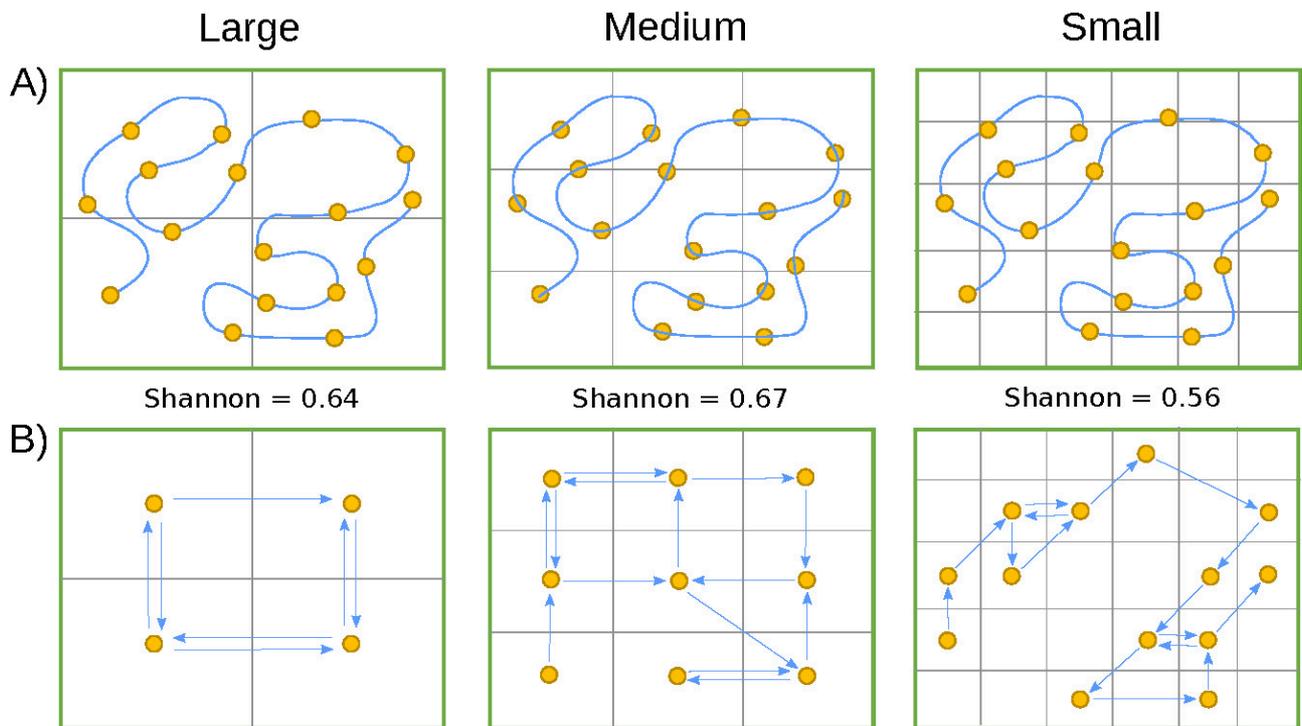
166 The first step consisted in transforming the raw movement data into a format that can be
167 automatically analysed with network metrics. To do so, we rasterized the animal coordinates on a
168 spatial grid. Because different grid resolutions affect the topological structure of the resulting
169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

171 Building a movement network from an animal trajectory has the risk of
172 oversimplifying the information depending on grid resolution (Fig. 1). Effects vary from large grid
173 size, where the entire trajectory can be summarized into movement loops starting and ending at a
174 single location, to small grid size, where each location of the raw trajectory corresponds to different
175 grid cell. The optimal grid resolution capturing biologically relevant behavioural patterns is
176 expected to lay somewhere in the middle. Previous studies have used the median of the step length
177 distribution as grid size, based on the fact that this value leads to robust results under the
178 assumption of Brownian movements (Bastille-Rousseau et al., 2018). However, many animal
179 trajectories show more complex patterns. To address this issue, for each trajectory we tested nine
180 grid resolutions. Each grid resolution corresponded to one specific quantile of the step length
181 distribution of the trajectory (i.e. $p = 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9$). The animal

182 coordinates were thus transformed into nodes and movements between them into directed edges
 183 (see Fig. 1B). We attributed the same node identity to each coordinate falling into the same grid
 184 cell. Empty cells were considered as non-visited cells at this stage. We then transformed the spatial
 185 network into a temporal edge list by associating a time to each movement of the sequence.

186

187



188

189

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

198

199 *Extract temporal sequence of network motifs from movement networks*

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

204 the context of movement networks, these sequences refer to sub-graphs that describe spatio-
 205 temporal movements (Pasquaretta et al., 2017) and can be used to understand non-random
 206 successions of patterns in a complex behavioural sequence (Patel et al., 2003).

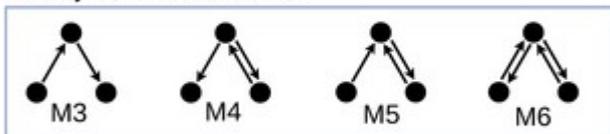
207 Among the 13 possible different motifs between three nodes, five are irrelevant for
 208 movement data (Fig. S4, see details in Wasserman & Faust, 1994). Four of the eight remaining
 209 motifs belong to the family of “loosely connected motifs”, i.e. sub-graphs missing one edge
 210 between two out of three nodes (Juszczyszyn, 2014; Fig. 2A). The four other motifs belong to the
 211 family of “closely connected motifs”, i.e. sub-graphs with edges between all nodes. In the context
 212 of movement data, the loosely connected motif M3 indicates movements across locations without
 213 any revisit to any location. All other motifs indicate more complex movement patterns characterised
 214 by at least one revisit to a location.

215 Temporal sequences of network motifs can be extracted by dividing the edge list into
 216 specific motif windows including at least three different connected nodes (Paranjape et al., 2017).
 217 Here we built sliding windows containing a maximum of three nodes, allowing us to create a
 218 temporal sequence of successive motifs based on the utilisation of three consecutive locations. To
 219 do so, we started from the first node of the network and iteratively analysed the entire sequence to
 220 create sub-sequences of three nodes. Each node in this subsequence can be visited only once (e.g.
 221 M3) or several times (e.g. M13). Once the first sub-sequence was created, we applied the same
 222 iterative algorithm to find all the successive motifs using the last node of the previous sub-graph as
 223 starting point for the next one (Fig. 2B).

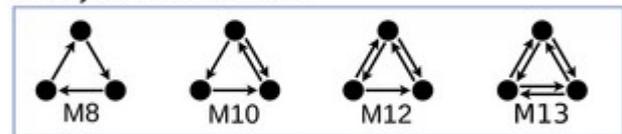
224

A) Motif patterns

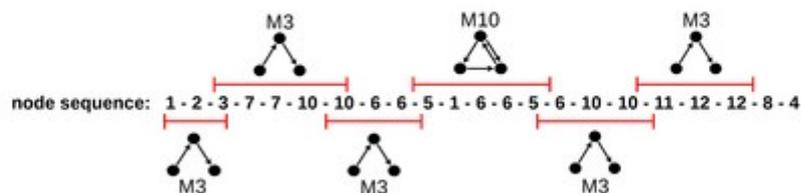
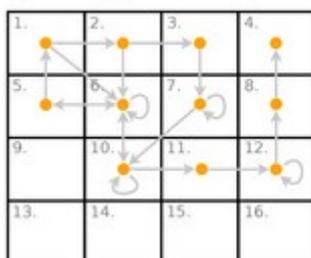
loosely connected motifs



closely connected motifs



B) Temporal sequence of motif patterns



225

226

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

232

233 Adjustment of grid resolution

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

240 We used this approach to create matrices of similarity between motif time series.
241 From these data, we finally selected the most suitable motif time series characterised by: 1) the
242 largest number of different motifs (abundance) and 2) the most equal proportion of each motif
243 (evenness). To do so, we created a list of temporal sequences of network motifs obtained from
244 different grid resolutions (i.e. 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9) and calculated a similarity matrix
245 using the DTW distance between them with the function “dist” of the R package *stats* (R Core
246 Team, 2018). We applied the Shannon Diversity Index (Shannon, 1948), using the R package *vegan*
247 (Oksanen et al., 2018), to select the optimal time series. Specifically, we used as optimal grid size
248 the step length corresponding to the highest value of Shannon Diversity Index (to illustrate the
249 robustness of the method, results from the second highest value are presented in Supplementary
250 Text S2). With this procedure, we ensured an objective way to select the best grid resolution value
251 returning the time series with the largest number of motifs which proportions were also more
252 equally represented. For each dataset, we identified the best grid resolution to analyse complex
253 movement patterns using sequences of behavioural patterns instead of the trajectory parameters
254 themselves (e.g. median step length, mean turning angle). We evaluated whether the proportion of
255 motifs differed across datasets with a Chi-square (χ^2) test, applied to a table with rows and columns
256 corresponding to motif counts and animals, using the “chisq.test” function in R.

257

258 Visualization of temporal behavioural patterns

259 To illustrate that our method can be used to identify spatio-temporal behavioural patterns from
260 complex animal trajectories we represented the evolution of motifs through time. Here, we focused
261 only on the seven motifs identified as indicative of complex movements: characterised by at least

262 one revisit to a node. We extracted the geographic locations involved in the construction of these
263 motifs and represented them in the network to describe spatio-temporal patterns of complex
264 behaviours. Loops (movements starting and ending at the same location) are structurally removed
265 when analysing network motifs (Wasserman & Faust, 1994). To account for such behavioural
266 patterns we first extracted the number of loops observed inside each motif and we later applied a
267 generalized linear model (GLM) for count data (Poisson error distribution) to estimate the
268 relationship between motif complexity and the number of loops performed using the *glm* function of
269 the R package *stats* (R Core Team, 2018). We also tested different temporal windows by
270 resampling the roe deer and wolf dataset (see supplementary Text S3).

271

272 Evaluation of temporal motifs with a null model

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

281 In temporal directed networks, where a temporal correlation between successive
282 motifs can be expected, an effective way to compare the experimental sequence with a randomized
283 sequence is by time-shuffling, that is randomly sample motifs in a sequence and change their
284 temporal position. The focus is then made on the structure of the motif sequence itself and on the
285 probability of temporal co-occurrence (conditional probability) of specific motif associations. Here
286 we used the conditional probabilities between each pair of motif to reveal the existence of non-
287 random transitions between specific behavioural patterns. We first calculated the probability matrix
288 to move from each motif to the next (8x8 matrix) and compared this matrix with 100 probability
289 matrices obtained from time-shuffled time series. For each pair of temporal patterns, we calculated
290 the 95% CIs and compared the probabilities from the original motifs time series to the
291 corresponding probabilities obtained from time-shuffled motifs time series. We used a one-tail
292 analysis and consider probabilities falling outside of the upper 95% confidence interval (CI) as
293 significant. The obtained resulting binary matrix thus assigns 1 to all the positive non-random
294 conditional probabilities and 0 to the others.

295 Comparing non-random probabilities with Brownian motion and Lévy walk

296 Brownian motion and Lévy walks are two main theoretical random movement patterns used to
297 describe trajectories observed in nature (Turchin, 1998; Fig. 3). Pure Brownian random walks have
298 been introduced to describe animal search strategies when no information is available. Brownian
299 motions are determined by successive steps in random directions whose step lengths and turning
300 angles are randomly drawn from a normal distribution (Bartumeus et al., 2002). Lévy walks are
301 defined by movements patterns following a power-law distribution (Shlesinger & Klafter, 1986;
302 Viswanathan et al., 1996; Reynolds, 2018). To estimate the degree by which the four original
303 trajectories differed from Brownian and Lévy random movements we compared the binary matrices
304 of transition between motifs obtained for each of the four animal trajectories with 100 probability
305 matrices obtained from both simulated Brownian and Lévy trajectories by calculating the Jaccard
306 index of similarity using the function *birewire.similarity* in the R package “BiRewire” (Gobbi et al.,
307 2017). We thus obtained four distributions of Jaccard indices (one for each dataset) and compared
308 them using t-statistic. We adjusted the α value using the sequential Bonferroni correction (Rice,
309 1989).

310

311

312

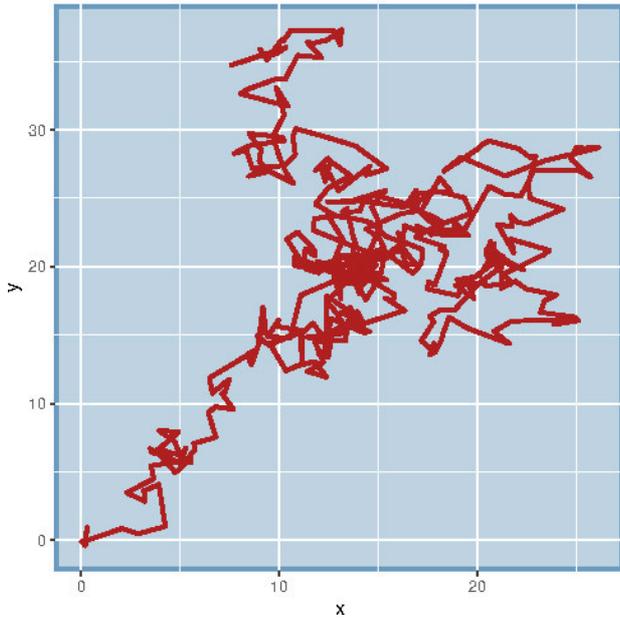
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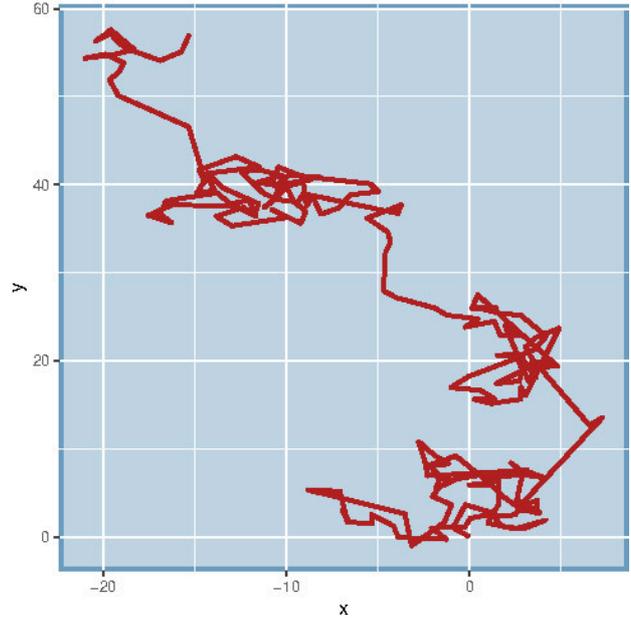
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316

Brownian motion



Lévy walk



317

318

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

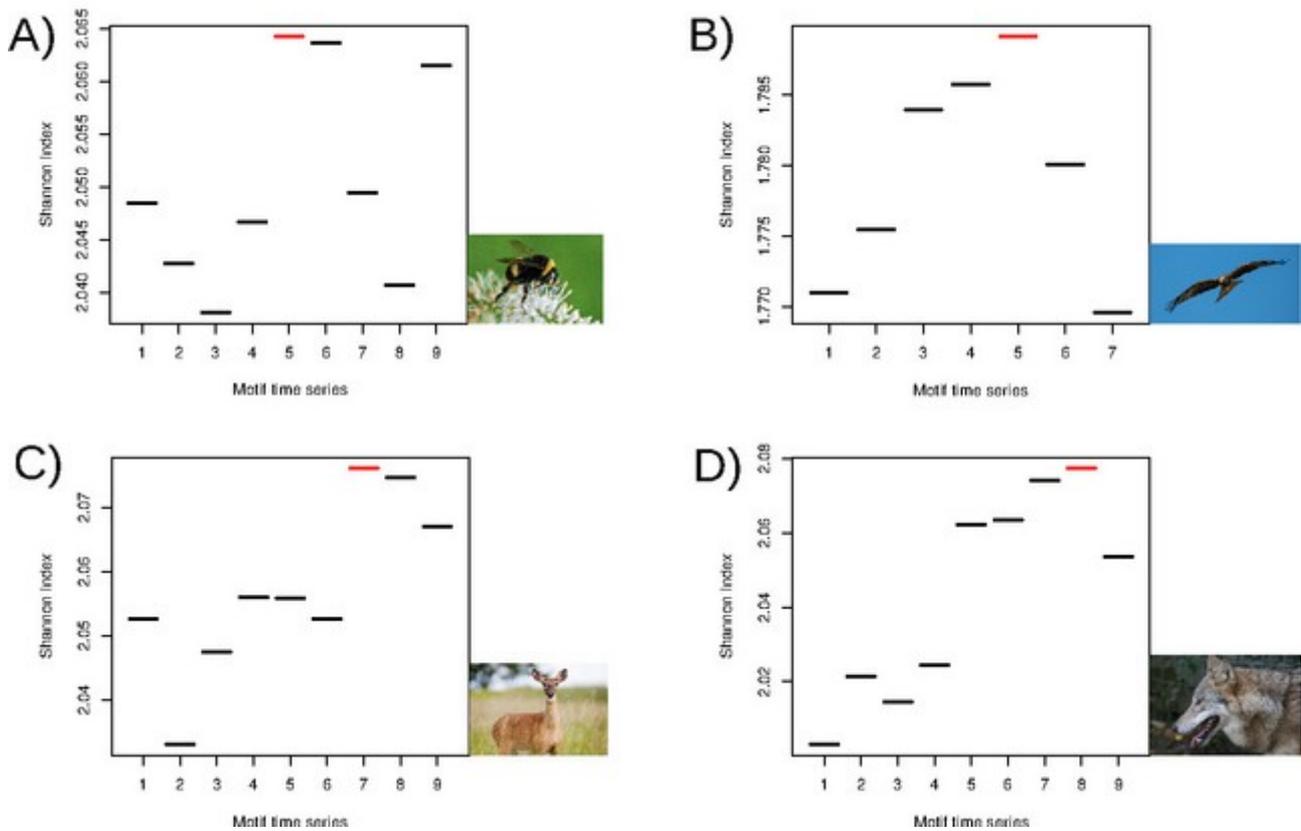
321

322 3. Results

323 3.1 Identification of optimal grid size

324 The crucial step in transforming an animal trajectory into a movement network involves the
325 selection of an optimal grid resolution that is small enough to obtain a suitable number of nodes to
326 create a network, and large enough to provide insightful details on the animal movement patterns.
327 For each dataset, we extracted the step length values of the nine quantiles of the step lengths
328 distribution of the trajectory, and removed any quantiles with step length value close to zero (i.e.
329 values lower than 10^{-6}). We obtained seven possible quantile values for the black kite, and nine
330 quantile values for the bumblebee, the roe deer and the wolf (Table S1). We used these quantile
331 values as cell size to build spatial grids and generate movement networks. From these networks, we
332 extracted temporal sequences of network motifs and compared them using the DTW distance to
333 select the optimal grid resolution given the data. We then applied the Shannon Diversity Index to
334 select the motif time series for each dataset as candidate sequence for subsequent analyses. The
335 Shannon Diversity Index retained the motif time series 5, 5, 7 and 8, corresponding to a cell size of
336 step length value of 11.209 (i.e. quantile 0.5) for the bumblebee, 0.0075 (i.e. quantile 0.7) for the
337 black kite, 0.0037 (i.e. quantile 0.7) for the roe deer and 0.2642 (i.e. quantile 0.8) for the wolf (Fig.

338 4; see Table S1 for the values of all quantiles). Thus, the optimal grid size selected for the temporal
339 analyses of network motifs varied across the four datasets.
340

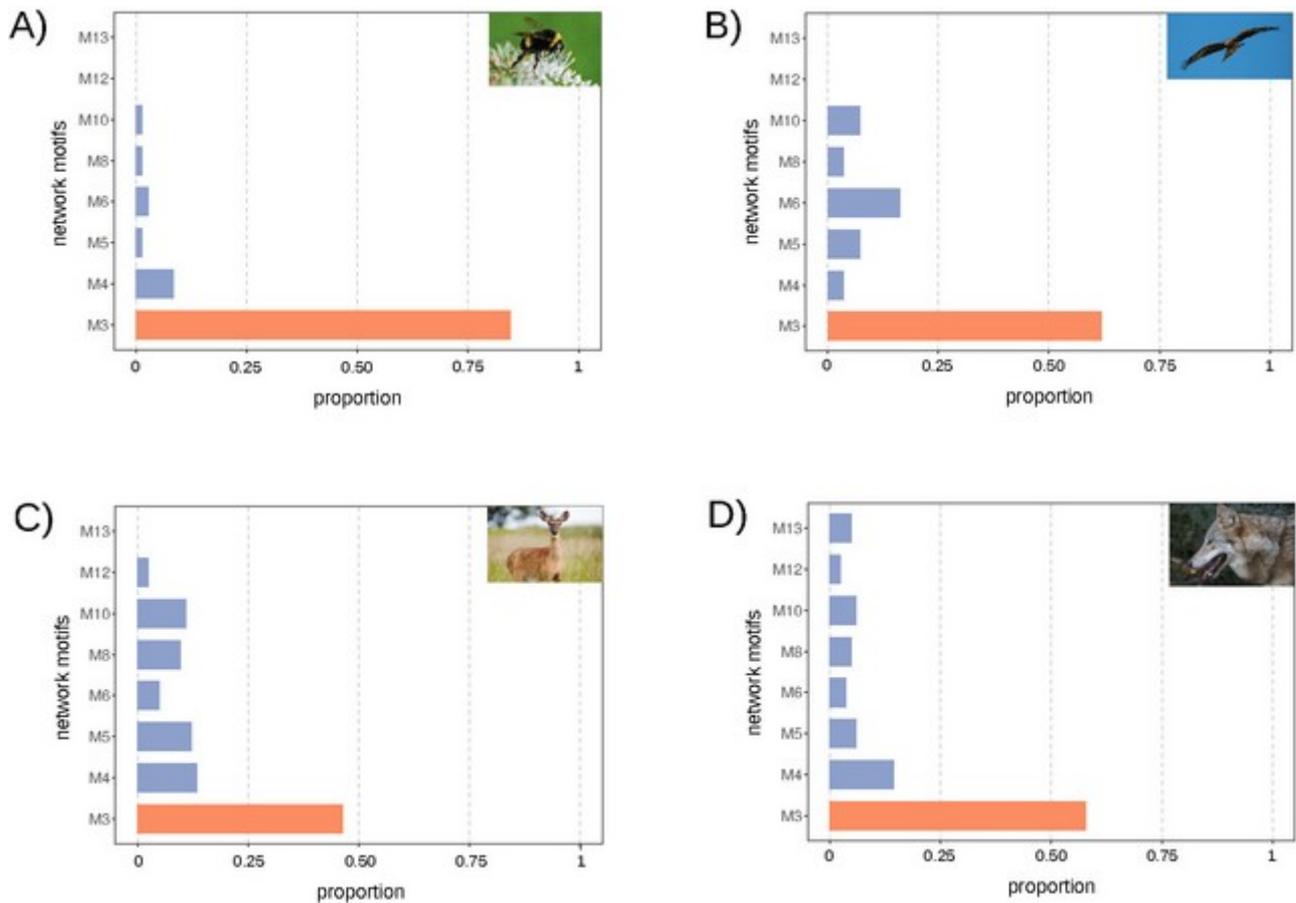


341
342 **FIGURE 4.** Motif time series selection. The Shannon Diversity Index was applied to motif time-series for each dataset:
343 A) bumblebee, B) black kite, C) roe deer, D) wolf. The highest Shannon Diversity Index value, used to select the most
344 suitable motif time series for each dataset, is highlighted in red.

345 346 **3.2 Analysis of behavioural patterns**

347 The proportion of motifs was different across the four datasets (Chi-squared = 56.77, df = 21, p-
348 value < 0.001). The dominant motif was the motif M3 (Fig. 5) that characterises unidirectional
349 movements across three nodes without revisits. This motif has different biological meanings
350 depending on the species under consideration. In the black kite and the roe deer, a succession of M3
351 motifs are characteristic of migratory movements patterns. In the wolf, however, this temporal
352 pattern is characteristic of movements towards familiar locations in a home range, such as hunting
353 areas. In the bumblebee, the succession of M3 motif is indicative of search flights.

354



355

356 **FIGURE 5.** Proportion of network motifs in each dataset. For each species, the proportion of motifs has been divided
 357 into two main categories: a motif describing a unidirectional movement (orange) and seven motifs describing more
 358 complex bidirectional patterns (blue).

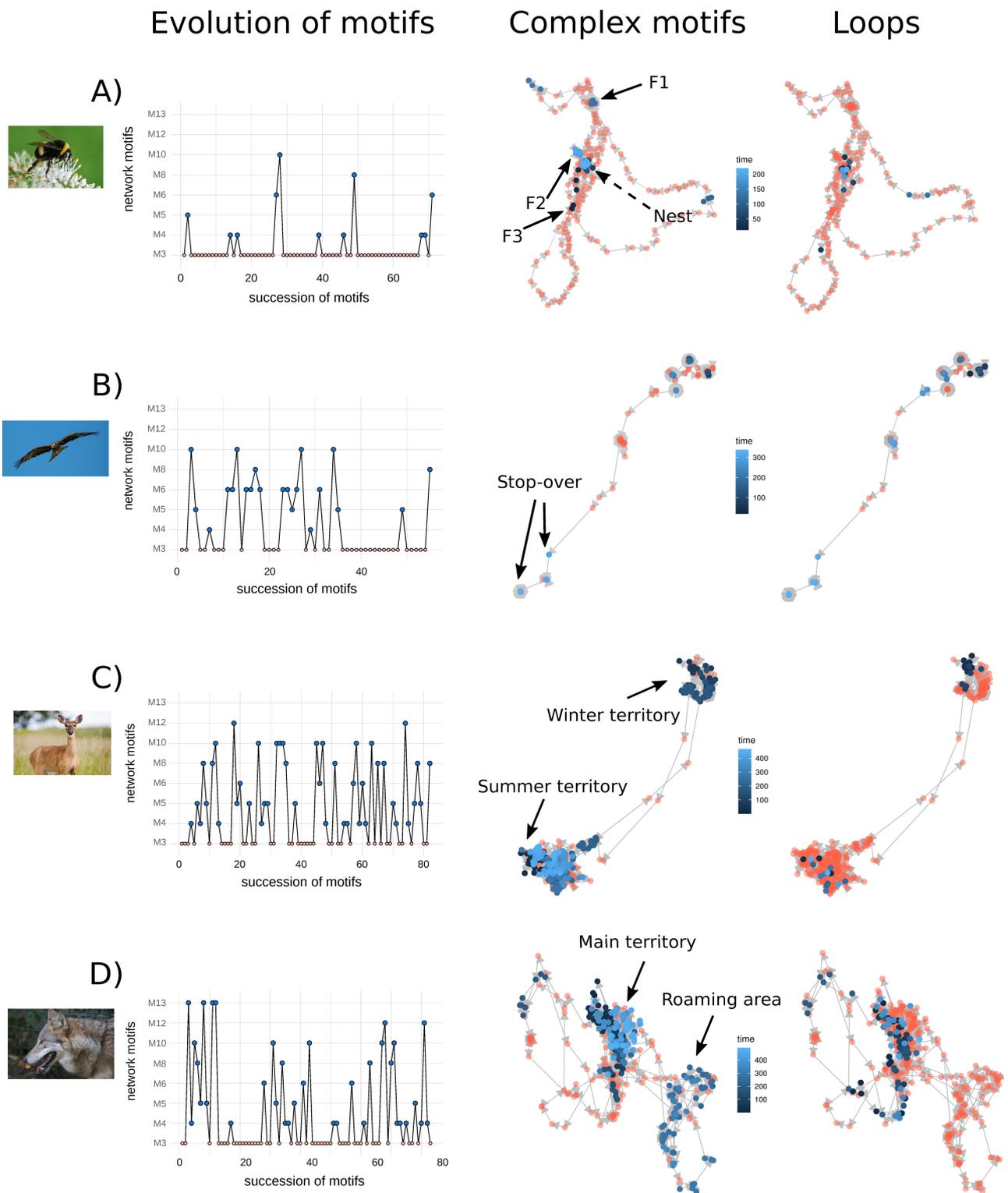
359

360 The seven other motifs characterise bidirectional movements with at least one revisit
 361 to the same node, indicating a temporal re-use of specific areas. The different proportions of such
 362 motifs in the movements may have different biological meanings in the different species and, once
 363 identified, are open to study.

364

365 To further explore and interpret the succession of temporal motifs, we constructed
 366 simplified trajectories highlighting the spatial locations of the simple (unidirectional) motif and the
 367 more complex (bidirectional) motifs in the original data. Because motif analysis does not allow to
 368 include loops (self-edges), we also constructed simplified trajectories highlighting the spatial
 369 locations of each loop (Fig. 6). The number of loops on the same location increased with the
 370 complexity of network motifs indicating that for all four trajectories more complex behavioural
 371 patterns represent areas of temporal interest in animals (GLM for count data - bumblebee: estimate
 372 = 0.243 , SE = 0.058 , z-value = 4.175 , p < 0.001 ; black kite: estimate = 0.203 , SE = 0.025 , z-
 value = 8.252 , p < 0.001 ; roe deer: estimate = 0.122 , SE = 0.019 , z-value = 6.296 , p < 0.001 ;

373 wolf: estimate = 0.275 , SE = 0.014 , z-value = 19.698 , p < 0.001). In the bumblebee trajectory,
374 bidirectional motifs occurred when the individual was in the nest area and near flowers, indicating
375 an association between complex behavioural patterns and familiar locations, while loops tended to
376 be concentrated around the nest only, a behavioural pattern reminiscent of orientation flights
377 (Osborne et al. 2013) (Fig. 6A). In the black kite trajectory, more complex bidirectional motifs
378 occurred in areas around the release point and few locations after the start of the migration and they
379 also correspond to single locations of intensive use (loops; Fig. 6B). In the roe deer trajectory,
380 complex motifs occurred intensely in two different areas while loops gathered around specific
381 smaller areas (Fig. 6C). In the wolf trajectory, complex bidirectional motifs were observed in two
382 spatially differentiated areas, while loops were only observed in one of them (Fig. 6D).
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 386 **FIGURE 6.** Spatio-temporal sequence of behavioural patterns. *Evolution of motifs*: temporal sequence of network
 387 motifs for each dataset. Blue: bidirectional motifs (M4, M5, M6, M8, M12, M13). Red: unidirectional motif (M3).
 388 *Complex motifs*: temporal motifs mapped on original trajectories. Blue gradient encodes the temporal sequence of the
 389 more complex bidirectional motifs. *Loops*: movements starting and ending at the same location mapped on original
 390 trajectories. Blue gradient encodes the temporal sequence of loops. A) Bumblebee data: bidirectional motifs are
 391 observed around the location of the nest and the artificial flowers (F1-F3) while loops are disproportionately observed

392 around the nest location. B) Black kite data: bidirectional motifs are observed before migration and at stopover
 393 locations along the migration route and loop behaviours tend to correspond to those locations. C) Roe deer data:
 394 bidirectional motifs are observed in both winter and summer territories while loops evidence some specific sub-areas of
 395 repeated intensive use. D) Wolf data: bidirectional motifs are observed in two territories (main and roaming areas)
 396 during specific periods of the year as well as some small area of temporary use sparse along the animal path. Loops here
 397 are observed only for the summer territory of the wolf (Kaczensky et al., 2006).

398

399 **Comparison with Brownian and Lévy walks**

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

411

412 **Table 1:** Students t-statistics between distributions of 100 Jaccard indices calculated from the comparison of each
 413 binary non-random motif conditional probabilities with 100 simulated matrices obtained from a Brownian and a Lévy
 414 random movement model. We applied a Bonferroni correction for 6 multiple comparison (new reference $\alpha = 0.008$).

Brownian motion	Lévy walk
Bumblebee – Black kite (t = 5.97 ; p < 0.001)	Bumblebee – Black kite (t = 6.68 ; p < 0.001)
Bumblebee – Roe deer (t = 2.59 ; p = 0.009) ns	Bumblebee – Roe deer (t = 8.97 ; p < 0.001)
Bumblebee – Wolf (t = 9.31 ; p < 0.001)	Bumblebee – Wolf (t = 5.24 ; p < 0.001)
Wolf – Black kite (t = -2.58 ; p = 0.009) ns	Wolf – Black kite (t = -1.14 ; p = 0.255) ns
Roe deer – Black kite (t = 3.75 ; p < 0.001)	Roe deer – Black kite (t = 1.40 ; p = 0.162) ns
Roe deer – Wolf (t = 7.32 ; p < 0.001)	Roe deer – Wolf (t = 2.55 ; p = 0.010) ns

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419 **4. Discussion**

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

426 Our approach builds on the utilisation of movement networks to analyse patterns of
427 space use by animals (Jacoby & Freeman, 2016; Pasquaretta et al., 2017; Bastille-Rousseau et al.,
428 2018). Starting from the proposition of Bastille-Rousseau et al. (2018) to isolate areas of intensive
429 use from static spatial network representations of animal movements, we propose to keep trace of
430 temporal information and create behavioural time series embedded in space. Our method is simple
431 to operate and thus expected to be embraced by a large community of ecologists. First the animal
432 trajectory is transformed into a spatial movement network in which nodes are geographic locations
433 and edges are movements between these locations. Next, the step length distribution of the
434 trajectory is used to calculate multiple movement networks, extract their motif time series and
435 compare them to estimate the optimal grid size providing the most diverse sequence of motifs. This
436 selection is used to objectively determine the most suitable resolution for the spatio-temporal
437 analysis of animal trajectories given the data. The temporal exploration of movement trajectories
438 from four case studies demonstrates that our approach is functional and insightful. The analysis of
439 movement patterns matched very well with our knowledge of the ecological context in which the
440 data were recorded, allowing us to identify simple behavioural patterns associated with search
441 routines and migration (unidirectional motifs), and more complex patterns (bidirectional motifs)
442 correlated with the exploitation of familiar areas (migration sites, home range), revisits to specific
443 locations (nest, flowers), resting phases during migrations (stopovers, sparse area of temporary use).

444 In the bumblebee dataset, complex motifs occurred when the individual was near to
445 biologically relevant locations (nest and flowers). These results are consistent with the well-
446 described observations that bumblebees searching for nectar resources often return to their nest and
447 previously discovered flowers (Lihoreau et al., 2012; Osborne et al., 2013), possibly to explore new
448 areas from known reference spatial locations (Lihoreau et al., 2016). Additionally, the loop analysis
449 revealed a strong tendency of the bumblebee to remain around the nest before flying longer
450 distances. This finding is in accordance with previous works demonstrating that bumblebees use
451 learning flights, in the form of loops around the nest, to learn and memorize the location of the nest

452 in the environment (Osborne et al., 2013). In the black kite dataset, complex movement patterns and
453 loops overlap almost perfectly, which likely indicates the existence of stopover sites along the
454 migratory route of the bird. The spatio-temporal analysis of the roe deer dataset highlighted the
455 existence of two successive migratory events during which similar use of spatially distinct home
456 ranges occurs. Interestingly, loops were concentrated around specific areas which might correspond
457 to areas of core usage (i.e. 50% of the time is spent in these specific areas) of the home range of the
458 animal during both summer and winter season. The wolf dataset presents complex bidirectional
459 motifs across a summer and a winter territory (Kaczensky et al., 2006). Sparse areas of temporary
460 use are also revealed along the trajectory suggesting possible resting areas during the roaming
461 process. In this case, interestingly, loop behaviours were only observed in the summer territory,
462 suggesting the possible existence of valuable resources in this area.

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

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

485 development of a truly comparative movement ecology based on statistics on standard network
486 metrics.

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

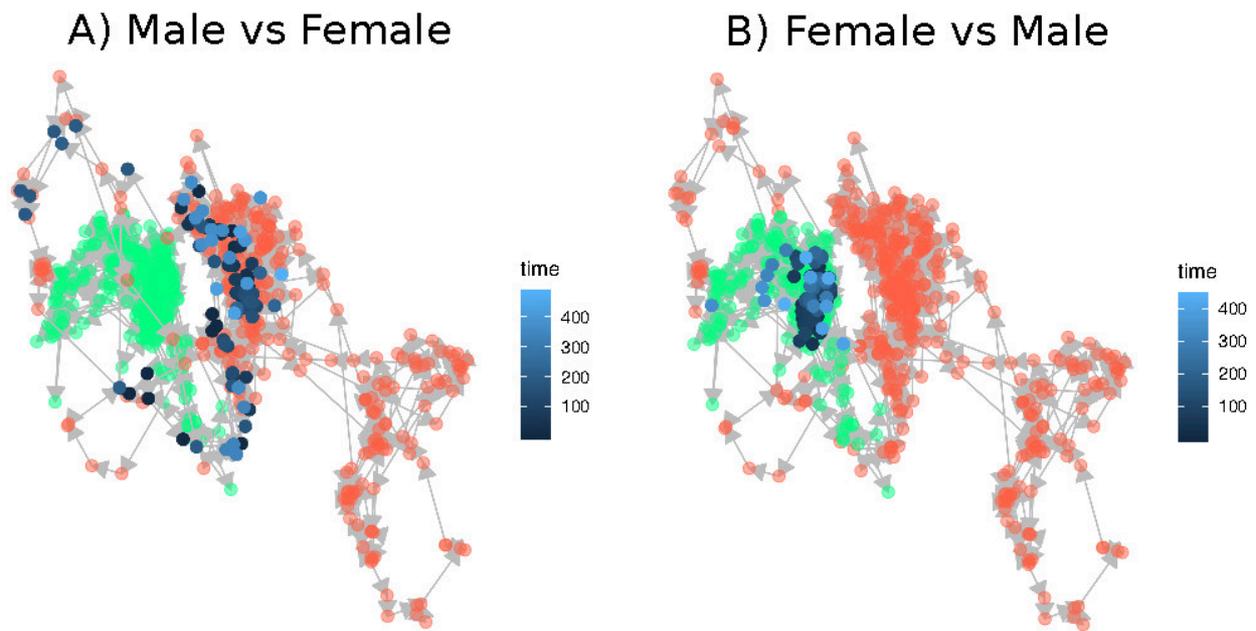
497 Importantly, our method enables to compare the spatio-temporal structure of
498 behavioural patterns to known theoretical movement models. In the future, a functional motif
499 analysis could be implemented to highlight cluster of functional roles (McDonnell et al., 2014).
500 Functional motifs could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

514 As illustrated above, another major advantage of our method is that it is broadly
515 applicable and can suit different types of movement data collected with different technologies
516 (GPS, PTT, harmonic radar), at different spatial scales (local territories, countries) and temporal
517 scales (minutes, years), on animals with different locomotion modes (walking, flying) and in
518 different ecological contexts (exploration, exploitation, migration). In principle, temporal analyses

519 of spatial network can be used to study virtually all type of animal movement data in which
520 individual animals are regularly re-located. If trajectories are incomplete, for instance because the
521 signal of the animal is lost for some period of time, linear interpolation can be used to fill gaps
522 (Strandburg-Peshkin et al., 2015; Strandburg-Peshkin et al., 2017). For any species, however, the
523 main limiting factor is the length of the trajectory (i.e. number of data points). If the trajectory has
524 too few data points, there is a high risk that simplification into a movement network does not
525 provide enough motifs to allow for an insightful exploration of the data.

526 We have shown that network analyses can be used to investigate the temporal
527 dimension of animal movements and get insights into how the animals interact with their ecological
528 environment (exploitation of known resources, migration routes, stopover sites, territories and
529 roaming areas). Since most animals (including those studied here) frequently interact with social
530 partners or competitors, a major challenge for future studies is to analyse the temporal behavioural
531 movement patterns of interacting animals. Important steps have been made to develop new methods
532 to extract social network from animal trajectories and future directions have been pointed towards
533 using social-telemetry data to identify preferred habitats for entire groups (Robitaille Webber &
534 Vander Wal, 2019). Our method can help analyse these data by allowing the characterization of
535 complex behavioural patterns of space use by multiple interacting individuals. For examples, a
536 preliminary analysis of the trajectories of two wolves (male and female) inhabiting the same area of
537 the Mongolia desert shows that the looping behaviours of both animals occur in separate zones.
538 Specifically, the male repeatedly used locations surrounding the female's territory and performed
539 the highest density of loops in an area facing the area where the female exhibited the highest density
540 of loops (blue locations in Fig. 7).

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544 **FIGURE 7:** Spatio-temporal sequence of loops of female and male wolves. A) Male vs Female visualisation. Red:
 545 locations in which the male did no loop. Blue: locations where the male did at least one loop. Green: locations where
 546 the female was observed. B) Female vs male visualisation. Green: locations in which the female did no loop. Blue:
 547 locations where the female did at least one loop. Red: locations where the male was observed. Blue gradient encodes the
 548 temporal sequence of the loops in both graphs. Locations with the same gradient of blue were collected on the same
 549 day.

550

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

564

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571 for comments that have helped improve the manuscript.

572

573 **Authors' contributions**

574 CP and ML conceived the ideas and designed the methodology. CP, TD, TGM, and ML collected
575 the bumblebee data. VP provided the black kite data. CP analysed the data. CP and ML led the
576 writing of the manuscript. All authors contributed critically to the drafts and gave final approval for
577 publication.

578

579 **Data availability**

580 We implemented our method in R. We provide the codes and the bumblebee and black kite datasets
581 in Dryad, DOI:10.5061/dryad.47d7wm390. The roe deer dataset was obtained from MOVEBANK
582 (Wikelski, M., and Kays, R. 2020). Animal Identifier: Sandro (M06), from Cagnacci et al. (2011).
583 The wolf dataset was obtained from MOVEBANK (Wikelski, M., and Kays, R. 2020), Animal
584 identifier: Zimzik, from Kaczensky et al. (2006).

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586 **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(4), 1075-1087.
- 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(11), 1299-1313.
- 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(3), 854-864.

- 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(9), 097901.
- Bovet, P., & Benhamou, S. (1988). Spatial analysis of animals' movements using a correlated random walk model. *Journal of Theoretical Biology*, 131(4), 419-433.
- 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(1550), 2157-2162.
- Cagnacci, F., Focardi, S., Heurich, M., Stache, A., Hewison, A. M., Morellet, N., ... & Delucchi, L. (2011). Partial migration in roe deer: migratory and resident tactics are end points of a behavioural gradient determined by ecological factors. *Oikos*, 120(12), 1790-1802.
- 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(3), 369-379.
- 587 • Dodge, S., Weibel, R., & Lautenschütz, A. K. (2008). Towards a taxonomy of movement
588 patterns. *Information visualization*, 7(3-4), 240-252.
- 589 • Edelhoff, H., Signer, J., & Balkenhol, N. (2016). Path segmentation for beginners: an
590 overview of current methods for detecting changes in animal movement patterns. *Movement
591 ecology*, 4(1), 21.
- 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.
- 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(6391), 911-914.
- 592 • Getz, W. M., & Saltz, D. (2008). A framework for generating and analyzing movement
593 paths on ecological landscapes. *Proceedings of the National Academy of Sciences of the
594 United States of America*, 105(49), 19066-19071.
- Giorgino, T. (2009). Computing and visualizing dynamic time warping alignments in R: the dtw package. *Journal of statistical Software*, 31(7), 1-24.
- 595 • Gobbi A, Iorio F, Albanese D, Jurman G, Saez-Rodriguez J (2017). `_BiRewire`: High-
596 performing routines for the randomization of a bipartite graph (or a binary event matrix),

- 597 undirected and directed signed graph preserving degree distribution (or marginal totals)_. R
598 package version 3.18.0
- Gurarie, E., Andrews, R. D., & Laidre, K. L. (2009). A novel method for identifying behavioural changes in animal movement data. *Ecology letters*, *12*(5), 395-408.
 - Jacoby, D. M., & Freeman, R. (2016). Emerging network-based tools in movement ecology. *Trends in Ecology & Evolution*, *31*(4), 301-314.
 - Janmaat, K. R., Byrne, R. W., & Zuberbühler, K. (2006). Evidence for a spatial memory of fruiting states of rainforest trees in wild mangabeys. *Animal Behaviour*, *72*(4), 797-807.
 - Juszczyszyn K. (2014). Motif Analysis. In: Alhajj R., Rokne J. (eds) Encyclopedia of Social Network Analysis and Mining. Springer, New York, NY
 - 599 • Kaczensky, P., Ganbaatar, O., Enksaikhaan, N. and Walzer, C. (2006). Wolves in Great
600 Gobi B SPAGPS tracking study 2003-2005 dataset. Movebank Data Repository
601 (www.movebank.org).
 - Kembro, J. M., Lihoreau, M., Garriga, J., Raposo, E. P., & Bartumeus, F. (2019). Bumblebees learn foraging routes through exploitation–exploration cycles. *Journal of the Royal Society Interface*, *16*(156), 20190103.
 - Lihoreau, M., Chittka, L., & Raine, N. E. (2010). Travel optimization by foraging bumblebees through readjustments of traplines after discovery of new feeding locations. *The American Naturalist*, *176*(6), 744-757.
 - 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*(9), e1001392.
 - 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.
 - McDonnell, M. D., Yaverovlu, Ö. N., Schmerl, B. A., Iannella, N., & Ward, L. M. (2014). Motif-role-fingerprints: the building-blocks of motifs, clustering-coefficients and transivities in directed networks. *PloS one*, *9*(12), e114503.
 - Milner-Gulland, E. J., Fryxell, J. M., & Sinclair, A. R. (Eds.). (2011). *Animal migration: a synthesis*. Oxford University Press.
 - 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 Networks and their Applications* (pp. 453-462). Springer, Cham.
- 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 (2018-03-15).
- 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*(11), e78681.
- Paranjape, A., Benson, A. R., & Leskovec, J. (2017). Motifs in temporal networks. In Proc. 10th ACM International Conference on Web Search and Data Mining 601–610
- 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.
- 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.
- Patel, P., Keogh, E., Lin, J., & Lonardi, S. (2002, December). Mining motifs in massive time series databases. In *2002 IEEE International Conference on Data Mining, 2002. Proceedings.* (pp. 370-377). IEEE.
- 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.
- 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*(5), 1506-1518.
- 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*(10), 2091-2101.
- R Core Team (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.

602
603

- 604 • Reynolds, A. M., Smith, A. D., Reynolds, D. R., Carreck, N. L., & Osborne, J. L. (2007).
605 Honeybees perform optimal scale-free searching flights when attempting to locate a food
606 source. *Journal of Experimental Biology*, 210(21), 3763-3770.
- 607 • Reynolds, A. M. (2008). Optimal random Lévy-loop searching: New insights into the
608 searching behaviours of central-place foragers. *EPL (Europhysics Letters)*, 82(2), 20001.
- 609 • Reynolds, A. M. (2018). Current status and future directions of Lévy walk research. *Biology
610 open*, 7(1), bio030106.
- 611 • Rice, W. R. (1989). Analyzing tables of statistical tests. *Evolution*, 43(1), 223-225.
- 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.
- Robitaille, A. L., Webber, Q. M., & Vander Wal, E. (2019). Conducting social network
analysis with animal telemetry data: applications and methods using spatso. *Methods in
Ecology and Evolution*, 10 (8), 1203–1211.
- 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.
- 612 • Schick, R. S., Loarie, S. R., Colchero, F., Best, B. D., Boustany, A., Conde, D. A., ... &
613 Clark, J. S. (2008). Understanding movement data and movement processes: current and
614 emerging directions. *Ecology Letters*, 11(12), 1338-1350.
- Shannon, C. E. (1948). A mathematical theory of communication. *Bell system technical
journal*, 27(3), 379-423.
- 615 • Shlesinger, M. F., & Klafter, J. (1986). Lévy walks versus Lévy flights. In *On growth and
616 form* (pp. 279-283). Springer, Dordrecht.
- 617 • Silk, M. J., Finn, K. R., Porter, M. A., & Pinter-Wollman, N. (2018). Can multilayer
618 networks advance animal behavior research?. *Trends in Ecology & Evolution*, 33(6), 376-
619 378.
- Strandburg-Peshkin, A., Farine, D. R., Couzin, I. D., & Crofoot, M. C. (2015). Shared
decision-making drives collective movement in wild baboons. *Science*, 348(6241), 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.

- Swingland, I. R., & Greenwood, P. J. (1983). *Ecology of animal movement*. Clarendon Press. Oxford. pp. 7-31
- 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.
- 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(1550), 2163-2176.
- 620 • Turchin, P. (1998). *Quantitative analysis of movement*. Sinauer Associates, Inc. Publishers,
621 Sunderland, MA, USA.
- 622 • Vallaeys, V., Tyson, R. C., Lane, W. D., Deleersnijder, E., & Hanert, E. (2017). A Lévy-
623 flight diffusion model to predict transgenic pollen dispersal. *Journal of the Royal Society*
624 *Interface*, 14(126), 20160889.
- Van Moorter, B., Visscher, D., Benhamou, S., Börger, L., Boyce, M. S., & Gaillard, J. M. (2009). Memory keeps you at home: a mechanistic model for home range emergence. *Oikos*, 118(5), 641-652.
- 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(10), e01498.
- 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(6581), 413.
- Wasserman, S., & Faust, K. (1994). *Social network analysis: Methods and applications* (Vol. 8). Cambridge university press.
- Wikelski, M., & Kays, R. (2020). Movebank: archive, analysis and sharing of animal movement data. World Wide Web electronic publication. <http://www.movebank.org>, accessed on July 2019.
- 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*, 105(49), 19108-19113.
- Woodgate, J. L., Makinson, J. C., Lim, K. S., Reynolds, A. M., & Chittka, L. (2017). Continuous radar tracking illustrates the development of multi-destination routes of bumblebees. *Scientific reports*, 7(1), 17323.