Extending {spatsoc} to measure intragroup social dynamics

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1 Abstract

1. Beyond proximity-based social networks and home range overlap, animal telemetry data can also be used to measure intragroup social dynamics including individual position within groups, individual and group level movement directions, leadership patterns and lagged follower behaviours.
2. We used a scoping review of literature across domains, including behavioural ecology, collective movement, and GISciences, to identify widely used metrics for measuring intragroup social dynamics that are not openly available in the R programming language.
3. We present a case study illustrating 18 new functions for the R package {spatsoc} measuring intragroup social dynamics with animal telemetry data.
4. The open availability of these new and flexible functions in {spatsoc} will allow researchers to easily measure intragroup social dynamics to more comprehensively measure the multifaceted animal social behaviours in their study systems.

2 Introduction

The R package {spatsoc} was developed to derive social networks from animal telemetry data using aggregated association rates, interindividual distances, and home range overlap (Robitaille et al., 2019). The methods in {spatsoc} have been used to measure social cohesion (Bracken et al., 2022), human-wildlife conflict (Boudreau et al., 2022), socioecology and resource availability

(Peignier et al., 2019), community structure (Sunga et al., 2021), the influence of stress on social proximity (Keshavarzi et al., 2023), and social patterns in non-social species (Heeres et al., 2024). Despite the substantive and varied applications of {spatsoc}, users lacked sufficient and accessible functionality for measuring the behaviour of individuals within social groups.

Many facets of group living need to be considered to better measure animal social systems (King et al., 2018). Beyond associations, there are additional types of dyadic relationships including genetic, affiliative, agonistic, and cooperative (Farine & Whitehead, 2015). There are also interactions between spatial phenotypes, social phenotypes, and environments (Webber et al., 2023). Using direct observations, researchers have studied intragroup social dynamics including social foraging (Barnard & Sibly, 1981; Giraldeau & Lefebvre, 1986; Hirsch et al., 2020), spatial position within groups (Krause, 1994; Mónus & Barta, 2008) and the influence of individual traits such as age, sex, and dominance (Furuichi, 1983; King & Cowlishaw, 2009; Teichroeb et al., 2015). Unfortunately, direct observations can be labour-intensive to collect and susceptible to observer bias (Smith & Pinter-Wollman, 2021), with low spatial and temporal resolution making them imperfect for studies of collective movement (King et al., 2018).

Pairing advanced remote tracking technologies with emerging methods expand opportunities to measure intragroup social dynamics. The availability and resolution of remote tracking data continues to improve (Kays et al., 2015; Kays et al., 2022; Nathan et al., 2022). There are over two decades of research on measuring interactions between moving individuals from the study of "moving point objects" in GISciences (Andersson et al., 2008; Dodge et al., 2008; Laube, 2005; Miller, 2021) to group coordination (Couzin et al., 2002; Herbert-Read et al., 2011), leadership, and decision making (King & Sueur, 2011; Nagy et al., 2010; Strandburg-Peshkin et al., 2015). Despite this, we suggest the lack of availability of open source tools (Hampton et al., 2015; Powers & Hampton, 2019; Wilson et al., 2017) is the missing piece between the call to integrate technology enhanced research with multidisciplinary approaches to better study animal social systems (Couzin & Heins, 2023; King et al., 2018).

We first conducted a scoping review to identify metrics that were applicable to spatiotemporal data, and focused on dyadic interactions, leadership patterns, and dominance hierarchies. Of the resulting metrics, we selected those with a high evidence of use, and lack of availability in the R programming language, either through R packages or supplemental materials in the literature. Here we present 18 new functions in the R package {spatsoc} (Robitaille et al., 2019) for measuring intragroup dynamics (Table 1). We will demonstrate these new functions through a case study and discuss biological interpretations.

3 Methods

We conducted a scoping review to identify metrics for measuring intragroup social dynamics including dyadic interactions, leadership patterns, and dominance hierarchies. We focused on metrics applicable to spatiotemporal data such as animal movement data. This scoping review expands on the review conducted by Joo et al. (2018) by using interdisciplinary sources (e.g. Miller (2021)), including metrics measuring group-level dynamics, leadership patterns, and lagged-follower behaviours, and by focusing on the open source availability of these metrics in the R programming language. See details scoping review methods in Supplement Section 9. and Metrics were selected for inclusion in {spatsoc} based on their relative importance as measured by frequency of use in the review, and their lack of availability in R packages when the review was conducted (Supplement Section 10). Some metrics were specifically not chosen for inclusion such as metrics relating to posture, metrics relating to static interaction or home range overlap and metrics based on statistical models such as Hidden Markov model and Granger causality. A full list of metrics not selected is in Supplement Section 11.

Table 1: Description of new functions in the R package {spatsoc} for measuring intragroup dynamics categorized by family. All avilable functions in the R package {spatsoc} including new and existing functions are listed in Table 15.

Function	Description
Spatial interface	

Function	Description
get_geometry()	Setup data for geometry interface
Edge-list generation	
edge_delay()	Directional correlation delay based edge-lists
edge_alignment()	Directional alignment based edge-lists
edge_direction()	Direction based edge-lists
edge_zones()	Behavioural zones based edge-lists
Dyad	
fusion_id()	Identify fusion events
Centroid	
centroid_group()	Group centroid
centroid_dyad()	Dyad centroid
centroid_fusion()	Fusion event centroid
Direction	
direction_step()	Direction step
direction_to_centroid()	Direction to group centroid
direction_to_leader()	Direction to group leader
direction_group()	Group mean direction
direction_polarization()	Polarization
Distance	
distance_to_centroid()	Distance to group centroid
distance_to_leader()	Distance to group leader
Leadership	
leader_direction_group()	Leadership along group direction
leader_edge_delay()	Leadership in directional correlation delay

4 Case study

Functions previously available in {spatsoc} can be used to identify spatiotemporal grouping, generate distance based edge-lists and conduct data-stream permutations (see existing functionality in Robitaille et al. (2019); Table S 15). These functions have allowed users to detect interactions between individuals, measure co-occurrence within and across species, and generate social networks from animal telemetry data (e.g. Albery et al., 2025; Bracken et al., 2022; Heeres et al., 2024; Merkle et al., 2024).

Spatiotemporal grouping can be performed given animal movement data, temporal and spatial thresholds, and one of three grouping functions: `group_pts()`, `group_lines()` or `group_polys()`. These return a unique identifier for each spatiotemporal group defined by point-based distances, linear trajectory overlap and home range overlap, respectively.

`get_geometry()` is a new helper function added to {spatsoc} to provide an alternative interface for providing coordinates and, optionally, coordinate reference system. Instead of providing the names to columns for the X and Y coordinates using the `coords` argument, the `get_geometry()` function adds a simple feature geometry list column (`sfc`) using the {sf} package (Pebesma, 2018). The geometry method is used by default for all {spatsoc} functions that require coordinates when the `coords` argument is left null. This interface also extends {spatsoc} to allow users to provide coordinates in any of the many coordinate reference systems, both projected and longlat degrees, that the {sf} package supports. The following examples and case study will illustrate the geometry interface throughout.

For example, the suggested `group_pts()` workflow with the example data from the package and the `get_geometry()` helper function to identify spatiotemporal groups (Table 2):

```
# Load packages
library(data.table)
library(spatsoc)
```

```r
# Read example data
DT <- fread(system.file("extdata", "DT.csv", package = "spatsoc"))

# Cast the character column to POSIXct
DT[, datetime := as.POSIXct(datetime, tz = 'UTC')]

# Set variables
temporal_threshold <- '20 minutes'
spatial_threshold <- 50
id <- 'ID'
coords <- c('X', 'Y')
utm <- 32736

# Setup DT for geometry interface
get_geometry(DT, coords = coords, crs = utm)

# Temporal grouping
group_times(DT, datetime = 'datetime', threshold = temporal_threshold)

# Spatial grouping with timegroup
group_pts(
  DT,
  threshold = spatial_threshold,
  id = id,
  coords = coords,
  timegroup = 'timegroup'
)
```

Table 2: Spatiotemporal groups measured using group_times() and group_pts(). group_times() returns a 'timegroup' column indicating temporal groups within the specified temporal threshold. group_pts() returns a 'group' column indicating spatiotemporal groups within the provided timegroup and specific distance threshold. Example output showing a subset of three spatiotemporal groups.

ID	datetime	geometry	timegroup	group
A	2016-11-16 18:01:54	POINT (705065.4 5506570)	190	190
C	2016-11-16 18:00:20	POINT (705070.8 5506511)	190	190
I	2016-11-16 18:00:41	POINT (705060.9 5506554)	190	190
E	2016-11-24 08:00:41	POINT (706785.9 5507420)	281	5355
H	2016-11-24 08:00:15	POINT (706789.2 5507414)	281	5355
B	2016-11-26 18:00:54	POINT (698209.9 5510867)	310	1706

Users can also measure interindividual distance using the `edge_dist()` function (Table 3) and identify nearest neighbours using `edge_nn()` function (Table 4). For example:

```
# Measure interindividual distance
interindividual_dist <- edge_dist(
  DT,
  threshold = spatial_threshold,
  id = id,
  timegroup = 'timegroup',
  returnDist = TRUE,
  fillNA = TRUE
)
```

Table 3: Distance based edge-lists measured using edge_dist(). Using the 'timegroup' column returned by group_times(), edge_dist() returns a distance based edge-list where individuals in the column 'ID1' are within the provided distance threshold from 'ID2'. Optionally, measured

distances can be returned in the column 'distance' if 'returnDist' is TRUE and NAs can be returned where an individual is not within the provided distance threshold if 'fillNA' is TRUE. Example output showing six observations of one timegroup with distances returned between focal individual 'ID1' and neighbour 'ID2'.

timegroup	ID1	ID2	distance
1424	B	E	44.67190
1424	B	G	27.13466
1424	D	NA	NA
1424	E	B	44.67190
1424	E	G	20.52638
1424	F	I	43.92168

```r
# Identify nearest neighbours
nearest_neighbours <- edge_nn(
  DT,
  id = id,
  timegroup = 'timegroup',
  returnDist = TRUE
)
```

Table 4: Distance based edge-lists measured using edge_nn(). Using the 'timegroup' column returned by group_times(), edge_nn() returns a distance based edge-list where individuals in the column 'NN' are the nearest neighbour to focal individuals in the column 'ID'. Optionally, measured distances can be returned in the column 'distance' if 'returnDist' is TRUE and a distance threshold can be provided using 'threshold'. Example output showing six observations of one timegroup with distances returned between focal individual 'ID' and nearest neighbour 'NN'.

timegroup	ID	NN	distance
1439	E	B	43.847993

timegroup	ID	NN	distance
1439	G	B	41.725396
1439	F	C	129.538328
1439	I	C	60.931938
1439	B	G	41.725396
1439	J	H	4.898148

Building on these, {spatsoc}'s new functions provide a more detailed measuring of an individual's behaviour with respect to their conspecifics. We aim to provide users with accessible, flexible functions that will help to identify leader-follower patterns, fission fusion dynamics and potentially dominance behaviours from animal telemetry data in their ecological systems.

4.1 Position within groups

Extending {spatsoc}'s abilities to identify spatiotemporal groups, a new set of functions are now available to measure individuals position relative within spatiotemporal groups. After identifying spatiotemporal groups with e.g. `group_pts()`, we can measure the group centroid, as defined by the mean of individual locations in a group, using `centroid_group()` (Table 5).

```
# Measure group centroids
centroid_group(DT)
```

Table 5: Group centroids measured using centroid_group(). Using the 'group' column returned by group_pts(), centroid_group() returns the column 'centroid' representing the centroid of all individual's locations in each spatiotemporal group. Example output showing a subset of the centroids for three spatiotemporal groups.

ID	timegroup	group	geometry	centroid
B	177	1573	POINT (700463.1 5507780)	POINT (700457.4 5507773)
G	177	1573	POINT (700451.8 5507767)	POINT (700457.4 5507773)

ID	timegroup	group	geometry	centroid
B	816	2212	POINT (697575.8 5511491)	POINT (697578.6 5511484)
G	816	2212	POINT (697581.4 5511477)	POINT (697578.6 5511484)
A	1280	1280	POINT (705981.4 5510214)	POINT (705991.2 5510219)
C	1280	1280	POINT (705985.9 5510213)	POINT (705991.2 5510219)

Then we can measure each individual's distance and direction to the group centroid using `distance_to_centroid()` and `direction_to_centroid()` (Figure 1). The distance to group centroid is the geographic distance from the focal individual to the group centroid. The direction to group centroid is the direction from the focal individual to the group centroid. The rank of individual's distances to the group centroid can be optionally returned using the argument `return_rank`. Spatial position within groups with respect to the group centroid has been studied in relation to predation risk (Heesen et al., 2015; Herbert-Read et al., 2017), leadership (Jolles et al., 2017; Kano et al., 2021) and group cohesion (Bracken et al., 2022; Harel et al., 2021).

```
# Measure distance to group centroid
distance_to_centroid(DT, return_rank = TRUE)

# Measure direction to group centroid
direction_to_centroid(DT)
```

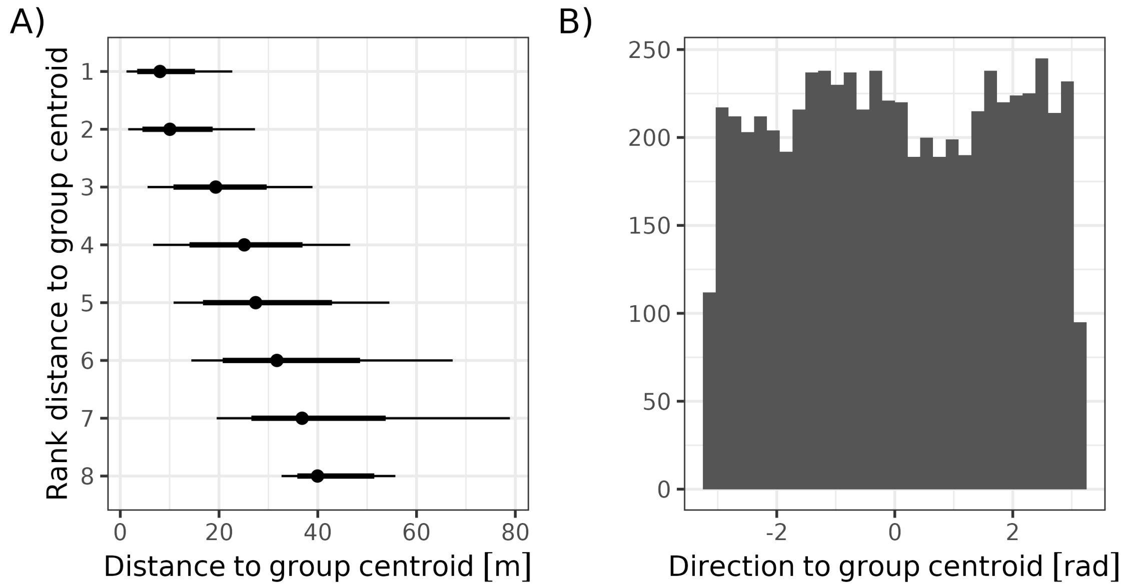


Figure 1: A) Distance and B) direction to group centroids measured using distance_to_centroid() and direction_to_centroid(). Using the ‘centroid’ column returned by centroid_group, distance_to_centroid() and direction_to_centroid() return the columns ‘distance_centroid’ and ‘direction_centroid’ representing the focal individual’s distance and direction to the group centroid. Optionally, the rank distance to the group centroid can be returned by distance_to_centroid() if ‘return_rank’ is true.

4.2 Directions

Next, we can use movement directions to measure how individuals and groups move together. We can measure an individual’s movement direction using `direction_step()` and the mean direction of each spatiotemporal group identified by `group_pts()` using `direction_group()` (Table 6).

```
# Measure movement direction
direction_step(DT, id = id)

# Measure mean movement direction of each spatiotemporal group
direction_group(DT)
```

Table 6: Individual and group mean directions measured using direction_step() and direction_group(). direction_step() returns the column 'direction' representing the movement direction of each individual to their next relocation. Using the spatiotemporal groups returned by group_pts, direction_group() returns the column 'group_direction' representing the mean direction of all individuals in each spatiotemporal group. Example output showing the movement directions of individuals and mean direction of two spatiotemporal groups.

ID	timegroup	group	direction	group_direction
B	1250	2597	−1.169144 [rad]	−1.240766 [rad]
E	1250	2597	−1.309294 [rad]	−1.240766 [rad]
J	1250	2597	−1.243852 [rad]	−1.240766 [rad]
C	1351	1351	3.006553 [rad]	2.682635 [rad]
F	1351	1351	3.005972 [rad]	2.682635 [rad]
I	1351	1351	1.381470 [rad]	2.682635 [rad]

We can measure polarization, the uniformity of movement directions in a group of individuals, using `direction_polarization()` (Figure 2). Polarization is represented on a scale of 0-1 where values near 0 indicate that individuals in a group are moving in completely different directions (or "non-aligned") and values near 1 indicate that individuals are moving in similar directions or ("aligned"). Polarization in the movement direction of groups of animals has been used to study cognition (Wang et al., 2022), learning (Vega-Trejo et al., 2020), the influence of habitat (Strandburg-Peshkin et al., 2017) and individual differences (Jolles et al., 2017) in collective behaviour.

```
# Measure direction polarization
direction_polarization(DT)
```

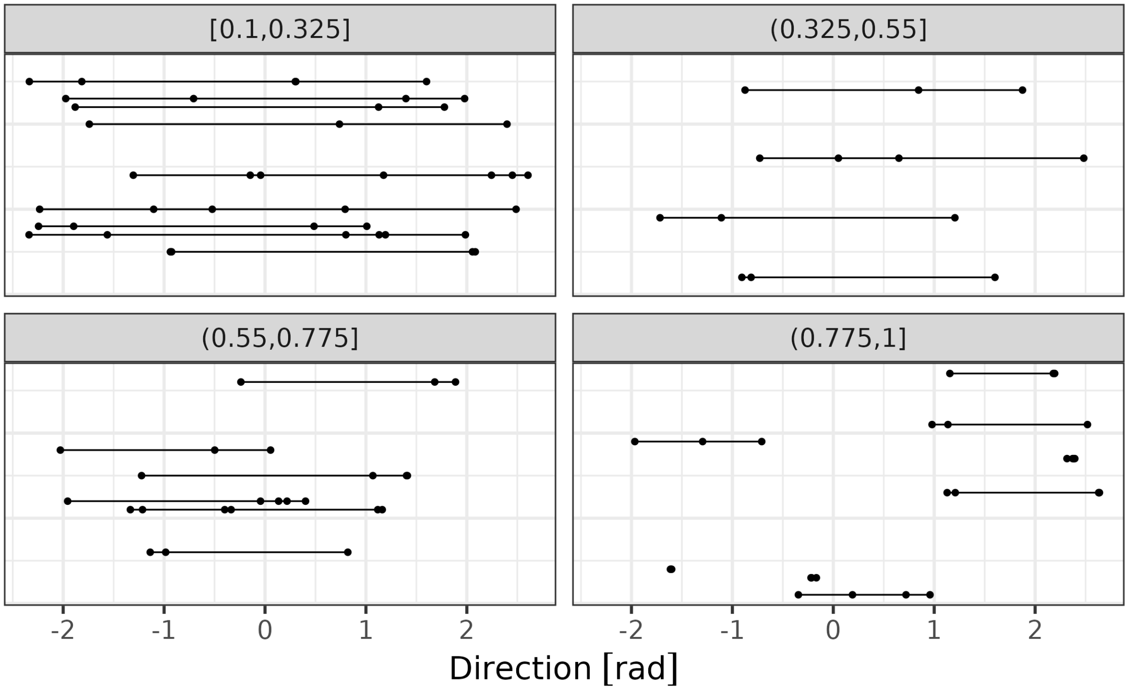


Figure 2: Direction polarization measured using direction_polarization(). Using the 'direction' column returned by direction_step() and 'group' column returned by group_pts(), direction_polarization() returns a column named 'polarization' indicating the polarization in directions in each spatiotemporal group. Ranges of directions shown for a sample of groups in four equal interval categories of direction polarization. Values of polarization range from 0 (non-alignment) to 1 (alignment).

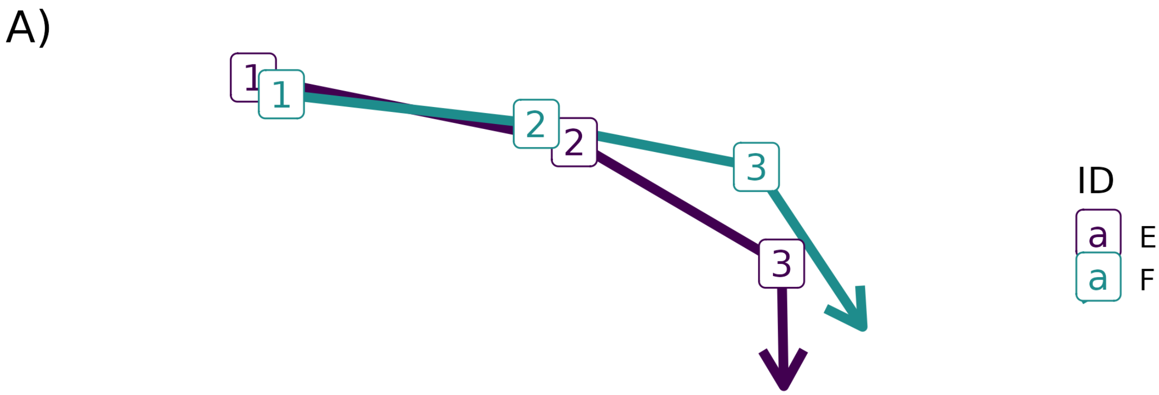
The interindividual direction, or direction from a focal individual to a neighbour, can be measured using `edge_direction()` (Figure 3). Like `edge_alignment()`, the interindividual directions are returned by in an edge-list format. Interindividual direction has been used to study risk exposure in schooling fish (Lemasson et al., 2014), coordinated movement (Herbert-Read, 2016) and mass migration (Torney et al., 2018).

```
# Measure interindividual direction
dyad_directions <- edge_direction(
  edges = interindividual_dist,
```

```
  DT = DT,
  id = id
)
```

The directional alignment, or relative difference between two individuals' directions, can be measured using `edge_alignment()` (Figure 3). The differences in movement directions are returned in an edge-list format similar to `edge_dist()` and other edge-list generating functions. Directional alignment has been used to study leadership (Šárová et al., 2010), decision making (Strandburg-Peshkin et al., 2015), and information transfer (Sumpter et al., 2018).

```
# Measure directional alignment
directional_align <- edge_alignment(
  DT = DT,
  id = id,
  signed = FALSE
)
```



B)

timegroup	ID1	ID2	direction_dyad	direction_diff
1	F	E	-1.06 [rad]	0.08 [rad]
1	E	F	2.08 [rad]	0.08 [rad]
2	F	E	1.99 [rad]	0.34 [rad]
2	E	F	-1.15 [rad]	0.34 [rad]
3	F	E	2.86 [rad]	0.57 [rad]
3	E	F	-0.28 [rad]	0.57 [rad]

Figure 3: A) Example locations for individuals 'E' (purple) and 'F' (blue) showing concurrent movement paths in timegroups 1, 2 and 3. B) Interindividual direction and directional_alignment() using edge_direction() and edge_alignment(). Using distance based edge-lists returned by edge_dist() or edge_nn() and the 'timegroup' column returned by group_times(), edge_direction() returns a column named 'direction_dyad' representing the direction between the focal individual ('ID1') and the neighbouring individual ('ID2'). Using the 'direction' column returned by direction_step(), the edge_alignment() function returns a column named 'direction_diff' representing the absolute different in movement directions between two individuals ('ID1' and 'ID2'). Optionally, the signed difference can be returned by edge_alignment() if the argument 'signed' is true.

4.3 Behavioural zones

The behavioural zones (Couzin et al., 2002), or non-overlapping behavioural regions around a focal individual, can measured using `edge_zones()` (Figure 4). The distance from the focal individual to each neighbour is used to assign the neighbours to behavioural zones. In addition, the direction from the focal individual to each neighbour can be used to determine if the neighbour is within a "blind volume" outside of the individual's visual perception. Couzin et al. (2002) defined three non-overlapping zones. The "zone of repulsion" is at a minimum distance around the focal individual within which neighbours are expected to move away to avoid collisions. The "zone of orientation" is around the focal individual beyond the "zone of repulsion" within which neighbours are expected to orient themselves to the movement of their neighbours. The "zone of attraction" is beyond the "zone of orientation" where neighbours are expected to be attracted to the position of the focal individual. The `edge_zones()` function is designed to allow for flexible definitions of zones including distance thresholds, zone labels and blind volume thresholds. The behavioural zones metric has been used to study the impact of individual movement speed and predator evasion (Klamser & Romanczuk, 2021) and identifying rules of interaction in large animal groups (Lukeman et al., 2010).

```r
# Define zone thresholds, labels and blind volume
zone_thresholds <- c(10, 25, 50)
zone_labels <- c('repulsion', 'orientation', 'attraction')
blind_volume <- 3

# Measure behavioural zones
zones <- edge_zones(
  dyad_directions,
  zone_thresholds = zone_thresholds,
  zone_labels = zone_labels,
  blind_volume = blind_volume
)
```

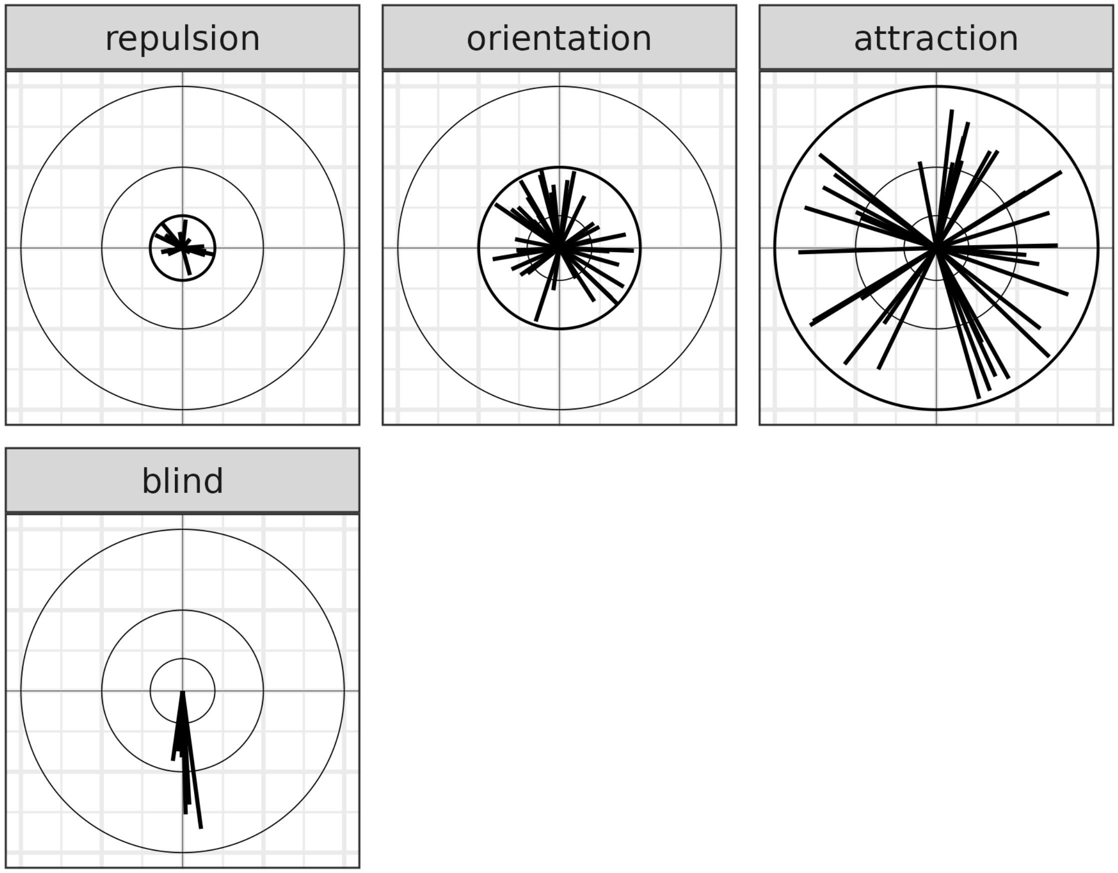


Figure 4: Behavioural zones measured using edge_zones(). Using the 'distance' column returned by edge_dist(), the edge_zones() function returns the column 'zone' representing the behavioural zone of the neighbour (ID2) with respect to the focal individual (ID1). Optionally, the 'direction_dyad' column returned by edge_direction() can be used to define the blind volume, or the range of interindividual directions that are beyond the visual perception of the focal individual. Example shows positions of neighbour 'E' in behavioural zones with respect to focal individual 'G' across the sample period.

4.4 Position relative to leader

After considering how individuals are positioned relative to the group centroid, we can also measure how individuals are positioned relative to the mean group direction. To do so, we first calculate each individual's movement direction with `direction_step()` and the group's mean direction with `direction_group()`. Then `leader_direction_group()` rotates the coordinate system around the group centroid by the group's mean direction. The distance along this new axis is the measure of front-back position of an individual within the group (Andrienko et al., 2013; Harel et al., 2021; Quera et al., 2023) (Figure 5). The rank of individual positions within spatiotemporal groups (Burns et al., 2012) can be optionally returned when the argument 'return_rank' is true.

```r
# Measure movement direction
direction_step(DT, id = id)

# Measure mean movement direction of each spatiotemporal group
direction_group(DT)

# Measure position relative to leader
leader_direction_group(DT, return_rank = TRUE)
```

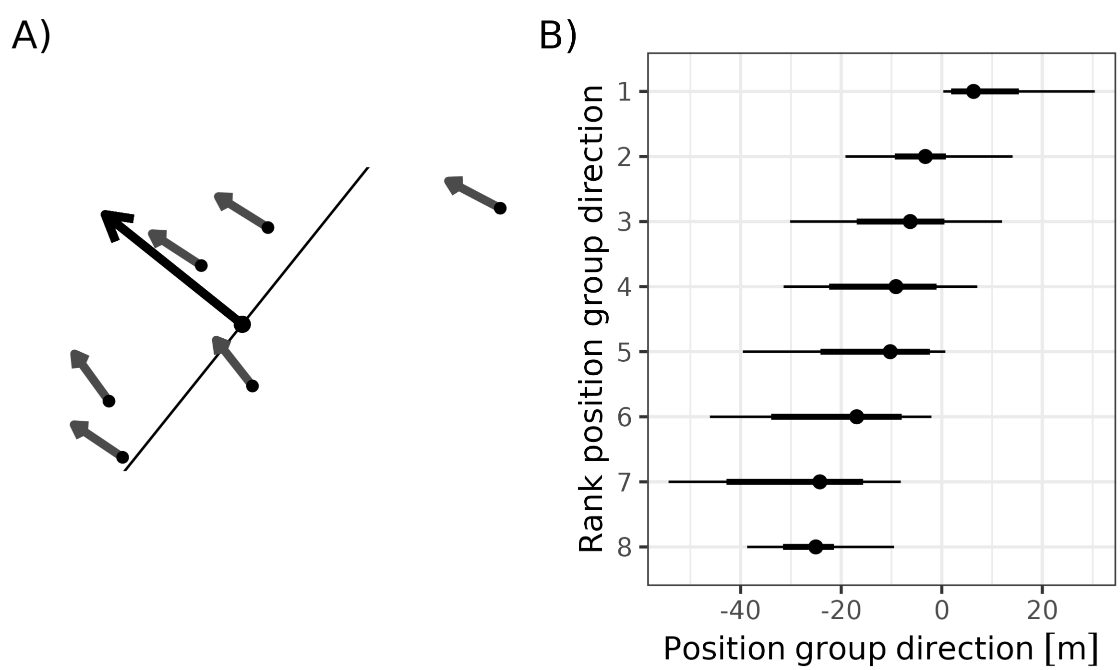


Figure 5: A) Example spatiotemporal group showing relative positions and movement directions of individuals (small points and grey arrows) with respect to the group centroid and mean group direction (large point and black arrow). B) Position along the group direction measured using leader_direction_group(). Using the 'direction' column returned by direction_step(), 'group_direction' column returned by direction_group() and 'centroid' column returned by centroid_group(), leader_direction_group() returns a column named 'position_group_direction' representing the front-back position along the mean group direction. Optionally, the rank position along the mean group direction if 'return_rank' is true.

Taking this simple, dynamic definition of leadership, we can identify the distance and direction of individuals to the leader of each spatiotemporal group using `distance_to_leader()` and `direction_to_leader()` (Figure 6). The distance to leader is the geographic distance from the focal individual to the group's leader and the direction to leader is the direction from the focal individual to the group's leader. The front-back position within the group, and distance and direction to the group leader has been used to study interaction rules (Weesner et al., 2023), leadership (Quera et al., 2023; Šárová et al., 2010), risk avoidance (Josephs et al., 2016), and how reproduction influences social structure (Pérez-Barbería & Walker, 2018). In addition, a user can calculate an individual's time spent leading by calculating the rate each individual was in the first ranked position out of the total observations.

```
# Measure distance to leader
distance_to_leader(DT)

# Measure direction to leader
direction_to_leader(DT)
```

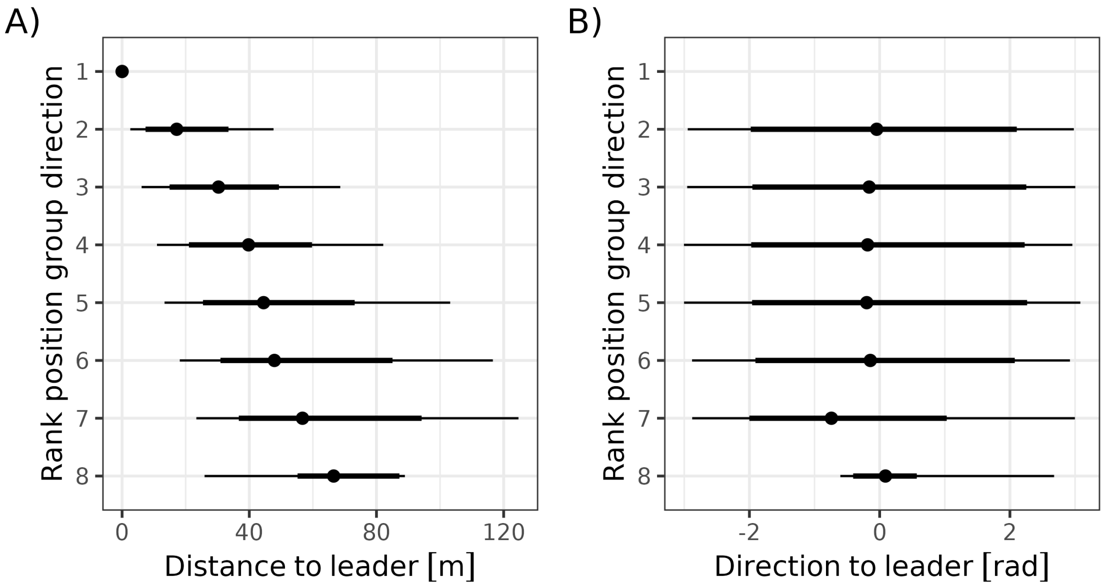


Figure 6: A) Distance and B) direction to group leaders measured using distance_to_leader and direction_to_leader. Using the 'rank_position_group_direction' column returned by leader_direction_group(), distance_to_leader() and direction_to_leader() return columns named 'distance_leader' and 'direction_leader' indicating the distance and direction of the focal individual to the leader of the spatiotemporal group. Note: for individuals identified as leader using 'position_group_direction', the distance is 0 and the direction is NA.

4.5 Fusion events

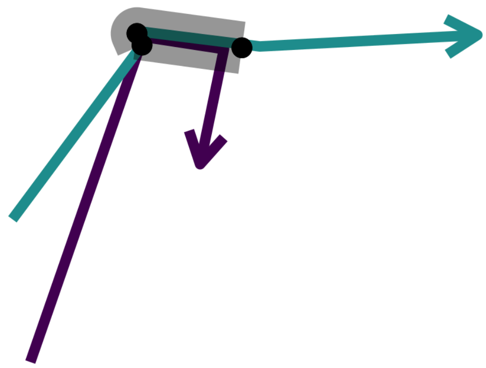
Fusion events, or temporal periods where two individiuals are within a given threshold distance from each other, can be identified using `fusion_id()` (Figure 7). Given the variability in defining fission fusion dynamics in the literature (Table S 14), the `fusion_id()` function flexibly allows users to use specific thresholds and definitions that match their study species and research questions. This will also allow users to easily compare their results to previously published work by using the same thresholds and definitions. The `threshold` argument defines the spatial distance threshold to establish a fusion event. The `n_min_length` argument defines the minimum number of successive fixes that are required to establish a fusion event. The `n_max_missing` defines the maximum number of allowable missed observations for either individual in a dyad within a fusion event. The `allow_split` argument defines if fusion events allow a temporary spatial splitting for one observation without resulting in a fission event. Identification of fusion events has been used to study resource seasonality (Baden et al., 2016), information transfer (Barocas et al., 2016), decision making (Merkle et al., 2015), and habitat selection (Fortin et al., 2009).

```r
# Identify dyads
dyad_id(interindividual_dist, id1 = 'ID1', id2 = 'ID2')

# Identify fusion events
fusion_events <- fusion_id(
  interindividual_dist,
  threshold = spatial_threshold,
  n_min_length = 3,
  n_max_missing = 1,
  allow_split = TRUE
)

# Measure centroids of fusion events
centroid_fusion(
  interindividual_dist,
  DT,
  id = id
)
```

A)



B)

timegroup	ID1	ID2	distance
1	J	NA	NA
2	J	C	11.26 [m]
3	J	C	9.98 [m]
4	J	C	35.89 [m]
5	J	NA	NA

Figure 7: A) Example fusion event for individuals ‘J’ and ‘C’ with black points representing the centroid of fusion observations returned by centroid_fusion(). B) A fusion event identified using fusion_id. Using the distance based edge-lists measured using edge_dist() and the dyad id returned by dyad_id(), fusion_id() a returns a column named ‘fusionID’ representing the fusion events defined with user specified constraints: the distance threshold (‘threshold’), the minimum number of observations defining a fusion event (‘n_min_length’), the maximum number of missing observations from either individual in a fusion event (‘n_max_missing’) and if a single observation where individuals are beyond the distance threshold should result in a fission event (‘allow_split’). In B), a fusion event is identified for individuals J and C given they are within the distance threshold at timegroups 2, 3, and 4. Individual J is shown at timegroups 1 and 5 with no neighbours within the threshold spatial distance (ID2 is NA).

4.6 Directional correlation delay

The directional correlation delay (Nagy et al., 2010), or the temporal delay at which two individual's movement directions are most similar, can be measured using `edge_delay()` (Figure 8). The function measures the similarity of movement directions of the focal individual at time t_0 and the movement direction's of a neighbour within a specified temporal window (e.g. $t_{-2}, t_{-1}, t_0, t_1, t_2$). The temporal delay is the difference in time where the neighbour's movement directions are most similar to the focal individual's. The directional correlation delay ranges from negative values indicating the focal individual's direction is most similar to the neighbour's previous movement direction to positive values indicating the focal individual's direction is most similar to the neighbour's future movement direction. The directional correlation delay can be aggregated to determine mean directional correlation delay using `leader_edge_delay()`. The mean directional correlation delay can be used to measure leadership patterns and generate hierarchical leadership networks depending on the study system (Ákos et al., 2014; Flack et al., 2013; Nagy et al., 2010; Nagy et al., 2013; Quera et al., 2023).

```r
# Measure directional correlation delay
delay <- edge_delay(
  edges = fusion_events,
  DT = DT,
  window = 3,
  id = id
)
```

```r
# Measure mean directional correlation delay
leader_delay <- leader_edge_delay(
  delay,
  threshold = 0.5
)
```

A)

timegroup	ID1	ID2	direction	direction_delay
2	C	G	-2.51 [rad]	0

B)

timegroup	ID	direction
1	G	-1.92 [rad]
2	G	-2.35 [rad]
3	G	-1.32 [rad]

C)

ID1	ID2	mean_direction_delay_dyad	mean_direction_del
C	G	-0.16	-0.08
G	C	0.16	0.09
C	I	-0.14	-0.08
I	C	0.14	-0.02
G	I	0.26	0.09
I	G	-0.26	-0.02

Figure 8: A) Example directional correlation delay for focal individual 'C' (ID1) and neighbour 'G' (ID2) indicating individual 'C' had a movement direction most similar to individual 'G' at the temporal delay of 0. Using the fusion events identified by fusion_id() and the 'direction' column returned by direction_step(), edge_delay() returns a column named 'direction_delay' representing the temporal delay at which the focal individual's movement direction is most similar to their neighbour's within a temporal window. B) Example movement directions for neighbour 'G' in the temporal window of timegroups 1-3 (set using argument 'window'). C) Aggregated directional delay using leader_edge_delay(). Using the 'direction_delay' column returned by edge_delay(), the leader_edge_delay() function returns a column named 'mean_direction_delay_delay' representing the mean directional correlation delay between two individuals and a column named 'mean_direction_delay' that represents the the mean correlation delay for each focal individual

and all observed neighbours. Optionally, a threshold difference in direction can be used to subset the temporal delays included in the calculation of mean directional delay with the argument 'threshold'.

5 Implications

The open source package {spatsoc} (Robitaille et al., 2019) for the R programming language (R Core Team, 2025) has improved accessibility to methods for spatiotemporal grouping and social network analysis with animal telemetry data (e.g. Albery et al., 2025; Bracken et al., 2022; Heeres et al., 2024; Merkle et al., 2024). Despite this, proximity based associations are only one dimension and studying intragroup social dynamics will allow researchers to further measure animal social systems. The new functions in {spatsoc} and the accompanying case study presented here make openly available a series of metrics that while commonly used in the literature have been largely absent from R packages. Paired with the continued development of animal tracking technology (Beardsworth et al., 2022; Nathan et al., 2022) and novel data collection methods (Koger et al., 2023; Pedrazzi et al., 2025), the open availability of these metrics in R will broaden their application across research questions, including, among others, long-standing ecological concepts such as:

- Social foraging theory and producer-scrounger dynamics where "producers" are those who discover patches and "scroungers" are those who join patches discovered by others (Barnard & Sibly, 1981; Giraldeau & Caraco, 2000; Vickery et al., 1991). This concept can be applied to animal telemetry data by evaluating the position of individuals within groups, the individual's arrival timing to forage patches and the characteristics of forage patches. Individuals balance predation risk and foraging success by adjusting their spatial position within groups (Hirsch et al., 2020; Teichroeb et al., 2015), and the foraging strategy selected by an individual can be influenced by the size of forage patches (Hansen et al., 2016).

- Leader-follower patterns in groups of moving animals can be studied both to determine factors that causally influence leadership, and for the influence of leader-follower strategies on foraging success and downstream fitness. Applied to animal telemetry data, leadership can be defined simply by identifying the individual at the foremost position along the front-to-back axis of the group's direction (Harel et al., 2021; Quera et al., 2023) or by calculating the directional correlation delay between individuals and building leadership hierarchies (Nagy et al., 2010). Leadership in a group of moving animals can inform animal decision making, group coordination, and migratory patterns (Flack et al., 2018; Kano et al., 2021; Quera et al., 2023; Weesner et al., 2023).

- Individual traits can influence behaviours related to intragroup dynamics. Dominance is related to foraging success (Caraco et al., 1989; Teichroeb et al., 2015) and choice of foraging strategy (Aplin & Morand-Ferron, 2017; King & Cowlishaw, 2009; Lee et al., 2016). Dominant, aggressive, grooming and other interindividual behaviours are typically measured using focal observations. However, some metrics have been developed for remotely estimating dominance behaviours. The directional correlation delay can be used to derive hierarchies of leadership which can be a proxy for dominance relationships in certain species (Ákos et al., 2014; Flack et al., 2013). Dominance relationships can also be inferred from animal telemetry data using movement initiations (Amornbunchornvej et al., 2018), approach-avoidance behaviours (Strandburg-Peshkin et al., 2015) and displacement events (Evans et al., 2018).

The lack of open source code and transparency of methods alongside research (Table S 4, Table S 5, Table S 6) continues to slow the progress of science by limiting the broader application of new methods. We hope that the availability of these metrics in {spatsoc} will allow researchers to apply them to diverse study species, systems or research questions, including novel applications that could have management and conservation implications for vulnerable species (Ramos et al., 2021).

6 Open science

All code used to produce this manuscript including figures and tables are available on GitHub at https://github.com/robitalec/extending-spatsoc-application-paper and on Zenodo at https://doi.org/10.5281/zenodo.19712779. The data used in this case study are included with the package and can be imported with:

```r
library(spatsoc)

library(data.table)

DT <- fread(system.file("extdata", "DT.csv", package = "spatsoc"))
```

The code for producing the scoping review results, figures, tables and manuscript was developed as a reproducible pipeline with the R package {targets} (Landau, 2021). Figures and tables were constructed using {ggplot2} (Wickham, 2016), {ggdist} (Kay, 2025), {patchwork} (Pedersen, 2025) and {tintytable} (Arel-Bundock, 2025). The manuscript was produced using {quarto} (Allaire & Dervieux, 2024). The {spatsoc} package gratefully depends on the R packages {adehabitatHR} (Calenge, 2024), {data.table} (Barrett et al., 2025), {igraph} (Csárdi et al., 2026), {sf} (Pebesma, 2018), {lwgeom} (Pebesma, 2025), {CircStats} (Lund & Agostinelli, 2025), {units} (Pebesma et al., 2016), and {rlang} (Henry & Wickham, 2026).

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8 Author contributions

Alec L. Robitaille, Quinn M.R. Webber and Eric Vander Wal contributed to conceptualization and writing. Eric Vander Wal contributed to methodology, funding acquisition, project administration and supervision. Alec L. Robitaille contributed to writing (original draft), software, investigation, formal analysis, data curation and visualization. # References {.unnumbered}

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9 Supplement: Scoping review methods

We conducted a scoping review to identify metrics used in ecology studies for measuring dyadic interactions, dominance hierarchies and leadership patterns. We focused on metrics applicable to spatiotemporal data such as GPS telemetry. We used two databases of academic literature: Web of Science and Scopus. We established a test list of nine benchmark papers (Supplement A: Table 1) that were relevant to our objectives and verified that each paper was indexed in our selected databases. We used an iterative search method to fine-tune search terms measuring the total number of papers returned and sensitivity of the search. Sensitivity is defined as the proportion of potentially relevant papers returned from the search estimated using the number benchmark papers returned from the test list (4.2.7 Collaboration for Environmental Evidence, 2022). Search terms were established in four categories: topic, population, method and exclusion. Topic included terms associated with dyadic interactions, dominance hierarchies and leadership patterns. Population included terms associated with animals, wildlife and ecology. Method included terms associated with data collection and data types. Finally, a list of exclusion terms were used to remove clearly irrelevant papers. Each category of terms were combined with OR operators and all three categories of terms were combined with AND operators. The set of papers used in further steps was the combination of the last iteration of search terms applied to both of the Web of Science (using the "TS" field) and Scopus (using the "TITLE-ABS-KEY" field) databases. Only articles between 1980-2023 were included using the PY (Web of Science) or PUBYEAR (Scopus) fields. The resulting set of references were imported into Covidence (Veritas Health Innovation, 2025) for deduplication, title and abstract screening, full text screening, and data extraction.

Before screening, articles were marked as duplicates using Covidence and manual screening. Covidence detected 799 duplicates based on title, year, volume, and authors, and manual screening identified an additional 128 duplicates.

Articles were screened out based on the following criteria:

- Study does not describe dyadic or group metric related to leadership or dominance (e.g. Papageorgiou & Farine (2020))
- Study describes metric that is not applicable to spatiotemporal data (e.g. Allanic et al. (2020) used focal observations and video recordings)
- Study does not describe metric beyond static interaction (e.g. Carter et al. (2013) used home range or spatial overlap)
- Study does not describe metric beyond group size (e.g.

  1)
- Study full text is not available in English (e.g. Bernard & Krafft (2002))
- Study is not a thesis
- Study is not a book chapter (e.g. Bernstein & Blue (2019))

Despite a focus on animal ecology, some studies discussed movement data more generically or, alternatively, specifically focused on human or robotic movement data (e.g. Long et al. (2022)). These studies were retained when the metrics described were deemed applicable to animal spatiotemporal movement data. Studies using mathematical models or simulations were largely beyond the scope of this review but studies were retained when the parameters used as inputs could be applied to spatial temporal data (e.g. Long (2015)). Review studies were read for building the scope of the introduction and discussion but not included in data extraction unless they explicitly discussed dyadic measures (e.g. King et al. (2018)).

The goals of data extraction were to record the breadth of dyadic social and dominance metrics applicable to spatiotemporal data, and the degree of code availability. General information about each study was recorded including the type of study (empirical, simulation, algorithm, model, or review), study species and study region. Dyadic social metrics for each study were listed including citations and interpretation for each metric used and data input required. Dominance metrics derived from spatiotemporal data were listed including citations and interpretation. Code availability was described including location of code (e.g. Zenodo, or GitHub), programming languages and software packages used.

Metrics identified were aggregated using a manual process to identify synonymous terms. This aggregation process was required due to variability in defining metrics during data extraction and differences between authors in describing metrics (e.g. distance to group "center", "centroid", or "center of mass"). Each study was geocoded using the {tidygeocoder} package (Cambon et al., 2021) and species were parsed using the {rgnparser} package (Chamberlain et al., 2023) which provides the GNparser (Mozzherin et al., 2026) functionality in R. We calculated frequency of data extracted for each categorical field including programming language, software package, analysis code availability, geographic region, study species and metric used. For many fields, authors did not provide sufficient to determine how metrics were calculated, e.g. not including the programming language or software package used. In all cases, counts are presented as an overall frequency including papers with missing fields.

Table S 1: Data extraction form for scoping review to identify metrics for studying intragroup dynamics

Category	Field
General	Covidence #
	Study ID
	Title
Study information	Type of study (Empirical, simulation, algorithm, model, review, other)
	Species
	Region
Dyadic social metrics	Metric used or described
	Software package(s) used
	Citation for metric if not introduced in this paper
	Interpretation

Category	Field
	Data input required
	Definitions of “leader”, “initiator”, etc
Dominance	Dominance metric
	Interpretation
	Citation for dominance metric if not introduced in this paper
Code availability	Analysis code availability
	Programming language
	Analysis code link
	Analysis code availability location (e.g. GitHub, Zenodo, FigShare)
	Other comments about code availability
Misc	Discussion points
	Etc

Table S 2: Benchmark papers used to evaluate iterative search results for scoping review

Citation	Indexed in WoS
Nagy, Máté, Zsuzsa Ákos, Dora Biro, and Tamás Vicsek. 2010. “Hierarchical Group Dynamics in Pigeon Flocks.” _Nature_ 464 (7290): 890–93. https://doi.org/10.1038/nature08891.	TRUE
Strandburg-Peshkin, Ariana, Damien R. Farine, Iain D. Couzin, and Margaret C. Crofoot. 2015. “Shared Decision-Making Drives Collective Movement in Wild Baboons.” _Science_ 348 (6241): 1358–61.	TRUE
Merkle, J.A., M. Sigaud, and D. Fortin. 2015. “To Follow or Not? How Animals in Fusion–Fission Societies Handle Conflicting Information during Group Decision-Making.” _Ecology Letters_ 18 (8): 799–806.	TRUE
Andersson, Mattias, Joachim Gudmundsson, Patrick Laube, and Thomas Wolle. 2007. “Reporting Leadership Patterns among Trajectories.” In	TRUE

Citation	Indexed in WoS
Proceedings of the 2007 ACM Symposium on Applied Computing, 3–7. SAC ’07. New York, NY, USA: Association for Computing Machinery. https://doi.org/10.1145/1244002.1244004.	
Flack, Andrea, Máté Nagy, Wolfgang Fiedler, Iain D. Couzin, and Martin Wikelski. 2018. “From Local Collective Behavior to Global Migratory Patterns in White Storks.” _Science_ 360 (6391): 911–14.	TRUE
Bracken, A.M., C. Christensen, M.J. O’Riain, I. Fürtbauer, and A.J. King. 2022. “Flexible Group Cohesion and Coordination, but Robust Leader-Follower Roles, in a Wild Social Primate Using Urban Space.” _Proc. R. Soc. B Biol. Sci._ 289 (1967). https://doi.org/10.1098/rspb.2021.2141.	TRUE
Long, Jed A., Trisalyn A. Nelson, Stephen L. Webb, and Kenneth L. Gee. 2014. “A Critical Examination of Indices of Dynamic Interaction for Wildlife Telemetry Studies.” _Journal of Animal Ecology_ 83 (5): 1216–33. https://doi.org/10.1111/1365-2656.12198.	TRUE
Dodge, Somayeh, Robert Weibel, and Anna-Katharina Lautenschütz. 2008. “Towards a Taxonomy of Movement Patterns.” _Information Visualization_ 7 (3–4): 240–52. https://doi.org/10.1057/PALGRAVE.IVS.9500182.	TRUE
Laube, Patrick, Stephan Imfeld, and Robert Weibel. 2005. “Discovering Relative Motion Patterns in Groups of Moving Point Objects.” _International Journal of Geographical Information Science_ 19 (6): 639–68. https://doi.org/10.1080/13658810500105572.	TRUE

Table S 3: Search strings for scoping review using Web of Science and Scopus

Source	String
Web of Science	TS=(“dominance hierarch*” OR “leadership” OR “dominance” OR “collective move*” OR “fusion-fission” OR “fission-fusion” OR (“fission*” AND “fusion*”) OR (“producer*” AND “scrounger”) OR “producer-scrounger” OR “leader-follower” OR “leader follower” OR (“leader*” AND “follower*”) OR (“finder*” AND “joiner*”) OR “group cohesion” OR “dynamic interaction” OR “leadership pattern*” OR “collective behav*” OR “spatiotemporal group*” OR “relative motion” OR “group dynamics”) AND TS=(“ecolog*” OR “animal*” OR “wildlife”) AND TS=((“spatial*” AND “network*”) OR “track*” OR “gps” OR “telemetry” OR “PIT” OR “video” OR “RFID” OR “biotelem*” OR “spatiotemporal” OR “spatio-temporal” OR “GPS” OR “movement pattern*”) NOT TS=(“human group*” OR “robot*” OR “genetic algorithm” OR “cell movement” OR “cellular” OR “sport*” OR “team sport*” OR “task force” OR “food web*” OR “host plant*” OR “fossil” OR “urbanism” OR “psychiatry” OR “bile”) AND PY=(1980-2023)
Scopus	TITLE-ABS-KEY (“dominance hierarch*” OR “leadership” OR “dominance” OR “collective move*” OR “fusion-fission” OR “fission-fusion” OR (“fission*” AND “fusion*”) OR (“producer*” AND “scrounger”) OR “producer-scrounger” OR “leader-follower” OR “leader follower” OR (“leader*” AND “follower*”) OR (“finder*” AND “joiner*”) OR “group cohesion” OR “dynamic interaction” OR “leadership pattern*” OR “collective behav*” OR “spatiotemporal group*” OR “relative motion” OR “group dynamics”) AND TITLE-ABS-KEY (“ecolog*” OR “animal*” OR “wildlife”) AND TITLE-ABS-KEY ((“spatial*” AND “network*”) OR “track*” OR “gps” OR “telemetry” OR “PIT” OR “video” OR “RFID” OR “biotelem*” OR “spatiotemporal” OR “spatio-temporal” OR “GPS” OR “movement pattern*”) AND NOT TITLE-ABS-KEY (“human group*” OR “robot*” OR “genetic algorithm” OR “cell movement”

Source	String
	OR “cellular” OR “sport*” OR “team sport*” OR “task force” OR “food web*” OR “host plant*” OR “fossil” OR “urbanism” OR “psychiatry” OR “bile”) AND PUBYEAR > 1980

10 Supplement: Scoping review results

Results

PRISMA

- 3870 references imported for screening as 3870 studies
  - 128 duplicates identified manually
  - 799 duplicates identified by Covidence
- 2943 studies screened against title and abstract
  - 2527 studies excluded
- 416 studies assessed for full-text eligibility
  - 275 studies excluded
    - 184 Does not discuss dyadic measure
    - 86 Metric not applicable to spatiotemporal data
    - 2 Book chapter
    - 2 Full text not in English
    - 1 Thesis
  - 0 studies ongoing
  - 0 studies awaiting classification
- 141 studies included

Table S 4: Count of code availability in references screened for full text extraction of scoping review

Code availability	N
No	114 (81%)
Yes	26 (19%)

Out of 141 articles, 52 did not list a programming language or GUI program. Of the 89 that did, 21 articles listed more than one programming language or GUI program, therefore the total count below will be greater than the number of articles.

Table S 5: Count of programming language or GUI program used in references screened for full text extraction of scoping review

Programming language	N
R	62 (36.26%)
NA	52 (30.41%)
MATLAB	15 (8.77%)
Python	6 (3.51%)
CUDA	4 (2.34%)
Ucinet	3 (1.75%)
Perl	3 (1.75%)
C++	3 (1.75%)
NetLogo	2 (1.17%)
SPSS	2 (1.17%)
SchoolTracker	1 (0.58%)
Bonsai	1 (0.58%)
Keras	1 (0.58%)
TensorFlow	1 (0.58%)
SYSTAT	1 (0.58%)
Fortran	1 (0.58%)

Programming language	N
Mathematica	1 (0.58%)
Brodgar	1 (0.58%)
Stata	1 (0.58%)
ArcGIS	1 (0.58%)
Pascal	1 (0.58%)
Matlab	1 (0.58%)
Hawth Tools for ArcGIS	1 (0.58%)
Wolfram Mathematica	1 (0.58%)
Ctrax	1 (0.58%)
StreamPix 5	1 (0.58%)
MoveMine	1 (0.58%)
Java	1 (0.58%)
Netlogo	1 (0.58%)

Out of 140 articles, 112 did not list a software package. Of the 28 that did, 14 articles listed more than one software package , therefore the total count below will be greater than the number of articles.

Table S 6: Count of software packages used in references screened for full text extraction of scoping review

(a)

Software package used	N
NA	112 (66.67%)
wildlifeDI	9 (5.36%)
geosphere	3 (1.79%)
adehabitat	2 (1.19%)

Software package used	N
moveVis	2 (1.19%)
ctmm	2 (1.19%)
CircStats	2 (1.19%)
corrMove	2 (1.19%)
adehabitatHR	2 (1.19%)
numpy	2 (1.19%)
h5py	2 (1.19%)
matplotlib	2 (1.19%)
pathlib	2 (1.19%)
swaRm	1 (0.60%)
forecast (cross correlation)	1 (0.60%)
move	1 (0.60%)
moveUD	1 (0.60%)
boot	1 (0.60%)
MASS	1 (0.60%)
BBMM	1 (0.60%)
momentuHMM	1 (0.60%)
adehabitatLT	1 (0.60%)
DescTools	1 (0.60%)
splancs	1 (0.60%)
vegan	1 (0.60%)
EloRating	1 (0.60%)
compete	1 (0.60%)
changepoint	1 (0.60%)
igraph	1 (0.60%)

Software package used	N
rethinking	1 (0.60%)
pdist	1 (0.60%)
polyclip	1 (0.60%)
geoR	1 (0.60%)
SDMTools	1 (0.60%)
FactoMineR	1 (0.60%)
OpenCV	1 (0.60%)
pamk	1 (0.60%)

Table S 7: Count of references screened for full text extraction across temporal period (1980-2023) of scoping review

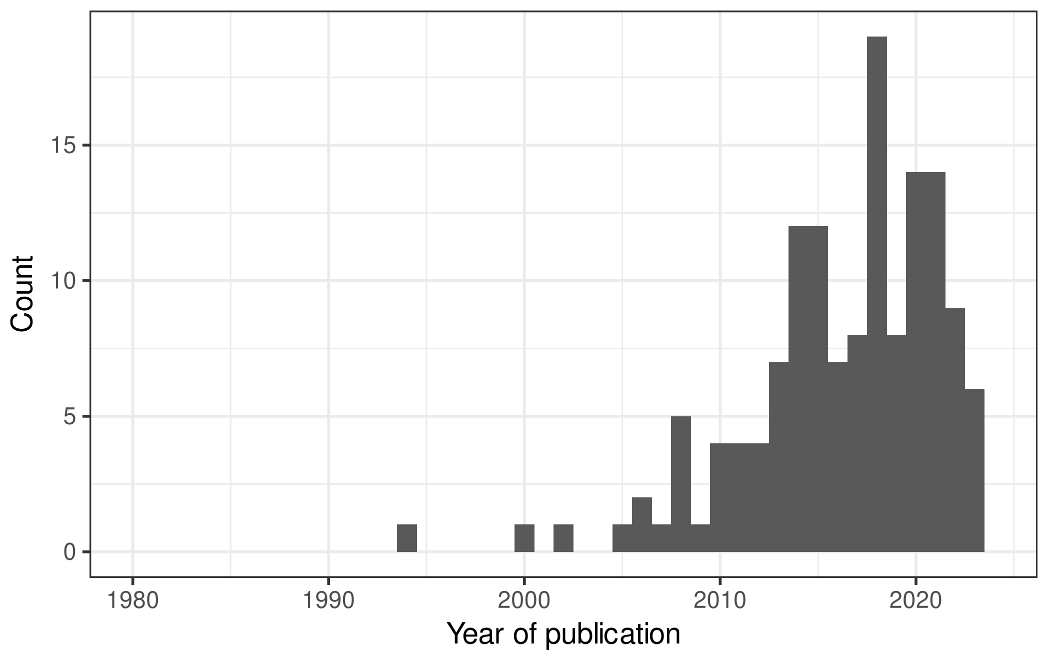

Table S 8: Map of study regions georeferenced using {tidygeocoder} from references screened for full text extraction of scoping review

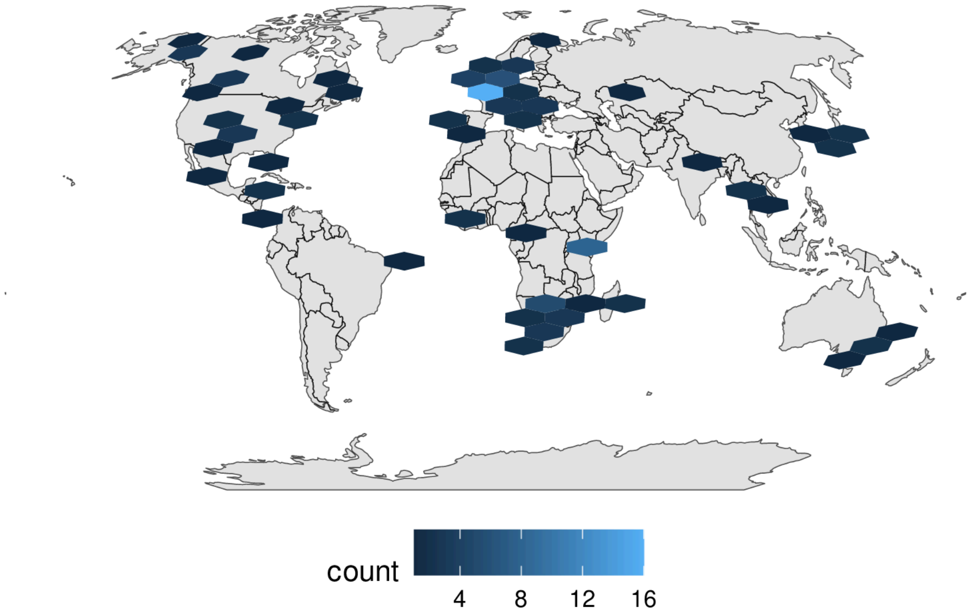

Table S 9: Count of species parsed using {rgnparser} in references screened for full text extraction of scoping review

Species	N
Columba livia	9 (7.09%)
Danio rerio	6 (4.72%)
Rangifer tarandus	6 (4.72%)
Gasterosteus aculeatus	5 (3.94%)
Papio anubis	5 (3.94%)
Poecilia reticulata	5 (3.94%)
Macaca fuscata	4 (3.15%)
Ovis aries	4 (3.15%)
Bos taurus	3 (2.36%)
Ateles geoffroy	3 (2.36%)
Equus ferus	3 (2.36%)

Species	N
Hemigrammus rhodostomus	3 (2.36%)
Loxodonta africana	3 (2.36%)
Odocoileus virginianus	3 (2.36%)
Bison bison	2 (1.57%)
Capra aegagrus	2 (1.57%)
Cervus elaphus	2 (1.57%)
Ciconia ciconia	2 (1.57%)
Equus hemionus	2 (1.57%)
Homo sapiens	2 (1.57%)
Panthera pardus	2 (1.57%)
Varecia variegata	2 (1.57%)
Acinonyx jubatus	1 (0.79%)
Acryllium vulturinum	1 (0.79%)
Ailurus fulgens	1 (0.79%)
Anser anser	1 (0.79%)
Astyanax mexicanus	1 (0.79%)
Aves NA	1 (0.79%)
Callisaurus draconoides	1 (0.79%)
Canis familiaris	1 (0.79%)
Canis lupus	1 (0.79%)
Canis mesomelus	1 (0.79%)
Cercocebus atys	1 (0.79%)
Cervus canadensis	1 (0.79%)
Chlorocebus pygerythrus	1 (0.79%)
Connochaetes taurinus	1 (0.79%)

Species	N
Corvus monedula	1 (0.79%)
Cryptoprocta ferox	1 (0.79%)
Eulemur rubriventer	1 (0.79%)
Eulemur rufifrons	1 (0.79%)
Gambusia holbrooki	1 (0.79%)
Gymnocorymbus ternetzi	1 (0.79%)
Hyaena brunnea	1 (0.79%)
Hyphessobrycon herbertaxelrodi	1 (0.79%)
Indotestudo elongata	1 (0.79%)
Llarus ridibundus	1 (0.79%)
Lontra canadensis	1 (0.79%)
Lutra lutra	1 (0.79%)
Lycaon pictus	1 (0.79%)
Macaca assamensis	1 (0.79%)
Macaca mulatta	1 (0.79%)
Melanitta perspicillata	1 (0.79%)
Melanotaenia duboulayi	1 (0.79%)
Meles meles	1 (0.79%)
Notemigonus crysoleucas	1 (0.79%)
Pan troglodytes	1 (0.79%)
Panthera leo	1 (0.79%)
Panthera tigris	1 (0.79%)
Papio hamadryas	1 (0.79%)
Papio ursinus	1 (0.79%)
Parahyaena brunnea	1 (0.79%)

Species	N
Pelvicachromis taeniatus	1 (0.79%)
Poecile atricapillus	1 (0.79%)
Poecilia formosa	1 (0.79%)
Sotalia guianens	1 (0.79%)
Sturnus vulgaris	1 (0.79%)
Suricata suricatta	1 (0.79%)
Syncerus caffer	1 (0.79%)
Tadarida brasiliensis	1 (0.79%)
Ursus arctor	1 (0.79%)
Vulpes vulpes	1 (0.79%)

Table S 10: Count of metrics used to measure intragroup dynamics in references screened for full text extraction of scoping review

Metric	N
interindividual distance	61 (14.73%)
nearest neighbour distance	19 (4.59%)
directional correlation delay	18 (4.35%)
speed	17 (4.11%)
position within group	16 (3.86%)
direction	15 (3.62%)
zones	15 (3.62%)
distance to group centroid	14 (3.38%)
fission fusion	13 (3.14%)
directional alignment	9 (2.17%)
DI	7 (1.69%)

Metric	N
group centroid	7 (1.69%)
polarization	7 (1.69%)
Don	6 (1.45%)
Prox	6 (1.45%)
velocity	5 (1.21%)
voronoi	5 (1.21%)
group velocity	5 (1.21%)
rank position within group	5 (1.21%)
direction to group centroid	5 (1.21%)
group size	5 (1.21%)
distance	5 (1.21%)
group direction	5 (1.21%)
acceleration	4 (0.97%)
time spent leading group	4 (0.97%)
Lixn	4 (0.97%)
interindividual direction	3 (0.72%)
HAI	3 (0.72%)
flock	3 (0.72%)
trend setting	3 (0.72%)
group speed	3 (0.72%)
IAB	3 (0.72%)
Cs	3 (0.72%)
DI in direction	3 (0.72%)
DI in displacement	3 (0.72%)
movement initiations pull and anchor	3 (0.72%)

Metric	N
relative angle	2 (0.48%)
Cr	2 (0.48%)
turning angle	2 (0.48%)
entropy	2 (0.48%)
coefficient of sociality	2 (0.48%)
concurrence	2 (0.48%)
constance	2 (0.48%)
convergence	2 (0.48%)
divergence	2 (0.48%)
attraction	2 (0.48%)
proximity	2 (0.48%)
diffusive movement correlation	2 (0.48%)
drift movement correlation	2 (0.48%)
overall component movement correlation	2 (0.48%)
optimal causal entropy	2 (0.48%)
change point detection	2 (0.48%)
temporal correlation delay	2 (0.48%)
cross correlation in speed	2 (0.48%)
position	2 (0.48%)
direction to leader	1 (0.24%)
distance to leader	1 (0.24%)
rank distance to group centroid	1 (0.24%)
difference coefficient	1 (0.24%)
dispersion	1 (0.24%)
group concurrence	1 (0.24%)

Metric	N
group turn	1 (0.24%)
independent	1 (0.24%)
motion azimuth	1 (0.24%)
opposition	1 (0.24%)
propagation	1 (0.24%)
turn	1 (0.24%)
cross correlation	1 (0.24%)
Granger causality	1 (0.24%)
neural network model	1 (0.24%)
patch occupancy	1 (0.24%)
mathematical model	1 (0.24%)
route selection	1 (0.24%)
path tortuosity	1 (0.24%)
group cohesion	1 (0.24%)
approaching event	1 (0.24%)
fleeing event	1 (0.24%)
withdrawal event	1 (0.24%)
group convex hull area	1 (0.24%)
synchronicity	1 (0.24%)
mFLICA	1 (0.24%)
HMM	1 (0.24%)
pointwise mutual information	1 (0.24%)
speed influence	1 (0.24%)
turn influence	1 (0.24%)
contact	1 (0.24%)

Metric	N
persistence index	1 (0.24%)
persistence velocity	1 (0.24%)
turning velocity	1 (0.24%)
group distance	1 (0.24%)
breakup	1 (0.24%)
encounter	1 (0.24%)
leadership	1 (0.24%)
track	1 (0.24%)
route efficiency	1 (0.24%)
Ca	1 (0.24%)
kappa coefficient	1 (0.24%)
milling	1 (0.24%)
herding	1 (0.24%)
nearest neighbour direction	1 (0.24%)
pertubation test of dynamic interaction	1 (0.24%)
stochastic process model	1 (0.24%)
approach-avoidance event	1 (0.24%)
movement disparity	1 (0.24%)
movement strength	1 (0.24%)
transfer entropy	1 (0.24%)
ORTEGA	1 (0.24%)
potential path area	1 (0.24%)
closed swarm	1 (0.24%)
synchronization ratio	1 (0.24%)
synchronized switch in direction	1 (0.24%)

Metric	N
convex hull	1 (0.24%)
group sphericity	1 (0.24%)
group stretch	1 (0.24%)
directedness	1 (0.24%)
elongation	1 (0.24%)
tilt	1 (0.24%)
adjusted order parameter	1 (0.24%)
following order parameter	1 (0.24%)

Table S 11: Count of metrics used to measure dominance in references screened for full text extraction of scoping review

Dominance metric	N
NA	112 (77.24%)
focal observations	14 (9.66%)
direction correlation delay	5 (3.45%)
fleeing events	2 (1.38%)
survey	2 (1.38%)
approach-avoidance events	2 (1.38%)
egalitarian leadership index	1 (0.69%)
movement initiations	1 (0.69%)
proportion of paired flights led	1 (0.69%)
spatially constrained trend-setter	1 (0.69%)
video observations	1 (0.69%)
displacement events	1 (0.69%)
directional consistency index	1 (0.69%)

Dominance metric	N
feeding-queuing events	1 (0.69%)

Table S 12: Review of definitions of spatiotemporal groups in references screened for full text extraction of scoping review

study_id	definition
Quaglietta 2014	interaction if within 100 m and 1 hour
Mielke 2020	group defined as all individuals within visual contact of focal individual
Leighty 2008	proximity defined as 8 m; approach/avoidance after event defined as changes in interindividual distance after an event
Hansen 2015	fish considered isolated if not within three body lengths of any other fish; group defined by within three body lengths
Bista 2022	temporal threshold 2 hour, distance threshold 100 m
Pinacho-Guendulain 2017	group using 30 m chain rule
Lemasson 2014	group when within 5 body lengths
Inoue 2019	proximity defined as two body lengths away

Table S 13: Review of definitions of leadership in references screened for full text extraction of scoping review

study_id	definition
Rahman 2020	leadership as tendency to be at the front of the group
Quera 2023	following Krause et al. (2000) and Collignon et al. (2019), the authors define a motion leader as an individual who initiates movement towards a certain direction and is followed by other group members

study_id	definition
Andrienko 2013	leader is an object that moves in front of others; trend setter is an object whose movements are copied by others
Amornbunchornvej 2018	following relation is where two individuals perform the same sequence of actions with some fixed delay; initiator is individual who first performs a sequence of actions and all other individuals follow
Kano 2021	leader from directional correlation delay
Pettit 2013	leadership based on directional correlation delay; leadership also based on tendency to use route taken on solo flight
Pérez-Barbería 2018	leadership is ranked position along front-back axis
Laube 2005	leadership extends flock with constance over previous time steps
Milner 2021	leader is animal that is dominant to at least one and subordinate to none
Strandburg-Peshkin 2018	an individual leads if it has repeated influence either directly or hierarchically on the behaviour of others
Andersson 2008	leader if and only if individual doesnt follow anyone and is followed by N others
Jolles 2017	leader in terms of propagation of movement changes in the group
King 2015	leader-follower dynamics from velocity-cross correlation
Bracken 2022	leader initiates movement away from another individual (follower) who joins or who doesn’t and leader returns
Flack 2018	leaders are birds who are ahead of the flock on average and followers those who are behind
ACM 2007	leader IFF x does not follow anyone and is followed by N others; leadership pattern if x is followed by minimum M others for K time unit intervals

study_id	definition
Jolles 2018	measure of leadership as proportion of time spent in front of group centroid

Table S 14: Review of definitions of fission-fusion in references screened for full text extraction of scoping review

study_id	definition
Baden 2016	NA
Aguilar-Melo 2018	fission when gte 1 were not observed with a group for 2 consecutive scans; fusion when gte 1 who were previously not observed with group are observed with group for 2 consecutive scans
Barocas 2016	fission and fusion defined as joining and leaving group in subsequent observations
Haydon 2008	fusion where solitary to grouped and fission where grouped to solitary
Fortin 2009	group/fusion when within 100 m; fission when two or more consecutive locations separated by > 100 m
Body 2015	fusion gte 2 groups merging into one; fission one group splitting into gte 2
DellaLibera 2023	define a fission and fusion event if one or more individuals left or joined the group, respectively. in the rare cases of missing data, missing individuals are not considered as having changed group membership, and individual 'disappearances' and 'reappearances' in the dataset are not considered as fission–fusion events
Wielgus 2020	group where simultaneously within 1 km or >= 1 km for <= 2 hr; fusion where together then different by one time step; fission reverse
Nishikawa 2014	converged when IID less than 20 m; separated when IID greater than 20 m; converged and separated synonymous with fission fusion
Krueger 2014	NA

study_id	definition
Lesmerises 2018	grouped/fission fusion if within 50 m for two relocations; to minimize the false fission events, considered dyad valid if together at t0, t2, but apart at t1; if one missing GPS location, dyad valid if before and after missing loc distance was <50 m
Merkle 2015	group defined as within 100 m within 24 hours

11 Supplement: Selected metrics

11.1 Selected metrics

The following metrics were not selected due to their availability in existing R packages:

- {wildlifeDI}: DI, Don, Prox, Lixn, Cs, DI in direction, DI in displacement, HAI, IAB, Cr, Ca
- {corrMove}: diffusive movement correlation, drift movement correlation, overall component movement correlation
- {changepoint}: change point analysis

The following metrics were not selected due to their availability in code availability accompanying publications:

- mFLICA provided in code accompanying Amornbunchornvej et al. (2018) and R package {mFLICA} (Amornbunchornvej, 2021)

The follow metrics were not selected due to the expected input data differing from existing {spatsoc} functions (XYT):

- metrics relating to posture

The selected metrics are listed in Table 1. All existing functions in {spatsoc} are listed below in Table S 15.

Table S 15: Description of all functions (new and previously existing) available in the R package {spatsoc} categorized by family.

Function	Description	Category
Spatial interface		
get_geometry()	Setup data for geometry interface	New
Edge-list generation		
edge_dist()	Distance based edge-lists	Existing
edge_nn()	Nearest neighbour based edge-lists	Existing
edge_delay()	Directional correlation delay based edge-lists	New
edge_alignment()	Directional alignment based edge-lists	New
edge_direction()	Direction based edge-lists	New
edge_zones()	Behavioural zones based edge-lists	New
Dyad		
dyad_id()	Identify dyads	Existing
fusion_id()	Identify fusion events	New
Centroid		
centroid_group()	Group centroid	New
centroid_dyad()	Dyad centroid	New
centroid_fusion()	Fusion event centroid	New
Direction		
direction_step()	Direction step	New
direction_to_centroid()	Direction to group centroid	New
direction_to_leader()	Direction to group leader	New
direction_group()	Group mean direction	New
direction_polarization()	Polarization	New
Distance		

Function	Description	Category
distance_to_centroid()	Distance to group centroid	New
distance_to_leader()	Distance to group leader	New
Leadership		
leader_direction_group()	Leadership along group direction	New
leader_edge_delay()	Leadership in directional correlation delay	New
Temporal grouping		
group_times()	Group times	Existing
Spatial grouping		
group_lines()	Group lines	Existing
group_pts()	Group points	Existing
group_polys()	Group polygons	Existing
Social network		
randomizations()	Data-stream randomizations	Existing
get_gbi()	Group by individual matrix	Existing
Build		
build_lines()	Build lines	Existing
build_polys()	Build polygons	Existing

Distance, direction and rank distance to group centroid

Our scoping review found 21 studies that used the group centroid, distance to group centroid, direction to group centroid, or rank distance to group centroid metrics, across 14 study species. 4 studies had code available. The {swaRm} package provides functionality to calculate the group centroid and the distance to the group centroid. At the time when the scoping review was conducted, to the best of our knowledge, there were no R packages that provide the rank to distance to group centroid metric.

Polarization, directional alignment and interindividual direction

Our scoping review found 20 studies that used the polarization, directional alignment or interindividual direction metrics, across 11 study species. 4 studies had code available. The {CircStats} and the {swaRm} packages provide functionality to calculate the polarization order parameter. At the time when the scoping review was conducted, to the best of our knowledge, there were no R packages that provide the directional alignment or interindividual direction metrics. After the scoping review was conducted, the {swaRmverse} package was released which provides the direction to nearest neighbour metric (Papadopoulou et al., 2025).

Behavioural zones

Our scoping review found 13 studies that used the behavioural zones metric, across 9 study species. 4 studies had code available. At the time when the scoping review was conducted, to the best of our knowledge, there were no R packages that provide the behavioural zones metric.

Position within group, rank position within group, distance and direction to leader

Our scoping review found 18 studies that used the position within group, rank position within group, distance to leader, or direction to leader metrics across 14 study species. Only 1 studies had code available. At the time when the scoping review was conducted, to the best of our knowledge, there were no R packages that provide these metrics.

Directional correlation delay

Our scoping review found 17 studies that used the directional correlation delay metric, across 12 study species. Only 1 study had code available using a combination of MATLAB (closed source), CUDA (closed source), and Python (open source). At the time when the scoping review was conducted, to the best of our knowledge, there were no R packages that provide this metric.