BIOL 452B Term Paper

The socio-spatial ecology of giant anteaters in the Brazilian Cerrado

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# Introduction

Mammalian sociality is complex and multifarious and can be shaped by biological factors, ecological conditions, and environmental change (Crook, Ellis & Goss-Custard, 1976). Understanding these drivers are fundamental in ethology and ecology (Darwin, 1859; Tinbergen, 1963). Spatial behaviour is highly intertwined with social behaviour, which influences movement behaviour and begets movement patterns (Webber *et al.*, 2023). Understanding socio-spatial ecology provides insight into how species are structured in space, how individuals interact with conspecifics and inform conservation policy (Bro-Jørgensen, Franks & Meise, 2019). Moreover, understanding such complexities can make it possible to predict how environmental forces may influence social behaviour and organization (Crook *et al.*, 1976) in the future under climate change.

Giant anteaters (*Myrmecophaga tridactyla*) are the largest extant anteater species reaching 2 m in length and 50 kg in weight (McNab, 1984; Toledo *et al.*, 2015). They are a carnivorous mammal and a specialized insectivore that feed on ants and termites (McNab, 1984). Although giant anteaters lack teeth, they have a well-developed olfactory system, suggesting an excellent sense of smell (Mcadam & Way, 1967). Moreover, they have an elongated snout and a tongue reaching 45 cm in length (Naples, 1999; Ferreira-Cardoso *et al.*, 2020). Giant anteaters have low basal metabolic rates, poor body temperature regulation (McNab, 1984), and use forest patches as a thermal refuge (Giroux *et al.*, 2021, 2022), making them vulnerable to environmental change.

Giant anteaters are native to Central and South America (Miranda, Bertassoni & Abba, 2014) and are generally found in open area grasslands and forest habitats (Mourão & Medri, 2007; Di Blanco, Jiménez Pérez & Di Bitetti, 2015). They have been experiencing population declines due to habitat loss, vehicle collisions, and fires (Miranda *et al.*, 2014; Noonan *et al.*, 2022). Giant anteaters are classified as vulnerable, with a risk of local extinction throughout their range (Miranda *et al.*, 2014). Their lifespan in the wild is currently unknown, they have a low reproductive rate, with females producing one pup a year (Miranda *et al.*, 2014) and low density (<1/km2) (Bertassoni, Bianchi & Desbiez, 2021). Therefore, the loss of forest patches due to human encroachment and climate change will further threaten their survival. Despite both the theoretical and applied values of understanding their socio-spatial ecology, little is known about how giant anteater social systems are structured in space and hamper conservation efforts.

Advances in global positioning system (GPS) technology have allowed the opportunity to study animals in their natural habitat, undisturbed, to explicate the socio-spatial behaviour with higher precision (Cooke *et al.*, 2004, 2017; Nathan *et al.*, 2022). The use of GPS technology provides new possibilities to tackle challenges that were once unfeasible to be overcome. Moreover, GPS tracking data can estimate fine-scaled interactions between individuals (Schlägel *et al.*, 2019). The analysis of wildlife tracking data can elucidate behaviour and behavioural changes across individuals, populations, and species in response to environmental change (Katzner & Arlettaz, 2020; Nathan *et al.*, 2022). Identifying changes within the socio-spatial dynamics within a population can serve as indicators of the environment (Nathan *et al.*, 2022). Moreover, the social-spatial differences and changes in individuals can have ecological consequences (Hertel *et al.*, 2020).

The recent advances in GPS technology have allowed giant anteaters to be studied in the wild in detail. We aim to describe giant anteater socio-spatial ecology using the first fine-scaled GPS tracking data collected from 2017 to 2018 at 20-minute intervals from 23 giant anteaters simultaneously in the Brazilian Cerrado. In this paper, we investigated the home range, the spatial relationship and the socio-spatial behaviour using continuous-time stochastic processes to

i) estimate and describe patterns in their home range overlap; ii) quantify the extent to which they co-occurred in both time and space; and iii) test for any correlations in their movement.

Findings are directly applicable for sustainable development as an integrated approach towards area-based management for the conservation of giant anteaters, other similar mammals and their habitat.

# Methods

## Study area

The data were collected in two sites in the Cerrado biome (savannah) within the Mato Grosso do Sul (MS) state of Brazil. MS has a tropical climate with average temperature ranges of 21 to 32&deg;C year-round, with the dry season from April to September and the wet season from October to March (Alvares *et al.*, 2013; Noonan *et al.*, 2022). The average annual rainfall ranges from 1000-1500 mm (Alvares *et al.*, 2013; Noonan *et al.*, 2022). The landscape was primarily dominated by agriculture and fragmented landscape with sparse densities of natural forest and savanna habitat (Noonan *et al.*, 2022). The area of the two study sites was mainly composed of riparian and savanna vegetation (Noonan *et al.*, 2022).

## Data collection

GPS tracking data was collected between 2017 to 2018 from wild giant anteaters equipped with GPS tracking harnesses. The data consisted of 847 683 GPS fixes for a total of 12 761 individual days. Of the 43 individuals within the data, 23 range-resident giant anteaters at two sites were selected, with a total of 528 324 GPS fixes. The dataset contained no outliers as they were removed based on error-informed distance from the median location and the minimum speed required for the displacement of each location.

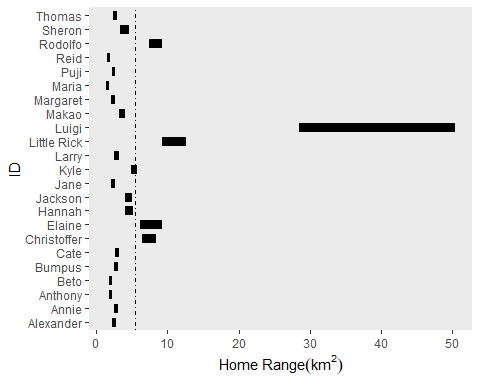
## Data analysis

All formal statistical analysis and plotting were carried out using R (version 4.2.2) and the following R packages 'ctmm' (version 1.1.0, Fleming and Calabrese 2022), 'lme4' (version 1.1.31, Bates et al. 2015), 'CorrMove' (version 0.1.0, Calabrese and Fleming 2023) and 'ggplot2' (version 3.4.2, Wickham 2016). All R scripts can be found in the GitHub repository at <https://github.com/QuantitativeEcologyLab/giantanteater>. Details of the analyzes are found in the Appendix.

First, we fitted a series of continuous-time movement models (CTMM) using the ctmm R package to the tracking data and selected the best CTMM (Calabrese & Fleming, 2023). We estimated the home range of each giant anteater by creating aligned utilization distribution using autocorrelated Kernel density estimation (AKDE) (Fleming et al., 2015). To evaluate the spatial relationship, we calculated the overlap of their home range from their AKDE. We were interested in understanding if the sex of the individual influenced the home range overlap. To determine whether the sex of the individuals was significant, we used a generalized linear mixed effects model with a binomial distribution using the lme4 R package to evaluate whether sex was a factor in the presence of home range overlap and if so, to what degree of overlap (Bates et al., 2015).

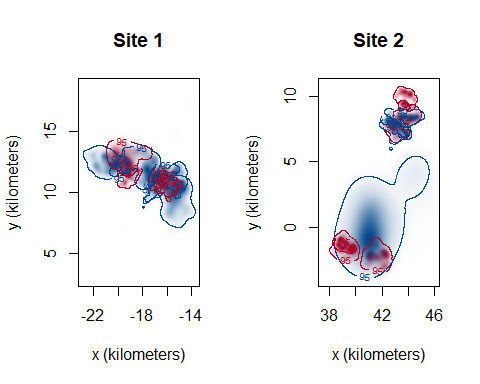
Focusing on the home range overlap dyadic relationships, we calculated the proximity statistics using the ctmm package across all individuals (Fleming & Calabrese, 2022). Using proximity as an indicator of a potential social interaction or response (Buderman et al., 2021), we used a proximity ratio estimation to identify individuals who had a difference in distance relative to each other. Proximity refers to the nearness or closeness in space-time, ergo, how close were each individual at each time-interval recording spatially (Joo et al., 2018). Once a dyad was identified, we calculated the instantaneous Euclidean distance between the dyad using the ctmm package to provide a measurement metric of nearness (Fleming & Calabrese, 2022) between the giant anteaters as an indicator of potential interaction (Long & Nelson, 2013). To determine if the movement giant anteaters are related or independent based on dyadic relationships, we calculated the correlative movement indices using the CorrMove package (Calabrese and Fleming 2023).

# Results



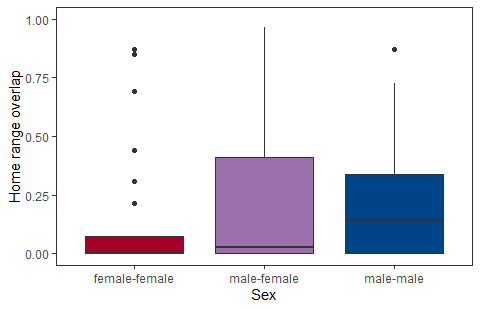
Scatter plots of home range size of each giant anteater. The dash line denotes the mean home range size.

The mean home range size was 5.46 km2 ranging from 4.55 to 6.46 km2 across all giant anteaters. The home range sizes differed between sex. The mean home range for males was 7.38 km2 ranging from 6.04 to 8.88 km2. The mean home range for females was 3.35 km2 ranging from 2.92 to 3.81 km2.



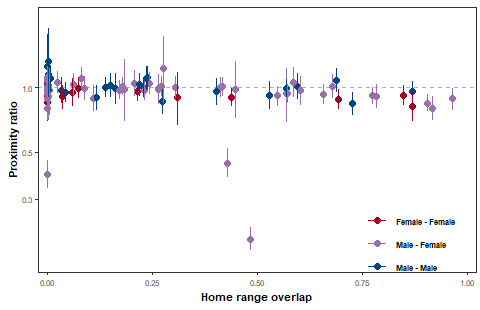
Home range overlap 95% CI estimate of giant anteaters using autocorrelated kernel density estimate (AKDE). Blue home range indicates male. Red home range indicates female. The deeper in colouration indicates the giant anteater spent more time in that area.

The home range overlap showed that all giant anteaters had a home range that overlapped with at least one other individual, and we found a total of 121 unique dyad overlaps.



Sex comparison of the home range overlap 95% CI estimate of giant anteaters using autocorrelated kernel density estimate (AKDE).

There was no evidence that home range overlap occurrence differed between sexes (p = 0.58).



Proximity ratio values. A value above 1 were further apart or values below 1 were closer on average than expected for independent movement (Fleming & Calabrese, 2022).

The proximity ratio showed that a dyad had a value above 1, and 11 dyads consisting of 17 individuals had a value below 1. The association between pairs of individuals was generally weak, with no sign of correlative movement. We found no trends in their spatial-temporal co-occurrences.

# Discussion

The evolution of social behaviour is neither unidirectional nor hierarchical, with eusociality being the ultimate phenotypic trait to evolve to (Wcislo & Danforth, 1997). Therefore, contrarious social behaviour can arise and present differently taxonomically. Understanding the socio-spatial ecology is essential for conservation efforts in protecting species and managing populations (Bro-Jørgensen et al., 2019), especially for species such as Giant anteaters that are vulnerable to habitat loss and climate change. Therefore, the knowledge gap in the spatial structure of the social system of giant anteaters presents conservation challenges.

From the fine-scaled GPS tracking data of 23 giant anteaters, we found no evidence of patterns in the home range overlap. The resource dispersion hypothesis predicts that if resources are not limited, multiple individuals can share the same space (i.e. home range overlap) with conspecifics (Elbroch et al., 2017), suggesting that giant anteaters may also experience resource richness within their environment. We found that every giant anteater had at least one dyadic relationship in home range overlap, suggesting they may not be a territorial species (Isbell et al., 2021; Schlichting et al., 2022). The lack of territoriality may also predict indifference or tolerance behaviour between individuals, which is not indicative of a territorial species (Minta, 1993; Isbell et al., 2021). Moreover, based on the kinship theory, individuals may be tolerant or willing to share space and resources due to relatedness (Hamilton, 1964; Rogers, 1987; Støen et al., 2005; Smith, 2014; Elbroch et al., 2017). Based on the correlative movement analysis, there was no evidence of agonistic behaviour or avoidance behaviour that is indicative of territoriality (Isbell et al., 2021). Consequently, the home range overlap did not show well-defined territories which may suggest that the area may be indefensible (Isbell et al., 2021). The defensibility of resources can provide insight into the mating system of giant anteaters (Clutton-Brock, 1989).

Our results revealed no sex-based patterns indicative of female defence theory (Palomares et al., 2017) in the home range overlap, which could infer a polygamy mating system (Crook et al., 1976; Ostfeld, 1987; Clutton-Brock, 1989). Moreover, our analysis found no evidence of mate guarding behaviour which is observed with territorial behaviour (Walther, 1991; Palomares et al., 2017). No evidence suggested cohesive or correlative movement that indicates mate guarding, aggregation or lekking, and herding to a mating site (Clutton-Brock, 1989; Walther, 1991). Social systems of mammals are often based on the reproductive strategies of the species (Clutton-Brock, 2009) as a foundation of social behaviours; however, they are not wholly derived from mating behaviour (Prox & Farine, 2020).

Most carnivores are described as solitary (Bekoff, Daniels & Gittleman, 1984; Sandell, 1989), where animals exhibit asynchronous or independent movement (Kappeler & van Schaik, 2002) and giant anteaters are no exception. Giant anteaters are described as mostly solitary in the wild except during mating season (Shaw, Machado-Neto & Carter, 1987; Braga, Santos & Batista, 2010). Solitary species may be more vulnerable to climate change due to their solitary behaviour than social species that may have the group support to attenuate the effects of a changing environment (Olivier, Schradin & Makuya, 2022). Therefore, understanding the socio-spatial ecology of a solitary species is crucial for conservation efforts (Olivier et al., 2022), especially if solitary behaviour does not lead nor evolve into adaptive social strategies (Elbroch et al., 2017).

Our findings suggest giant anteaters exhibit solitary behaviour regardless of sex. Based on kinship theory, the spatial distribution of solitary species is driven by neighbouring conspecifics where an individual may be more tolerant due to relatedness (Hamilton, 1964; Rogers, 1987; Elbroch et al., 2017). Solitary behaviour can occur with spatial relationships where conspecifics have overlapping home ranges (Minta, 1993). The giant anteaters do not actively avoid each other or exhibit cohesive movements indicative of social behaviour (Giardina, 2008). When individuals are within close proximity of each other for interaction, they exhibit independent movement, which suggests asocial behaviour (Sandell, 1989; Yoerg, 1999). Arguably, there have been observational reports of courtship behaviour where cohesion movement is recorded in terms of following behaviour during mating season (Júnior & Bertassoni, 2014). Furthermore, agonistic behaviour and social interactions between individuals during the mating season have also been documented (Shaw et al., 1987; Júnior & Bertassoni, 2014). Shaw et al. (1987) highlight that activity patterns differ geographically; therefore, our findings may be only reserved for the individuals that have been tracked, and the social behaviour exhibited does not reflect the whole population or species (i.e., differ across the range).

# Conclusion

While many social behaviour hypotheses try to explain the evolution of social behaviour in animals, they also explain solitary behaviour. Using fine-scaled GPS tracking data allowed us to make inferences on the socio-spatial ecology of giant anteaters. There were no sex-based trends, mate guarding or territorial behaviour, signifying that giant anteaters have a polygamy mating system. Our findings suggest giant anteaters are solitary species that readily share space with conspecifics. Such information is crucial for area-based management strategies for sustainable development while maintaining ecological integrity and the conservation of giant anteaters and their habitats. Future studies should include the genetics of giant anteaters to provide further insight into socio-spatial behaviour as a consequence of kinship.

# References

Alvares, C.A., Stape, J.L., Sentelhas, P.C., De Moraes Gonçalves, J.L. & Sparovek, G. (2013). Köppen’s climate classification map for Brazil. *metz* **22**, 711–728.

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using **lme4**. *J. Stat. Soft.* **67**.

Bekoff, M., Daniels, T.J. & Gittleman, J.L. (1984). Life History Patterns and the Comparative Social Ecology of Carnivores. *Annu. Rev. Ecol. Syst.* **15**, 191–232.

Bertassoni, A., Bianchi, R.D.C. & Desbiez, A.L.J. (2021). Giant Anteater Population Density Estimation and Viability Analysis Through Motion‐Sensitive Camera Records. *Jour. Wild. Mgmt.* **85**, 1554–1562.

Braga, F.G., Santos, R.E.F. & Batista, A.C. (2010). Marking behavior of the giant anteater Myrmecophaga tridactyla (Mammalia: Myrmecophagidae) in Southern Brazil. *Zoologia (Curitiba, Impr.)* **27**, 07–12.

Bro-Jørgensen, J., Franks, D.W. & Meise, K. (2019). Linking behaviour to dynamics of populations and communities: application of novel approaches in behavioural ecology to conservation. *Phil. Trans. R. Soc. B* **374**, 20190008.

Buderman, F.E., Gingery, T.M., Diefenbach, D.R., Gigliotti, L.C., Begley-Miller, D., McDill, M.M., Wallingford, B.D., Rosenberry, C.S. & Drohan, P.J. (2021). Caution is warranted when using animal space-use and movement to infer behavioral states. *Movement Ecology* **9**, 30.

Calabrese, J.M. & Fleming, C.H. (2023). corrMove: Analyze Correlated Movements in Multi-Individual Datasets.

Clutton-Brock, T. (2009). Structure and function in mammalian societies. *Phil. Trans. R. Soc. B* **364**, 3229–3242.

Clutton-Brock, T.H. (1989). Review Lecture: Mammalian mating systems. *Proceedings of the Royal Society of London. Series B, Biological sciences* **236**.

Cooke, S.J., Hinch, S.G., Wikelski, M., Andrews, R.D., Kuchel, L.J., Wolcott, T.G. & Butler, P.J. (2004). Biotelemetry: a mechanistic approach to ecology. *Trends in Ecology & Evolution* **19**, 334–343.

Cooke, S.J., Nguyen, V.M., Kessel, S.T., Hussey, N.E., Young, N. & Ford, A.T. (2017). Troubling issues at the frontier of animal tracking for conservation and management: Troubling Issues at the Frontier of Animal Tracking. *Conservation Biology* **31**, 1205–1207.

Crook, J.H., Ellis, J.E. & Goss-Custard, J.D. (1976). Mammalian social systems: Structure and function. *Animal Behaviour* **24**, 261–274.

Darwin, C. (1859). *On the origin of species by means of natural selection, or, The preservation of favoured races in the struggle for life*. 1st edn. London: John Murray.

Di Blanco, Y.E., Jiménez Pérez, I. & Di Bitetti, M.S. (2015). Habitat selection in reintroduced giant anteaters: the critical role of conservation areas. *JMAMMAL* **96**, 1024–1035.

Elbroch, L.M., Levy, M., Lubell, M., Quigley, H. & Caragiulo, A. (2017). Adaptive social strategies in a solitary carnivore. *Sci. Adv.* **3**, e1701218.

Ferreira-Cardoso, S., Fabre, P.-H., De Thoisy, B., Delsuc, F. & Hautier, L. (2020). Comparative masticatory myology in anteaters and its implications for interpreting morphological convergence in myrmecophagous placentals. *PeerJ* **8**, e9690.

Fleming, C.H. & Calabrese, J.M. (2022). ctmm: Continuous-Time Movement Modeling.

Fleming, C.H., Fagan, W.F., Mueller, T., Olson, K.A., Leimgruber, P. & Calabrese, J.M. (2015). Rigorous home range estimation with movement data: a new autocorrelated kernel density estimator. *Ecology* **96**, 1182–1188.

Giardina, I. (2008). Collective behavior in animal groups: Theoretical models and empirical studies. *HFSP Journal* **2**, 205–219.

Giroux, A., Ortega, Z., Bertassoni, A., Desbiez, A.L.J., Kluyber, D., Massocato, G.F., De Miranda, G., Mourão, G., Surita, L., Attias, N., Bianchi, R. de C., Gasparotto, V.P. de O. & Oliveira‐Santos, L.G.R. (2022). The role of environmental temperature on movement patterns of giant anteaters. *Integr. Zool.* **17**, 285–296.

Giroux, A., Ortega, Z., Oliveira-Santos, L.G.R., Attias, N., Bertassoni, A. & Desbiez, A.L.J. (2021). Sexual, allometric and forest cover effects on giant anteaters’ movement ecology. *PLoS ONE* **16**, e0253345.

Hamilton, W.D. (1964). The genetical evolution of social behaviour. I. *Journal of Theoretical Biology* **7**, 1–16.

Hertel, A.G., Niemelä, P.T., Dingemanse, N.J. & Mueller, T. (2020). A guide for studying among-individual behavioral variation from movement data in the wild. *Movement Ecology* **8**, 30.

Isbell, L.A., Bidner, L.R., Loftus, J.C., Kimuyu, D.M. & Young, T.P. (2021). Absentee owners and overlapping home ranges in a territorial species. *Behav Ecol Sociobiol* **75**, 21.

Joo, R., Etienne, M.-P., Bez, N. & Mahévas, S. (2018). Metrics for describing dyadic movement: a review. *Movement Ecology* **6**, 26.

Júnior, J.F.M. & Bertassoni, A. (2014). Potential Agonistic Courtship and Mating Behavior between Two Adult Giant Anteaters ( *Myrmecophaga tridactyla* ). *Edentata* **15**, 69–72.

Kappeler, P.M. & van Schaik, C.P. (2002). Evolution of Primate Social Systems. *International Journal of Primatology*.

Katzner, T.E. & Arlettaz, R. (2020). Evaluating Contributions of Recent Tracking-Based Animal Movement Ecology to Conservation Management. *Front. Ecol. Evol.* **7**, 519.

Long, J.A. & Nelson, T.A. (2013). Measuring Dynamic Interaction in Movement Data. *Transactions in GIS* **17**, 62–77.

Mcadam, D.W. & Way, J.S. (1967). Olfactory Discrimination in the Giant Anteater. *Nature* **214**, 316–317.

McNab, B.K. (1984). Physiological convergence amongst ant‐eating and termite‐eating mammals. *Journal of Zoology* **203**, 485–510.

Minta, S.C. (1993). Sexual differences in spatio-temporal interaction among badgers. *Oecologia* **96**, 402–409.

Miranda, F., Bertassoni, A. & Abba, A.M. (2014). *Myrmecophaga tridactyla* ( No. e. T14224A47441961). , The IUCN Red List of Threatened Species. International Union for Conservation of Nature and Natural Resources.

Mourão, G. & Medri, Í.M. (2007). Activity of a specialized insectivorous mammal (Myrmecophaga tridactyla) in the Pantanal of Brazil. *Journal of Zoology* **271**, 187–192.

Naples, V.L. (1999). Morphology, evolution and function of feeding in the giant anteater ( *Myrmecophaga tridactyla* ). *Journal of Zoology* **249**, 19–41.

Nathan, R., Monk, C.T., Arlinghaus, R., Adam, T., Alós, J., Assaf, M., Baktoft, H., Beardsworth, C.E., Bertram, M.G., Bijleveld, A.I., Brodin, T., Brooks, J.L., Campos-Candela, A., Cooke, S.J., Gjelland, K.Ø., Gupte, P.R., Harel, R., Hellström, G., Jeltsch, F., Killen, S.S., Klefoth, T., Langrock, R., Lennox, R.J., Lourie, E., Madden, J.R., Orchan, Y., Pauwels, I.S., Říha, M., Roeleke, M., Schlägel, U.E., Shohami, D., Signer, J., Toledo, S., Vilk, O., Westrelin, S., Whiteside, M.A. & Jarić, I. (2022). Big-data approaches lead to an increased understanding of the ecology of animal movement. *Science* **375**, eabg1780.

Noonan, M.J., Ascensão, F., Yogui, D.R. & Desbiez, A.L.J. (2022). Roads as ecological traps for giant anteaters. *Animal Conservation* **25**, 182–194.

Olivier, C.-A., Schradin, C. & Makuya, L. (2022). Global Change and Conservation of Solitary Mammals. *Front. Ecol. Evol.* **10**, 906446.

Ostfeld, R.S. (1987). On the Distinction between Female Defense and Resource Defense Polygyny. *Oikos* **48**, 238.

Palomares, F., Lucena-Pérez, M., López-Bao, J.V. & Godoy, J.A. (2017). Territoriality ensures paternity in a solitary carnivore mammal. *Sci Rep* **7**, 4494.

Prox, L. & Farine, D. (2020). A framework for conceptualizing dimensions of social organization in mammals. *Ecol Evol* **10**, 791–807.

Rogers, L.L. (1987). Effects of Food Supply and Kinship on Social Behavior, Movements, and Population Growth of Black Bears in Northeastern Minnesota. *Wildlife Monographs* 3–72.

Sandell, M. (1989). The Mating Tactics and Spacing Patterns of Solitary Carnivores. In *Carnivore Behavior, Ecology, and Evolution*: 164–182. Gittleman, J.L. (Ed.). Boston, MA: Springer US.

Schlägel, U.E., Signer, J., Herde, A., Eden, S., Jeltsch, F., Eccard, J.A. & Dammhahn, M. (2019). Estimating interactions between individuals from concurrent animal movements. *Methods Ecol Evol* **10**, 1234–1245.

Schlichting, P.E., Boughton, R.K., Anderson, W., Wight, B., VerCauteren, K.C., Miller, R.S. & Lewis, J.S. (2022). Seasonal variation in space use and territoriality in a large mammal (Sus scrofa). *Sci Rep* **12**, 4023.

Shaw, J.H., Machado-Neto, J. & Carter, T.S. (1987). Behavior of Free-Living Giant Anteaters (Myrmecophaga tridactyla). *Biotropica* **19**, 255.

Smith, J.E. (2014). Hamilton’s legacy: kinship, cooperation and social tolerance in mammalian groups. *Animal Behaviour* **92**, 291–304.

Støen, O.-G., Bellemain, E., Sæbø, S. & Swenson, J.E. (2005). Kin-related spatial structure in brown bears Ursus arctos. *Behav Ecol Sociobiol* **59**, 191–197.

Tinbergen, N. (1963). On aims and methods of Ethology. *Zeitschrift für Tierpsychologie* **20**, 410–433.

Toledo, N., Bargo, M.S., Vizcaíno, S.F., De Iuliis, G. & Pujos, F. (2015). Evolution of body size in anteaters and sloths (Xenarthra, Pilosa): phylogeny, metabolism, diet and substrate preferences. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **106**, 289–301.

Walther, F.R. (1991). On herding behavior. *Applied Animal Behaviour Science* **29**, 5–13.

Wcislo, W.T. & Danforth, B.N. (1997). Secondarily solitary: the evolutionary loss of social behavior. *Trends in Ecology & Evolution* **12**, 468–474.

Webber, Q.M.R., Albery, G.F., Farine, D.R., Pinter‐Wollman, N., Sharma, N., Spiegel, O., Vander Wal, E. & Manlove, K. (2023). Behavioural ecology at the spatial–social interface. *Biological Reviews* brv.12934.

Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York.

Yoerg, S.I. (1999). Solitary is not Asocial: Effects of Social Contact in Kangaroo Rats (Heteromyidae: Dipodomys heermanni). *Ethology* **105**, 317–333.