

Conducting social network analysis with animal telemetry data: applications and methods using `spatsoc`

Alec L. Robitaille ^a, Quinn M.R. Webber ^b & Eric Vander Wal ^{a b}

^a Department of Biology, Memorial University of Newfoundland, St. John's, NL, Canada

^b Cognitive and Behavioural Ecology Interdisciplinary Program, Memorial University of Newfoundland, St. John's, NL, Canada

Summary

1. We present `spatsoc`: an R package for conducting social network analysis with animal telemetry data.
2. Animal social network analysis is a method for measuring relationships between individuals to describe social structure. Proximity-based social networks are generated from animal telemetry data by grouping relocations temporally and spatially, using thresholds that are informed by the characteristics of the species and study system.
3. `spatsoc` fills a gap in R packages by providing flexible functions, explicitly for animal telemetry data, to generate edge lists and gambit-of-the-group data, perform data-stream randomization and generate group by individual matrices.
4. The implications of `spatsoc` are that current users of animal telemetry or otherwise georeferenced data for movement or spatial analyses will have access to efficient and intuitive functions to generate social networks.

Introduction

Animal social network analysis is a method for measuring the relationships between individuals to describe social structure (Wey et al. 2008; Croft, James, and Krause 2008; Pinter-Wollman et al. 2014; Farine and

Whitehead 2015). Association networks are built from a set of observed elements of social community structure and are useful to understand a variety of ecological and behavioural processes, including disease transmission, interactions between individuals and, community structure (Pinter-Wollman et al. 2014). Among the most common types of social network data collection is gambit-of-the-group, where individuals observed in the same group are assumed to be associating or interacting (Franks, Ruxton, and James 2010). Similar to gambit-of-the-group, proximity based social networks (PBSNs) are association networks based on close proximity between individuals (Spiegel et al. 2016). PBSNs rely on spatial location datasets that are typically acquired by georeferenced biologging methods such as radio-frequency identification tags, radiotelemetry, and Global Positioning System (GPS) devices (hereafter, animal telemetry).

Biologging using GPS devices allow simultaneous spatiotemporal sampling of multiple individuals in a group or population, thus generating large datasets which may otherwise be challenging to collect. The advent of biologging technology allows researchers to study individuals of species that range across large areas, migrate long distances, or spend time in inaccessible areas (Cagnacci et al. 2010; Cooke et al. 2013; Hebblewhite and Haydon 2010). Moreover, the recent increase in the number of studies using GPS telemetry to study movement ecology (Kays et al. 2015; Tucker et al. 2018) indicates the potential for a large number of existing datasets that may be retro-actively analyzed to test a priori hypotheses about animal social structure. As animal telemetry data have become more accessible and available at a fine scale, a number of techniques and methods have been developed to quantify various aspects of animal social structure (Webber and Vander Wal 2018). These include dynamic interaction networks (Long et al. 2014), PBSNs (Spiegel et al. 2017) and the development of traditional randomization techniques to assess non-random structure of PBSNs constructed using animal telemetry data (Spiegel et al. 2016). Despite the recent increase in the number of studies using animal telemetry data and GPS relocation data (Webber and Vander Wal 2019), there is no comprehensive R package that generates PBSNs using animal telemetry data.

Here, we present `spatsoc` (v0.1.9), a package developed for the R programming language (R Core Team 2018) to (i) convert animal telemetry data into gambit-of-the-group format to build PBSNs, (ii) implement data-stream social network randomization methods of animal telemetry data (Farine and Whitehead 2015; Spiegel et al. 2016), and (iii) provide flexible spatial and temporal grouping of individuals from large datasets. Animal telemetry data can be complex both temporally (e.g., data can be partitioned into monthly, seasonal or yearly segments) and spatially (e.g., subgroups, communities or populations). Functions in `spatsoc` were developed taking these complexities into account and provide users with flexibility to select relevant parameters based on the biology of their study species and systems and test the sensitivity of results across spatial and temporal scales.

Functions

The `spatsoc` package provides functions for using animal telemetry data to generate PBSNs. Relocations are converted to gambit-of-the-group using grouping functions which can be used to build PBSNs. Alternatively, edge functions can be used to generate edge lists to build PBSNs. Raw data streams can be randomized where animal telemetry data is swapped between individuals at hourly or daily scales (Farine and Whitehead 2015), or within individuals using a daily trajectory method (Spiegel et al. 2016).

Grouping

Gambit-of-the-group data is generated from animal telemetry data where individuals are grouped based on temporal and spatial overlap. The `spatsoc` package provides one temporal grouping function:

1. `group_times` groups animal telemetry relocations into time groups (Figure 1). The function accepts date time formatted data and a temporal threshold argument. The temporal threshold argument allows users to specify a time window within which relocations are grouped, for example: 5 minutes, 2 hours or 10 days.

`group_times` compares the date and time of each relocation to a regular interval defined by the temporal threshold. For example, a five minute threshold will compare the date and time of each relocation to five minute time intervals throughout each day. Each relocation is grouped to the nearest time interval at a maximum temporal distance of half the threshold before or past the time interval.

The `spatsoc` package provides three spatial grouping functions:

1. `group_pts` measures the geographic distance between animal telemetry relocations within each time group based on a spatial threshold provided by the user (Figure 2). A distance matrix is constructed to measure the distance between all individuals. The threshold is used to binarize the distance matrix and the connected components are labelled to form spatial groups. The connected components represent individuals within the threshold distance from one another. We apply the chain rule (Croft, James, and Krause 2008) where three or more individuals that are all within the defined threshold distance of at least one other individual are considered in the same group. For point based spatial grouping with a distance threshold that does not use the chain rule, see `edge_dist` below.
2. `group_lines` groups overlapping movement trajectories generated from animal telemetry data (Figure 3). Movement trajectories for each individual within each time group, e.g. 8 hours, 1 day or 20 days, are generated and grouped based on spatial overlap of lines produced from trajectories. If a spatial

distance threshold is provided, trajectories are buffered by this distance before spatial overlap.

3. `group_polys` generates and groups overlapping home ranges using kernel utilization distributions or minimum convex polygons generated in `adehabitatHR` of individuals and optionally returns a measure of proportional area overlap (Figure 4). Home ranges are generated for each individual in each timegroup, providing efficient comparison of home ranges through time, e.g. multiple days, seasons or years.

For spatial grouping functions, individuals that are not within the distance threshold, or that do not overlap with any other individuals are assigned to a group on their own.

Edge lists

The `spatsoc` package provides two edge list generating functions:

1. `edge_nn` calculates the nearest neighbour to each individual within each time group (Figure 5). If the optional distance threshold is provided, it is used to limit the maximum distance between neighbours. `edge_nn` returns an edge list of each individual and their nearest neighbour.
2. `edge_dist` calculates the geographic distance between animal telemetry relocations within each time group and returns all paired relocations within the spatial threshold (Figure 5). `edge_dist` uses a distance matrix like `group_pts`, but, in contrast, does not use the chain rule to group relocations. Instead, it returns an edge list of each individual and all others within the spatial distance threshold.

For edge list generating functions, individuals that are not within the distance threshold, or that do not have a nearest neighbour (or within the distance threshold if provided), are returned as NA.

Randomizations

Randomization procedures in social network analysis are important to test assumptions of spatial and temporal non-independence of social association data (Farine and Whitehead 2015). Data-stream randomization is the recommended randomization technique for social network users (Farine and Whitehead 2015) and involves swapping individuals and group observations within or between temporal groups and individuals (Farine 2017). Animal telemetry data has inherent temporal structure and is well suited to randomization methods. The `spatsoc` package provides three data-stream randomization methods:

1. Step - randomizes identities of animal telemetry relocations between individuals within each time step.

2. Daily - randomizes daily animal telemetry relocations between individuals, preserving the order of time steps.
3. Trajectory - randomizes daily trajectories generated from animal telemetry relocations within individuals (Spiegel et al. 2016).

The `randomizations` functions return the input data with random fields appended, ready to use by the grouping functions or to build social networks. Step and daily methods return a “randomID” field that can be used in place of the ID field and the trajectory method returns a “randomDatetime” that can be used in place of the datetime field. The `randomizations` function in `spatsoc` allow users to split randomizations between spatial or temporal subgroups to ensure that relocations are only swapped between or within relevant individuals.

Using `spatsoc` in social network analysis

`spatsoc` is integrated with social network analysis in R to generate and randomize PBSNs. First, users will generate temporal groups with `group_times`. Next, users will generate PBSNs from spatial groups:

1. Generate gambit-of-the-group data with spatial grouping functions (`group_pts`, `group_lines` and `group_polys`)
2. Generate group by individual matrices (`get_gbi`)
3. PBSN data-stream randomization (`randomizations`)

or edge lists:

1. Generate edge lists (`edge_nn` and `edge_dist`)
2. PBSN data-stream randomization (`randomizations`)

Before spatiotemporal grouping or edge list generation, users should first determine relevant temporal and spatial grouping thresholds.

Selecting and evaluating spatial and temporal thresholds

Functions provided by `spatsoc` emphasize flexibility to allow users the ability to modify functions to better suit their specific use case. The temporal threshold argument of `group_times` accepts units of minutes, hours or days to generate temporal groups at different scales. The spatial threshold defines the distance used to generate spatial groups and edge lists. The spatial and temporal thresholds used for generating PBSNs with `spatsoc` must be considered carefully and we recommend the thresholds used are based on

the nuances of the animal telemetry data, study species, system and specific research questions. Despite this, there are no hard and fast rules for selecting thresholds for spatiotemporal grouping (but see below for recommendations). Evaluating candidate thresholds is recommended and has been shown to provide valuable insights for selecting temporal (Psorakis et al. 2015) and spatial (Davis, Crofoot, and Farine 2018) thresholds.

It is important that the temporal threshold matches the spatial grouping or edge list function used. In the case of point based spatial grouping and edge list generating functions, the temporal threshold must be at least less than the fix rate of the telemetry device. If not, an individual may have multiple relocations in a timegroup and potentially grouped with itself. The temporal threshold for these functions will likely be in units of minutes or hours. For line and polygon based spatial grouping, the temporal threshold will necessarily encompass multiple relocations for each individual. Lines must be built with at least two points and there are specific requirements for number and distribution of relocations for building home ranges (Laver and Kelly 2008; Cumming and Corn  lis 2012).

While, the spatial and temporal thresholds are informed by the biology of the study species and research questions, there are a number of behavioural, morphological, and ecological factors that could influence threshold distance. For example, these include, but are not limited to, body size, daily movement rate, communication distance (Cameron and Toit 2005), gregariousness (Godde et al. 2013), and degree of fission-fusion (Haddadi et al. 2011). Some empirical examples from the literature include five body lengths for white-faced capuchin monkeys (*Cebus capucinus*, Crofoot et al. 2011), within arm's reach for chimpanzees (*Pan troglodytes*, Fraser, Schino, and Aureli 2008), 2m for sleepy lizards (*Tiliqua rugosa*, Leu et al. 2010), 100m for bison (*Bison bison*, Merkle, Sigaud, and Fortin 2015). Leu et al. (2010) also measured the median GPS device precision to estimate an effective range of 2-26m when using a spatial threshold of 2m. In summary, it is clear that smaller bodied species have shorter threshold distances than larger bodied species, while highly active and gregarious species, including most primates, tend to also have shorter threshold distances.

Finally, *spatsoc* can be used to compare networks generated with different grouping methods across a range of spatial and temporal thresholds. Davis, Crofoot, and Farine (2018) compared association networks generated from wild baboon (*Papio anubis*) telemetry data using spatial thresholds with the chain rule (as in *group_pts*), spatial thresholds without the chain rule (as in *edge_dist*) and nearest neighbours (as in *edge_nn*). For example, Castles et al. (2014) compared proximity networks of chacma baboons (*Papio ursinus*) built with the chain rule (as in *group_pts*) and without (as in *edge_dist*) and using nearest neighbours with a maximal distance (as in *edge_nn*).

Generating networks

Here, we will provide an example of point based spatial grouping with `spatsoc`'s example caribou telemetry data (Table 1). The data consists of 10 individuals with relocations recorded every 2 hours. The coordinates "X" and "Y" are in units of meters and the coordinate system is UTM Zone 21N.

In this case, we will use a temporal threshold of 5 minutes and a spatial distance threshold of 50 m given the size and behaviour of the study species (Peignier et al. 2019). The combination of spatial and temporal thresholds means that any individuals within 50 m of each other within 5 minutes will be assigned to the same group. Please note that `spatsoc` is designed to work with the `data.table` package, specifically in the following example for reading the input data and casting the datetime column from character to date time formatted, as well as internally in `spatsoc` functions.

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

# Import spatsoc's example data
DT <- fread(system.file("extdata", "DT.csv", package = "spatsoc"))

# Cast datetime column to POSIXct
DT[, datetime := as.POSIXct(datetime)]

# Temporal groups
group_times(
  DT,
  datetime = 'datetime',
  threshold = '5 minutes'
)

# Spatial groups using 'timegroup' generated by group_times
group_pts(
  DT,
  threshold = 50,
  id = 'ID',
```

```

coords = c('X', 'Y'),
timegroup = 'timegroup'
)

```

After the temporal and spatial grouping is completed with `group_times` and `group_pts`, a group by individual matrix is generated (described by Farine and Whitehead (2015)). A group by individual matrix forms columns of individuals and rows of groups and a boolean will indicate membership of each individual to a group.

```

gbi <- get_gbi(
  DT,
  group = 'group',
  id = 'ID'
)

```

After generating the group by individual matrix, it is passed directly to `asnipe`, the animal social network package (Farine 2013), to generate a proximity based social network. Note, in this example we use the simple ratio index (SRI) as an association index because all individuals are correctly identified and observed at each relocation event (i.e. the equivalent to an observational period for networks generated using focal observations).

```

library(asnipe)
net <- get_network(
  gbi,
  data_format = "GBI",
  association_index = "SRI"
)

```

Data-stream randomization

To perform network data-stream permutations, the `randomizations` function is used to permute spatial and temporal groupings and rebuild PBSNs at each iteration. In this example, we use the “step” method to randomize between individuals at each time step for 500 iterations. The output `randStep` contains the observed and randomized data and can subsequently be used to generate group by individual matrices, networks and calculate network metrics. An extended form of this example is provided in the vignette “Using `spatsoc` in social network analysis” (see Resources).


```
# Step type randomizations
randStep <- randomizations(
  DT,
  type = 'step',
  id = 'ID',
  group = 'group',
  datetime = 'timegroup',
  iterations = 500,
  splitBy = 'year'
)
```

The `splitBy` argument can be used in the `randomizations` function (as well as edge list generating and spatial grouping functions) to delineate spatial, e.g. groups or populations, or temporal segments of data, e.g. weekly, monthly, or yearly, by which PBSNs will be generated. For example, in large datasets with individuals in two distinct populations with data over many years, users may use the `splitBy` argument to generate PBSNs for each population-by-year combination as opposed to generating each PBSN separately.

Implications

`spatsoc` represents a novel integration of tools for generating PBSNs from animal telemetry data. The grouping and randomization functions allow users to efficiently and rapidly generate a large number of PBSNs within the `spatsoc` environment. `spatsoc` will be of interest and use to a wide range of behavioural ecologists who either already use social network analysis or those who typically work with GPS relocation data but are interested in becoming social network users. We advocate for the use of `spatsoc` in conjunction with the most recent ‘how to’ on social network analysis (Farine and Whitehead 2015) as well as other R packages, such as `asnipe` (Farine 2013) and `igraph` (Csárdi and Nepusz 2006), to facilitate greater sharing of computational and statistical efficiencies and ideas for users of social network analysis.

Resources

`spatsoc` is a free and open source software available on CRAN (stable release) and at <https://github.com/ropensci/spatsoc> (development version). It is licensed under the GNU General Public License 3.0. `spatsoc` depends on other R packages: `data.table` (Dowle and Srinivasan 2018), `igraph` (Csárdi

and Nepusz 2006), *rgeos* (Bivand and Rundel 2018), *sp* (Bivand, Pebesma, and Gomez-Rubio 2013) and *adehabitatHR* (Calenge 2006). Documentation of all functions and detailed vignettes (including “Introduction to spatsoc”, “Frequently asked questions” and “Using spatsoc in social network analysis”) can be found on the companion website at spatsoc.robitallec.ca. Development of spatsoc welcomes contribution of feature requests, bug reports, and suggested improvements through the issue board at <https://github.com/ropensci/spatsoc/issues>.

Future directions

In the future, we intend on producing vignettes which highlight the role of spatsoc for generating social networks for other types of data collection commonly used in social network analysis. For example, data collected using passive-integrated transponders (e.g. Aplin et al. 2013) is increasingly being used to generate animal social networks (Webber and Vander Wal 2019) and spatsoc could represent a novel and computationally efficient way to generate social networks for large PIT-tag datasets. The basic principles of spatsoc and grouping functions can be applied to other data types, including PIT-tags, as long as both spatial and temporal information are known. We are also developing additional grouping methods including dyadic grouping and clustering methods. The dyadic grouping method will extract multiple simultaneous relocations for a dyad through time (e.g. for similar application see Lesmerises, Johnson, and St-Laurent 2018) and will have applications for collective and coordinated movement of dyads. Meanwhile, the clustering method will identify spatially and temporally clustered relocations for individuals, or groups of individuals, and could have applications for identifying preferred habitats for groups as well as locations of scavenging or predation (e.g. for similar applications see Knopff et al. 2009; Kermish-Wells et al. 2018; Cristescu, Stenhouse, and Boyce 2014).

Acknowledgements

We thank all members of the Wildlife Evolutionary Ecology Lab, including Juliana Balluffi-Fry, Sana Zabihi-Seissan, Erin Koen, Michel Laforge, Christina Prokopenko, Julie Turner, Levi Newediuk, Richard Huang and Chris Hart for their comments on previous versions of this manuscript. We thank Michel Robitaille for comments on the French version of the abstract. We thank Tyler Bonnell, Martin Leclerc and Shane Frank for testing the package ahead of its release as well as two anonymous reviewers for comments that greatly improved the manuscript and the package. We also thank the rOpenSci organization for their package on-boarding process including rOpenSci reviewers, Priscilla Minotti and Filipe Teixeira, and editor,

Lincoln Mullen, for their code review, which contributed to improving this package. Funding for this study was provided by a Vanier Canada Graduate Scholarship to QMRW and a NSERC Discovery Grant to EVW.

Author contributions

ALR, QMRW, and EVW conceived of the original package concept. ALR developed the package. ALR and QMRW drafted the manuscript and all co-authors contributed critically to the drafts and gave final approval for publication.

Data accessibility

All data and code used to produce figures are available on GitHub at <https://github.com/robitalec/spatsoc-application-paper> and on Zeonodo at <https://doi.org/10.5281/zenodo.2824869>. The data is also included with the package and can be imported with:

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

Citation

Users of spatsoc should cite this article directly. A formatted citation and BibTex entry is provided in R:

```
citation('spatsoc')
```

References

- Aplin, L. M., D. R. Farine, J. Morand-Ferron, E. F. Cole, A. Cockburn, and B. C. Sheldon. 2013. "Individual personalities predict social behaviour in wild networks of great tits (*Parus major*)."
Ecology Letters 16 (11): 1365–72.
- Bivand, R., and C. Rundel. 2018. *rgeos: Interface to Geometry Engine - Open Source ('GEOS')*. <https://cran.r-project.org/package=rgeos>.
- Bivand, R. S., E. Pebesma, and V. Gomez-Rubio. 2013. *Applied spatial data analysis with R, Second edition*. Springer, NY. <http://www.asdar-book.org/>.
- Cagnacci, F., L. Boitani, R. A. Powell, and M. S. Boyce. 2010. "Animal ecology meets GPS-based radiotelemetry: A perfect storm of opportunities and challenges." *Philosophical Transactions of the Royal Society B: Biological Sciences* 365 (1550): 2157–62. <https://doi.org/10.1098/rstb.2010.0107>.
- Calenge, C. 2006. "The package adehabitat for the R software: tool for the analysis of space and habitat use by animals." *Ecological Modelling* 197: 1035.
- Cameron, E. Z., and J. T. du Toit. 2005. "Social influences on vigilance behaviour in giraffes, *Giraffa camelopardalis*." *Animal Behaviour* 69 (6): 1337–44.
- Castles, M., R. Heinsohn, H. H. Marshall, A. E.G. Lee, G. Cowlishaw, and A. J. Carter. 2014. "Social networks created with different techniques are not comparable." *Animal Behaviour* 96: 59–67.
- Cooke, S. J., J. D. Midwood, J. D. Thiem, P. Klimley, M. C. Lucas, E. B. Thorstad, J. Eiler, C. Holbrook, and B. C. Ebner. 2013. "Tracking animals in freshwater with electronic tags: Past, present and future." *Animal Biotelemetry* 1 (1): 1–19. <https://doi.org/10.1186/2050-3385-1-5>.
- Cristescu, B., G. B. Stenhouse, and M. S. Boyce. 2014. "Predicting multiple behaviors from GPS radiocollar cluster data." *Behavioral Ecology* 26 (2): 452–64.
- Crofoot, M. C., D. I. Rubenstein, A. S. Maiya, and T. Y. Berger-Wolf. 2011. "Aggression, grooming and group-level cooperation in white-faced capuchins (*Cebus capucinus*): insights from social networks." *American Journal of Primatology* 73 (8): 821–33.
- Croft, D. P., R. James, and J. Krause. 2008. *Exploring Animal Social Networks*. Princeton University Press. <https://books.google.ca/books?id=CViwRbohZkC>.
- Csárdi, G., and T. Nepusz. 2006. "The igraph software package for complex network research." *InterJournal Complex Systems*: 1695. <http://igraph.org>.

- Cumming, G. S., and D. Corn  lis. 2012. "Quantitative comparison and selection of home range metrics for telemetry data." *Diversity and Distributions* 18 (11): 1057–65.
- Davis, G. H., M. C. Crofoot, and D. R. Farine. 2018. "Estimating the robustness and uncertainty of animal social networks using different observational methods." *Animal Behaviour* 141: 29–44.
- Dowle, M., and A. Srinivasan. 2018. *data.table: Extension of 'data.frame'*. <https://cran.r-project.org/package=data.table>.
- Farine, D. R. 2013. "Animal social network inference and permutations for ecologists in R using *asnipe*." *Methods in Ecology and Evolution* 4 (12): 1187–94. <https://doi.org/10.1111/2041-210X.12121>.
- . 2017. "A guide to null models for animal social network analysis." *Methods in Ecology and Evolution* 8 (10): 1309–20. <https://doi.org/10.1111/2041-210X.12772>.
- Farine, D. R., and H. Whitehead. 2015. "Constructing, conducting and interpreting animal social network analysis." *Journal of Animal Ecology* 84 (5): 1144–63. <https://doi.org/10.1111/1365-2656.12418>.
- Franks, D. W., G. D. Ruxton, and R. James. 2010. "Sampling animal association networks with the gambit of the group." *Behavioral Ecology and Sociobiology* 64 (3): 493–503. <https://doi.org/10.1007/s00265-009-0865-8>.
- Fraser, O. N., G. Schino, and F. Aureli. 2008. "Components of relationship quality in chimpanzees." *Ethology* 114 (9): 834–43.
- Godde, S., L. Humbert, S. D. C  t  , D. R  ale, and H. Whitehead. 2013. "Correcting for the impact of gregariousness in social network analyses." *Animal Behaviour* 85 (3): 553–58.
- Haddadi, H., A. J. King, A. P. Wills, D. Fay, J. Lowe, A. J. Morton, S. Hailes, and A. M. Wilson. 2011. "Determining association networks in social animals: choosing spatial–temporal criteria and sampling rates." *Behavioral Ecology and Sociobiology* 65 (8): 1659–68.
- Hebblewhite, M., and D. T. Haydon. 2010. "Distinguishing technology from biology: A critical review of the use of GPS telemetry data in ecology." *Philosophical Transactions of the Royal Society B: Biological Sciences* 365 (1550): 2303–12. <https://doi.org/10.1098/rstb.2010.0087>.
- Kays, R., M. C. Crofoot, W. Jetz, and M. Wikelski. 2015. "Terrestrial animal tracking as an eye on life and planet." *Science* 348 (6240): aaa2478. <https://doi.org/10.1126/science.aaa2478>.
- Kermish-Wells, J., A. Massolo, G. B. Stenhouse, T. A. Larsen, and M. Musiani. 2018. "Space–time clusters for early detection of grizzly bear predation." *Ecology and Evolution* 8 (1): 382–95.
- Knopff, Kyle H, Aliah Adams Knopff, Mike B Warren, and Mark S Boyce. 2009. "Evaluating Global

Positioning System Telemetry Techniques for Estimating Cougar Predation Parameters." *The Journal of Wildlife Management* 73 (4): 586–97.

Laver, P. N., and M. J. Kelly. 2008. "A critical review of home range studies." *The Journal of Wildlife Management* 72 (1): 290–98.

Lesmerises, F., C. J. Johnson, and M.-H. St-Laurent. 2018. "Landscape knowledge is an important driver of the fission dynamics of an alpine ungulate." *Animal Behaviour* 140: 39–47.

Leu, Stephan T, Jim Bashford, Peter M Kappeler, and C Michael Bull. 2010. "Association networks reveal social organization in the sleepy lizard." *Animal Behaviour* 79 (1): 217–25.

Long, J. A., T. A. Nelson, S. L. Webb, and K. L. Gee. 2014. "A critical examination of indices of dynamic interaction for wildlife telemetry studies." *Journal of Animal Ecology* 83 (5): 1216–33. <https://doi.org/10.1111/1365-2656.12198>.

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.

Peignier, Mélissa, Quinn M. R. Webber, Erin L. Koen, Michel P. Laforge, Alec L. Robitaille, and Eric Vander Wal. 2019. "Space Use and Social Association in a Gregarious Ungulate: Testing the Conspecific Attraction and Resource Dispersion Hypotheses." *Ecology and Evolution* 9 (9): 5133–45. <https://doi.org/10.1002/ece3.5071>.

Pinter-Wollman, N., E. A. Hobson, J. E. Smith, A. J. Edelman, D. Shizuka, S. De Silva, J. S. Waters, et al. 2014. "The dynamics of animal social networks: Analytical, conceptual, and theoretical advances." *Behavioral Ecology* 25 (2): 242–55. <https://doi.org/10.1093/beheco/arto47>.

Psorakis, I., B. Voelkl, C. J. Garroway, R. Radersma, L. M. Aplin, R. A. Crates, A. Culina, et al. 2015. "Inferring social structure from temporal data." *Behavioral Ecology and Sociobiology* 69 (5): 857–66. <https://doi.org/10.1007/s00265-015-1906-0>.

R Core Team. 2018. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. <https://www.r-project.org/>.

Spiegel, O., S. T. Leu, A. Sih, and C. M. Bull. 2016. "Socially interacting or indifferent neighbours? Randomization of movement paths to tease apart social preference and spatial constraints." *Methods in Ecology and Evolution* 7 (8): 971–79. <https://doi.org/10.1111/2041-210X.12553>.

Spiegel, O., A. Sih, S. T. Leu, and C. M. Bull. 2017. "Where should we meet? Mapping social network

interactions of sleepy lizards shows sex-dependent social network structure." *Animal Behaviour* 136: 207–15. <https://doi.org/10.1016/j.anbehav.2017.11.001>.

Tucker, M. A., K. Böhning-Gaese, W. F. Fagan, J. M. Fryxell, B. Van Moorter, S. C. Alberts, A. H. Ali, et al. 2018. "Moving in the Anthropocene: Global reductions in terrestrial mammalian movements." *Science* 359 (6374): 466–69. <https://doi.org/10.1126/science.aam9712>.

Webber, Q. M.R., and E. Vander Wal. 2018. "An evolutionary framework outlining the integration of individual social and spatial ecology." *Journal of Animal Ecology* 87 (1): 113–27. <https://doi.org/10.1111/1365-2656.12773>.

———. 2019. "Trends and perspectives on the use of animal social network analysis in behavioural ecology: a bibliometric approach." *Animal Behaviour* 149: 77–87.

Wey, T., D. T. Blumstein, W. Shen, and F. Jordán. 2008. "Social network analysis of animal behaviour: a promising tool for the study of sociality." *Animal Behaviour* 75 (2): 333–44. <https://doi.org/10.1016/j.anbehav.2007.06.020>.

Table captions

- Table 1

Table 1: expected data input for spatsoc; the relocations for each individual with a timestamp column. These rows are a subset from the package's example caribou movement data of 10 individuals collected every 2 hours. The individual identifier ("ID") and timestamp ("datetime") columns are character type and the coordinates ("X" and "Y") are numeric. This example shows the first three relocations for four individuals (E, F, G, and H).

Figure Captions

- Figure 1

Figure 1: temporal grouping with `group_times`. A) A full temporal data stream of regular fixes at two hour intervals for four individuals (example data described in Table 1). B) An example showing the temporal deviation around the set fix rate. Temporal grouping with a threshold of five minutes groups these relocations to the nearest five minute interval. Times within the temporal threshold, e.g. five minutes in this case, are grouped together. C) temporal grouping with a threshold of eight hours showing the relocations being grouped to the nearest eight hour interval. D) temporal grouping with a threshold of ten days with all relocations being grouped in ten day chunks.

- Figure 2

Figure 2: point based spatial grouping with `group_pts`. A) Three relocations for four individuals in three time groups (example data described in Table 1). The relocation in the second timegroup for all individuals is buffered, to depict the distance threshold (in this case 50m) to generate spatial groups. The temporal threshold used is five minutes (see Figure 1 B). B) A distance matrix of relocations for all four individuals at timegroup 2 where highlighted rows are pairwise distances that meet the user defined criteria for spatial grouping, i.e. are less than the spatial threshold. C) The connected components showing the chain rule implementation of point based distance grouping with `group_pts`. The connected components show individuals E, F and G grouped (group 2 coloured blue), despite individual F and G being further apart than the spatial threshold, since they were both within the threshold distance from E. Individual H is assigned a group on their own, since they are not within the spatial threshold of any other individuals (group 9 coloured pink). D) Output spatiotemporal groups from `group_pts` showing individuals ("ID"), timegroups ("timegroup") and spatiotemporal groups ("group").

- Figure 3

Figure 3: line based spatial grouping with `group_lines`. A) Three daily trajectories for four individuals generated using a time threshold of one day (see Figure 1 C) and `group_lines` (example data described in Table 1). A spatial threshold of 50m is used, represented by the buffered portions around each individual's trajectory on the second day, or timegroup 2. B) Output spatial groups from `group_pts` showing individuals ("ID"), timegroups ("timegroup") and spatiotemporal groups ("group").

- Figure 4

Figure 4: home range based spatial grouping with `group_polys`. A) Home ranges for four individuals

generated using a temporal threshold of 30 days (see Figure 1 D). `group_pts` generates and groups overlapping home ranges of individuals. It either returns B) binary overlap or C) a measure of proportional area containing the area of overlap (km^2) and proportion of overlap among individuals.

- Figure 5

Figure 5: Edge list generating functions `edge_nn` and `edge_dist`. Panels show relocations and output edge lists for four individuals (E, F, G, H) for one timegroup from example data described in Table 1. Note the distances between individuals shown here is presented in Figure 2 panel B. A) and B) show edges generated with `edge_dist`. Edges between individuals are generated if the distance between relocations is within the spatial threshold. C) and D) show edges generated with `edge_nn`. Edges are created by identifying the nearest neighbour to each individual in each timegroup. Optionally, users may specify a maximum distance within which to consider a nearest neighbour relevant.