Density-dependent network structuring within and across wild animal systems

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Abstract

Theory predicts that high population density leads to more strongly connected spatial and social networks, but how local density drives individuals' positions within their networks is unclear. This reduces our ability to understand and predict density-dependent processes. Here, we show that density drives greater network connectedness at the scale of individuals within wild animal populations. Across 36 datasets of spatial and social behaviour in >58,000 individual animals, spanning 30 species of fish, reptiles, birds, mammals and insects, 80% of systems exhibit strong positive relationships between local density and network centrality. However, >80% of relationships are nonlinear and 75% are shallower at higher values, indicating saturating trends as demographic and behavioural processes counteract density's effects. These are stronger and less saturating in spatial than social networks, as individuals become disproportionately spatially connected rather than socially at higher densities. Consequently, ecological processes that depend on spatial connections are likely more density-dependent than those involving social interactions. These findings suggest fundamental scaling rules governing animal social dynamics and could help to predict network structures in novel systems.

Keywords: Behavioural ecology, Spatial ecology, Disease ecology, Epidemiology, Population dynamics, Social network structure, Network analysis, Spatial analysis

Introduction

The number of individuals occupying a given space – i.e., population density – is a central factor governing social systems. At higher densities, individuals are expected to more frequently share space, associate, and interact, producing more-connected spatial and social networks and thereby influencing downstream processes such as mating, learning, and competition. In particular, density-driven increases in network connectedness should provide more opportunities for parasites [1–5] or information [6] to spread between hosts[1–4,9] Despite the fundamental nature of such density-dependent processes, evidence is relatively limited that individuals inhabiting higher-density areas have more spatial and social connections. Furthermore, density effects should differ for asynchronous space sharing (e.g. home range overlap) *versus* social associations (e.g. den sharing or grouping) or interactions (e.g. mating or fighting). While several studies have compared animal populations at different densities to demonstrate variation in social association rates among populations (e.g., [7–9]) or groups (e.g., [10–12]), attempts to identify such density effects *within* continuous populations of individuals are rarer (but see [9,13–16]), and their findings have never been synthesised or compared for spatial and social behaviours. We therefore have an incomplete understanding of how density, as a fundamental ecological parameter, determines socio-spatial dynamics within and across systems. This inhibits our ability to identify and predict how changes in density – e.g. through culling, natural mortality, dispersal, or population booms – influence downstream processes that depend on shared space and social interactions.

The rate at which an individual interacts with conspecifics depends on its spatial and social behaviour within the context of the surrounding environment and population. Adding more individuals into the same space should cause them to more frequently spatially overlap and socially associate or interact (Figure 1). Often, individuals are modelled as randomly moving and interacting molecules ("mass action" or "mean field"). In this conceptualisation, direct contact between two molecules is analogous to a social interaction or association; rates of such interactions are often assumed to increase with density ("density-dependent"; e.g., [17]), and/or to be homogenous in space (e.g., [12]). In reality individuals are unlikely to behave and interact randomly in space, and instead will be influenced by spatially varying factors including local density [18] and competition for resources [9]. Changes in density may cause individuals to alter their foraging behaviour [19–21], dispersal [22,23], social preference or avoidance [15,24], mating behaviour [25], or preferred group size [8]. In some cases, density may have no effect on interaction rates, because individual animals alter their behaviour in a density-dependent manner to maintain a desired interaction rate [26]. These and related processes might produce strong nonlinearities in density-interaction relationships, which can complicate the predictions of density dependence models of pathogen transmission, for example [2,4,5]. For example, individuals or groups can learn to avoid where competitors might go, resulting in greater spatial partitioning under higher densities [27]. Nevertheless, nonlinearities such as these are poorly understood and rarely considered.

Several wild animal studies have suggested relationships between density and social association rates are often nonlinear and saturating [9–12,15]. Such relationships imply that association rates do not increase passively with density, but rather that behavioural or demographic processes likely change as density increases, with the ultimate consequence of slowing association rates. However, these nonlinearities are difficult to examine between populations or between species because they introduce a range of confounders and have few replicates along the density axis [2]. On the other end, lower densities may provide less ability to exert social preferences, but low-density populations may be harder to study due to (for example) low return on sampling investment; alternatively, the failure to achieve sufficient interaction rates may result in Allee effects and ultimately drive populations toward decline [28,29].

Characterising gradients of density across individuals within a population offers a workaround to these problems, and facilitates an appreciation of the fact that interactions occur between individuals rather than at the population level. Examining between-individual variation is one reason that social network analysis – which allows characterisation and analysis of individual-level social traits, amongst other things – has become so popular in animal ecology in recent years [30–34]. Additionally, recent years have seen a substantial growth in understanding of socio-spatial behaviours, including harmonising the concepts of spatial and social density [2,18,35]. Applying network analyses coupled with this socio-spatial understanding of density could provide an individual-level picture of density's effects on spatial and social connectedness, offering far higher resolution and statistical power and greater ability to detect within-system nonlinearities and between-system differences [2]. By providing new understanding of the correlates and emergent consequences of variation in density, this expansion could help to identify general rules underlying social structuring and network scaling in space.

Critically, different types of interactions or associations should show different relationships with density: for example, the need to compete for food at higher densities could drive a disproportionate increase in aggression [36], but this is unlikely to be true of mating interactions. In contrast, higher density and food scarcity should lead to lower exclusivity in resources and more overlapping home ranges, thus enhancing the effect of density on spatial network [37]. This rationale is well-understood in disease ecology, as differences in density-contact relationships are thought to drive differences in density dependence of infection – where "contact" is defined as an interaction or association that could spread a pathogen (Figure 1). "Contacts" then form the basis of spatial and social networks used to investigate pathogen transmission dynamics, which should likewise diverge with density just as contacts do. For example, density should drive greater transmission of respiratory pathogens but not sexually transmitted pathogens [1,38]. Establishing these density-contact relationships is integral to understanding disease dynamics and developing control measures [1,39], but we still have a poor understanding of how different interactions (and therefore contact events for different pathogens) are driven by density. This direct/indirect interaction dichotomy is most fundamental to disease ecology [35,40], but given building interest in the spatial-social interface and relationships between spatial and social networks in behavioural ecology [18], the framework is readily related to other fields (e.g. direct versus indirect cues that can lead to social learning [41]). Previously established density-interaction relationships are diverse and include feral dog bites [13], ant antennations [42] and trophallaxis [26], ungulate group memberships [14,19], rodent co-trapping [10,43], and agamid association patterns [15,16], but no study has yet synthesised how the rates of multiple interaction or association types relate to density, within or across systems.

Identifying the general rules underlying density dependence requires quantifying density's relationship with proxies of interaction rates at fine scales across a diversity of systems, then identifying the factors determining their slope and shape. To this end, we collate a meta-dataset of over 58,000 individual animals across 36 wildlife systems globally (Figure 2) to ask how within-population variation in density determines between-individual interaction rates based on connectedness in spatial and social networks. We fit multiple competing linear and nonlinear relationships to identify the slope and shape of density effects within each system, and we use meta-analyses to investigate general rules determining their slope and shape across systems. In particular, we focus on comparing space sharing with social interactions and associations as a cross-system case study. Ultimately, we present a *de novo* cross-system analysis of individuals' social and spatial behaviour that traverses fields of behavioural, population, and disease ecology, which could help to inform general rules governing the structure of social systems, and eventually shape management and conservation decisions in a wide range of systems.

Results and Discussion

We compiled a comparative meta-dataset of over 14 million observations of 151,835 individual animals' spatial and social behaviour, across a wide range of ecological systems and taxonomic groups of animals. We then ran a standardised pipeline to align their spatial and social observations, identifying strong and predictable relationships between local density and network connectedness at the individual level.

We observed strong positive relationships between individuals' local population density and their connectedness in spatial and social networks across a wide range of wild animals: of our 64 replicates, 51 (78%) were significantly positive when analysed using linear models (Figure 3A). Meta-analyses identified a highly significant positive mean correlation between density and connectedness, both for social networks (Estimate 0.22; 95% CI 0.17, 0.27) and spatial networks (0.45; 0.36, 0.53; Figure 3B). Our study therefore provides fundamental evidence that high local population density broadly drives greater connectedness within ecological systems, at the individual level. Slopes were highly variable across systems for both spatial and social networks (Figure 3A; Q-test of heterogeneity across systems: Q_{37} = 5627.33 and Q_{25} = 1281.83, both P<0.0001), indicating that quantifying these slopes within and between multiple systems and comparing them is important for understanding animal socio-spatial structure. That is, relationships between density and individual connectedness differ substantially between populations, and the biological mechanisms underlying these divergent trends are likely important. As well as adding resolution and allowing comparisons of density effects across systems, our methodology facilitated fitting of nonlinear relationships (using generalised additive models (GAMs); see below). This approach has only rarely been applied before, and then at much coarser resolution (see [10,11,13]). As such, this study fills an important empirical gap by providing insights into the slope and shape of density-connectedness relationships for a diverse variety of animal groups and their social and spatial behaviours (Figure 4). Nevertheless, despite this diversity, we were able to identify several further general trends in our data.

Remarkably, density's effect more than doubled in size for spatial compared to social networks (Figure 3B; r=0.45 *versus* 0.22); there was a difference of 0.26 (CI 0.16, 0.36, P<0.0001) for this effect when we meta-analysed the two contact types together. This finding indicates that as density increases, wild animals are more likely to share space with each other, but that social connections increase at a much slower rate. Similarly, we discovered that saturating shapes were extremely common: as density increased, its effect on connectedness decreased, such that 48/64 systems (75%) had a steeper slope at low density values than at high ones. This effect was strong for both social networks (effect on r= -0.11; CI -0.19, -0.03; P=0.01) and for spatial networks, with substantial overlap between their estimates (-0.22; -0.37, -0.07; P=0.0042). Due to the greater overall effect for space sharing, the latter half of density's spatial effect was still higher than the first half of its social effect (Figure 3C). Together, these observations suggest that density-dependent processes act to limit the increase in social connectedness with density, but without limiting spatial overlaps to the same extent. Consequently, higher-density areas are characterised disproportionately by individuals asynchronously sharing space rather than socially associating, while in lower-density areas individuals are disproportionately more socially connected proportional to their shared space.

There are many possible social reasons for saturating nonlinearity in density-dependent network structuring: for example, individuals in higher density areas may begin to avoid each other, seeking to avoid competition or aggression [36] or exposure to infectious disease [44]. For instance, Eastern water dragons (*Intellagama lesueurii*) show greater avoidance at higher densities [15], supporting avoidance-related mechanisms. Alternatively, in species with high social cognition or stable bonds, saturation could reflect lower social effort or ability to keep track of social affiliates at higher densities [45]. In general, individuals likely have a preferred social interaction rate or group size – a preference that they may increasingly exert at higher densities [8]. It remains to be seen how this preference varies among individuals, and whether individuals vary in their preferred social network position given a certain density. Given that individuals vary in their movement and spatial phenotypes [46–48], and social phenotypes [48–50] in ways that should manifest for density-dependent behaviours specifically [18], it seems likely that these slopes could vary between individuals as they do between populations. Future analyses might fit variable density-connectedness slopes among individuals to identify socio-spatial syndromes across systems, as has been done previously in single systems including caribou (*Rangifer tarandus*) [51] and American red squirrels (*Tamiasciurus hudsonicus*) [52]. Additionally, we could dissect the social network and its relationship to the spatial network to identify levels of attraction [53,54] or avoidance [55] and how they depend on density.

We considered that density-dependent changes in spatial behaviours might explain these trends: for example, density could create greater competition over resources and therefore reduce energy to roam (and contact others). Individuals may partition their niches [56], or reduce their territory or home range sizes [52,57,58], potentially driven by years of plentiful resources supporting higher densities alongside smaller home ranges sufficiently providing ones' resource needs, which could drive lower association rates. However, our findings do not seem to support explanations related to small home ranges, because such explanations should produce an equivalent or stronger reduction in (relative) spatial connectedness. In contrast, we observed that density drove individuals to become spatially connected faster than socially, such that the underlying mechanisms likely involve behaviours and demographic processes that specifically affect social collocation in space and time. Testing the precise underlying mechanism will likely require finer-scale behavioural observations, as described below. Regardless of mechanism, these saturating density-connectedness relationships strongly support the idea that examining density effects at the individual level – rather than between populations – is highly informative. For many systems, "mean field" expectations of homogenous interactions under increasing density likely produce an inaccurate (i.e., inflated) picture of density's effects. Importantly, our study included many examples of proximity-based social networks – most notably "gambit of the group" measures [59] – but relatively few "direct" interactions such as mating, grooming, or fighting. It is interesting that these differences manifested even among two ostensibly spatially-defined contact metrics (gambit of the group and home range overlap). This observation supports the assertion that social association metrics defined by spatiotemporal proximity are valuable for informing on social processes separately from more spatial behaviours *sensu stricto* such as ranging behaviour [14]; we expect that "more direct" interactions could show even further differences in relationships with density. Incorporating a larger number of "direct" metric-based systems could help to address this question (see Supplementary Discussion).

The fact that spatial networks show stronger and more linear density dependence than social networks could heavily influence the ecology of animal systems. For example, indirectly transmitted (i.e., environmentally latent) parasites may exhibit greater density dependence than directly transmitted ones, given that individuals likely experience disproportionately more indirect contact at higher densities. This observation contrasts with orthodoxy that directly transmitted parasites are most likely to be density dependent [60], and supports the value of investigating nonlinear changes in socio-spatial behaviour and grouping patterns in response to density when considering density dependence. Saturating density-connectedness functions further have implications for disease modelling and control. Specifically, our findings lend behavioural support to the growing consensus that many diseases are density-dependent at lower densities, but not at higher densities (i.e., that the slope flattens with density) [17,61]. Rather than assuming constant behavioural mixing at higher densities, epidemiological models could benefit from incorporating density-dependent shifts in behaviours and demography that influence direct and indirect interaction frequencies, as previously suggested empirically and by epidemiological theory [17]. These relationships could influence our targets for culling or vaccination coverage [62]. Given that animals at high density seem likely to have a relatively shallow relationship between density and contact rates, reducing population density – for example by culling – might therefore be ineffective at reducing pathogen transmission initially, particularly when considering socially transmitted pathogens, where contact rates are particularly likely to have become saturated (Figure 3C). Similar problems with culling have already been acknowledged in specific systems – e.g. in canine rabies [39,63,64] – but our study implies that shallow nonlinear density-contact trends could be more general than previously thought and could be driven by flexible density-dependent changes in behaviour and demography. Conversely, culling could be disproportionately effective at intermediate densities and identifying the inflection points of the curve might help to design optimal management strategies. Future studies should investigate whether the divergence in spatial and social connectedness with density drives a concurrent divergence in the prevalence of directly and indirectly transmitted parasites, as well as addressing several other biases in our selection of systems (e.g. [65]; see Supplementary Discussion).

Beyond these general trends, we ran generalised additive models (GAMs) that revealed that 52/64 density effects on network connectedness (81%) were significantly nonlinear (ΔAIC>2); these relationships took a wide variety of shapes, representing a range of nonlinear functions that are hard to generalise (Figure 4). Notably, while many GAM smooths were eventually significantly negative (Figure 4), the vast majority of linear models fitted to the second half of the data were positive (Figure 3C); this result is likely an artefact of restricted model fitting, rather than true downturns in connectedness with density. Nonlinearity did not cluster according to connection type definitions, or according to animal group. These observations were largely corroborated by our meta-analytical models, which found no factors influencing the slope and shape of density effects overall ($P>0.05$; Supplementary Table 3), including no clear phylogenetic signal (ΔAIC=2.71). This observation speaks to the complexity of these relationships within and across systems, while accentuating that simple functional relationships are often likely to be complicated by contravening ecological factors like habitat selection [66,67], group formation [9], parasite avoidance [68], and demographic structuring [69]. While we were unable to identify specific between-system predictors of nonlinearity of density-connectedness relationships, the finding that most such relationships are strongly nonlinear is an important consideration for future work.

Density is a universal factor underlying the dynamics of animal populations, and its linear and nonlinear effects on spatial and social network structure are likely to impact myriad processes in behaviour, ecology, and evolution. Similar to other studies that have reported general scaling patterns in network analysis [70] and in food web ecology [71], the patterns we report strongly suggest that animal systems generally become more connected spatially than socially under increasing density. These trends might extrapolate to human networks, given that other scaling patterns in animal networks do [70]. As these patterns seemingly manifest regardless of animal group and interaction type, they may reflect a generalisable rule governing the socio-spatial structure of ecological systems. Further refining and implementing these models could facilitate prediction of network structure in novel systems.

Finally, this study is relatively unique in conducting an expansive meta-analysis of behavioural data from individual animals across a diverse selection of systems. As datasets accumulate comparative analyses are increasing in frequency in social network ecology [72], but often revolve around analysing whole networks rather than individuals [73], and never (to our knowledge) in conjunction with analyses of spatial behaviour. These analyses therefore hold exceptional promise for disentangling spatial and social behaviour across diverse systems; for example, given that our dataset includes many repeatedly sampled known individuals, future analyses could investigate individual-level repeatability or multi-behaviour "behavioural syndromes" across a variety of different taxa and environments [18,74]. Additionally, capitalising on the wide range of methodological approaches to behavioural data collection (e.g. censuses, trapping, and GPS telemetry), the methodological constraints of socio-spatial analyses could be tested in this wide meta-dataset as they have been in other recent comparative analyses of wild ungulates [75]. As well as being diverse, our meta-dataset had several replicate examples of (for example) marine mammals and trapped rodents, which could be used for finer-scale and more targeted comparative analyses within these smaller taxonomic groupings. For now, it is highly encouraging that we uncovered general trends across these disparate animal systems, and further explorations of these socio-spatial patterns may help to inform a wide range of exciting and longstanding questions at the spatial-social interface [18].

Methods

Data standardisation and behavioural pipeline

Data were manipulated and analysed using R version 4.2.3 [76], and all R code is available at https://github.com/gfalbery/DensityMetaAnalysis. Our 36 datasets each involved at least one continuous uninterrupted spatial distribution of observations in a single population; some datasets comprised multiple such populations; all systems had at least one social network measure, and two had two different types of social interaction. These datasets covered 30 different animal species, including sharks, carnivores, cetaceans, ungulates, rodents, elephants, birds, reptiles, and one orthopteran insect (Figure 2). In one case (The Firth of Tay and Moray Dolphins) we used two distinct replicates despite being composed of overlapping groups of individuals, because of their distinct spatial distributions, which made it difficult to fit a coherent density distribution.

To standardise the timescale across studies, all systems were analysed as annual replicates – i.e., social and spatial networks were summarised within each year. Our analyses used 64 system-behaviour replicates, listed in Supplementary Table 1, and totalled 151,835 unique system-individual-year-behaviour data points.

All spatial coordinates were converted to the scale of kilometres or metres to allow comparison across systems. To provide an approximation of local density, following prior methodology [14,77], we took each individual's average location across the year (their centroid) and created a spatial density kernel using the `adehabitathr` package [78], which provides a probabilistic distribution of population density across each study system based on the local frequencies of observed individuals. Each individual was assigned an annual estimate of local density based on their centroid's location within this spatial density distribution. We made these density distributions as comparable as possible between systems by incorporating the density raster using metre squares; however, there were large differences in density across populations that were difficult to resolve and put on the same scale (e.g. interactions per individual/km^2 unit of density). Consequently, we scaled and centred density to have a mean of zero and a standard deviation of one within each population, which allowed us to focus on differences in relative slope and shape across systems.

To validate the local density measures estimated using the kernel density approach, we also estimated local density for individuals across all populations based on the locations of individual annual centroids within a designated area. To do so, we first estimated the area of the minimum bounding box (MBB) within which all individuals were censused during the study period based on their annual centroids. For each individuals mean location, we then estimated a circular boundary of radius r=1/20 * area of MBB. We then calculated the number of individuals present within this boundary as an individual's local density measure. We estimated the Pearson correlation coefficients between the local density measures derived using the KDE approach and the proportional area - based approach (Supplementary Figure 1).

To provide a measure of asynchronous space sharing, we constructed home range overlap (HRO) networks based on proportional overlap of two individuals' minimum convex polygon (MCP; i.e., the bounding polygon around all observations of each individual in a given year). These HRO networks were restricted to only individuals with five or more observations in a given year to allow us to create convex polygons effectively; 10/36 (28%) systems did not have sufficient sampling for this analysis. We also repeated our analyses with a series of higher sampling requirements for observation numbers to ensure that our findings were robust to this assumption. The MCP approach is relatively low-resolution, and assumes uniform space use across an individual's home range; however, this approach is less data intensive – and less sensitive to assumptions – than density kernel-based approaches that would estimate variation in space use across the home range, allowing us to apply the models across more systems, more generalisably, and more conservatively.

To provide a measure of social connectedness, we built social networks using various approaches as defined by the original studies: direct observations of dyadic interactions (e.g. fighting or mating); gambit of the group (GoG; i.e., membership of the same group) [59]; co-trapping (i.e., trapped together or in adjacent traps within a given number of trapping sessions); or direct contact measured by proximity sensors (defined by a certain distance-based detection threshold). Notably some analyses use indirect interactions – i.e., spatial overlap – to *approximate* direct interactions, which requires spatiotemporal coincidence, which we caution against particularly when modelling pathogen transmission [35,79]. While the two do often correlate, here we are not using HRO to approximate direct interaction rates, but rather as a measure of indirect interactions (e.g., indicative of transmission of environmental parasites).

For each social network, we scaled connection strength relative to the number of observations of each individual in a dyad (i.e., simple ratio index [80]). Our response variable therefore took the form of strength centrality, scaled to between 0-1 for each dyad, for each social and spatial network. We focus on comparing density effects on social interactions and associations with density's effects on space sharing.

Density-connectedness models: what forms do density effects take?

We developed a workflow to allow us to derive and compare density's effects on connectedness – and their drivers – in a standardised way across our animal systems. We fitted models with three main forms: **linear models** fitted to the whole dataset, nonlinear **Generalised additive models** fitted to the whole dataset, and linear **saturation models** fitted separately to low- and high-density subsets of each dataset.

Linear models: For each system-behaviour replicate, we first fitted a linear model using the \`lm\` function in R, fitting scaled density as an explanatory variable to estimate linear density effect slopes. The linear fits are displayed in the supplement (Supplementary Figure 2), as are the residuals (Supplementary Figure 3).

Generalised additive models (GAMs): We fitted GAMs in the \`mgcv\` package [81] to identify whether each density effect was better described by a linear or nonlinear relationship, and to identify the shape of these nonlinear relationships. For each model, we fitted a default thin plate spline with k=4 knots. This knot number was selected to reduce overfitting in our models, which formed several fits to the data that were difficult to reconcile with functional formats. To assess whether nonlinear models fit better than linear models, we used Akaike Information Criterion (AIC), with a contrast of $2\Delta AIC$ designated to distinguish between models.

Saturation models: To quantify whether density effects were generally saturating (i.e., that density had steeper relationships with individuals' connectedness at lower density values), we split the data into two portions: all values below the median density value, and all values above the median. We then re-ran linear models examining the relationship between density and strength in each portion. We attempted to investigate nonlinear patterns (especially saturating effects) across all our systems using a range of other methods (e.g., comparing specific functional relationships with nonlinear least squares), but found that they were generally incapable of fitting well to the data in a standardised way across the many datasets (i.e., non-convergence of nonlinear least squares using semi-automated starting estimates across systems). As such, this approach represented a tradeoff between tractable, generalisable model fitting, interpretability, and accurate representation of the relationship's shape. All else being equal, we posit that investigating the relative slopes of two otherwise-identical portions of the data is a conservative and informative method of identifying saturation, which was our main hypothesis for the expected shape of density effects.

Heteroskedasticity and log-log models: To ensure that our estimates were robust to non-normality and to provide another source of information concerning possible saturation effects, we also conducted tests of heteroskedasticity on our linear models and accompanied them with simulations and fitted log-log linear models. First, we carried out a simple simulation study to test how: a) the skew in residuals; b) a saturating relationship; and c) heteroscedasticity impact whether we may under- or overestimate the slope of an assumed linear relationship between density and strength (See Supplementary Methods - Heteroskedasticity Simulations). These demonstrated that our models were resilient to skew and saturating effects, but that heteroskedasticity in residuals could drive overestimated linear effects in our models.

To examine this possibility further, we derived the Breusch-Pagan statistic for each linear model as a measure of heteroskedasticity, and then plotted it against the meta-analysis covariates and fixed effects. There was no evidence that the density effect was being skewed to be greater for spatial behaviours due to heteroskedasticity, and neither were the second portions of the data more heteroskedastic, which would be expected if this was driving the saturating effect (Supplementary Figure 4). Finally, we fitted log-log linear models with the same formulations as our main linear models defined above, but with both density and strength log(X+1)-transformed, rather than scaled to have a mean of 0 and a standard deviation of 1 (Supplementary Figure 5). Our results showed broadly identical findings of greater estimates for spatial behaviours, and the fact that the slopes were largely under 1 is indicative of a saturating effect. As such, these tests strongly support our findings' resilience to uneven data distributions.

Meta-analysis: what factors determine the slope of density-connectedness relationships?

To characterise the typical relative slope of density effects across systems and identify the factors influencing their variation, we fitted hierarchical meta-analytical models using the `metafor` package in R. The response variable was the standardised slope of the linear density effect; because both individual network strength and density were scaled to have mean of zero and standard deviation of one in the linear regression, this is equivalent to the correlation coefficient (r) [82]. We converted all correlation coefficients into Fisher's Z (Z_r) and computed associated sampling variance.

For our hierarchical meta-analysis models, we used an initial model that nested observations within a system-level random effect to account for within- and between-system heterogeneity [83], as 26/36 systems had more than one density effect. We used another random effect for species to account for repeat observations per animal species.

We then added a separate random effect for animal phylogeny [84]. This effect used a phylogenetic correlation matrix of our 30 animal species derived from the Open Tree of Life via the `rotl` package [85], with the `ape` package used to resolve multichotomies and provide branch lengths [86].

We then fitted intercept-only models using the `rma.mv()` function with restricted maximum likelihood (REML), weighted by inverse sampling variance, and used variance components to quantify I^2, the contribution of true heterogeneity to the total variance in effect size. We used

Cochran's Q to test whether such heterogeneity was greater than that expected by sampling error alone.

We next fitted models with the same random effects structure that included explanatory variables. To detect whether some animals were more likely to experience density effects, we fitted **Animal group** as a factor with six categories, representing a combination of species' taxonomy and general ecology: aquatic (fish and dolphins), birds, large herbivores (elephants and ungulates), small mammals (rodents and hyraxes), carnivores, and ectotherms (insects and reptiles). We also fitted several explanatory variables indicative of greater statistical power that might increase the strength of density effects: **Geographic area** (km^2, log_{10}-transformed), **Number of years** of study, and **Number of individuals**, all of which we fitted as continuous covariates. Broadly, the animal group model was highly uninformative and competed with the other effects, and we expected that the phylogeny would be more informative, so we report the results of the model without the animal group effect fitted.

We ran several different versions of these meta-analyses: first, we fitted meta-analytical models to the **overall linear models** of spatial and social interaction types separately, and then together, to investigate differences between the spatial and social networks in terms of their mean density slope. Next, we fitted duplicated versions of these models, but with the **saturation models**. These models were identical, but each system replicate had two linear estimates: one taken from the first 50% of the data (up to the median), and one from the latter 50%. By fitting a binary fixed effect of "data portion" to the meta-analytical models, this model would tell us whether the slopes were generally higher in the first portion of the data than the last (and therefore showed generally saturating shapes). We were unable to fit meta-analytical models to our GAMMs, as methods for the meta-analysis of nonlinear estimates are not yet well defined.

Data availability

The data required to run the meta-analysis models are available on Zenodo at https://doi.org/10.5281/zenodo.15847435 on GitHub at github.com/gfalbery/DensityMetaAnalysis. Datasets are available from contributing coauthors upon request.

Code availability

All code is available on Zenodo at https://doi.org/10.5281/zenodo.15847435 and on GitHub at github.com/gfalbery/DensityMetaAnalysis.

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Author contributions

GFA conceived of and led the study, collated and analysed the datasets, and wrote the manuscript, supervised by SB. ARS helped with cleaning the data. DJB helped with meta-analysis of the data. SR conducted an independent assessment of the density metric. JAF, DDM, MJS, EVW, and QW advised throughout. All other coauthors donated data. All authors commented on drafts of the manuscript.

Competing interests

The authors declare no competing interests.

Figure legends

Figure 1: Schematic detailing the rationale underlying this study, outlining how population density drives the formation of spatial and social networks. This depiction uses the Wytham Wood great tits as an example. Panel A presents the outline of the woods. In panel B, the points represent individual birds' locations, with some jittering added; the red shading represents local population density. In panel C, the different purple shades correspond to different individuals' home ranges. In panel D, red lines depict connections among individuals, with each individual located at their centroid. Ultimately, one of our main aims is to ask whether spatial or social connections generally show a stronger relationship with density, partly functioning as a proxy for indirect and direct contact events with the potential to transmit pathogens. This framework moves between concepts of network and contact formation traversing behavioural ecology, spatial and social network ecology, and disease ecology.

Figure 2: The phylogenetic (A) and geographic (B) distribution of our 36 examined datasets of spatial and social behaviour, with (C) schematic depicting the methodology for deriving local density values, using the Isle of Rum red deer data as an example. The X and Y axes are bivariate spatial coordinates. The panels within (C) show raw observations of individuals in space that we then average at the individual level to make centroids; we use the centroids to generate annual density distributions, which are then assigned to individuals in the form of local density measures. Animal silhouettes are from phylopic.org; a list of attributions is in the supplement (Supplementary Table 2). NB the Potomac dolphins are now defined as *Tursiops erebennus*; they are currently incorporated in Panel A as *T. truncatus*, following the Open Tree of Life nomenclature.

Figure 3: Meta-analysis revealed drivers of variation in linear density effects on individual network connectedness across N=36 systems comprising N=64 system-behaviour replicates. A) Our fitted linear model estimates of density effects on network strength. Each point represents the mean estimate from a given system; the error bars denote 95% confidence intervals. Opaque error bars were significant (i.e., do not overlap with 0); transparent ones were not. The estimates are in units of standard deviations for both density and network strength. The colour of the point denotes whether the network being examined was defined using spatial or social connections. B) Meta-analyses revealed that centrality in spatial networks (i.e., home range overlap; red points) had a significantly steeper relationship with density than social networks (blue points). C) We fitted linear models separately to two portions of the data within each study population ("first" and "last" represent values below and above the median). The slopes for the latter portion (pink points) were generally less positive than the former portion (purple points), implying a general saturation shape. In panels B) and C), each coloured point represents a study replicate fitted to the strength estimate; points are sized according to sample size, and jittered slightly on the x axis to reduce overplotting. The large black points represent the mean slope estimated from the meta-analysis, and the error bars represent 95% confidence intervals.

Figure 4: Relationships between density and network connectedness varied substantially across N=64 animal systems comprising N=151,835 individual animals. Density in individuals per area is on the x axis; network connectedness (strength centrality) is on the y axis. Both values have been standardised to have a mean of zero and a standard deviation of 1 within each system; the axis ticks are in units of 1 standard deviation. Each point represents an individual-year-behaviour replicate; the lines portray the model fit from our generalised additive models (GAMs). Red lengths of the smooth=significantly positive; grey=not significantly different from zero; blue=significantly negative. Points are semi-transparent to enhance visibility. Panels are arranged phylogenetically following the

tree displayed in Figure 2A; GOG=gambit of the group; HRO=home range overlap. Animal silhouettes are from phylopic.org; a set of links and attributions are in the Supplement.

References

1. Lloyd-Smith JO, Cross PC, Briggs CJ, Daugherty M, Getz WM, Latto J, Sanchez MS, Smith AB, Swei A. 2005 Should we expect population thresholds for wildlife disease? *Trends Ecol Evol* **20**, 511–519. (doi:10.1016/j.tree.2005.07.004)

2. Albery GF. 2022 Density dependence and disease dynamics: moving towards a predictive framework. *EcoEvoRxiv Preprints* (doi:10.32942/OSF.IO/GAW49)

3. Hopkins SR, Fleming-Davies AE, Belden LK, Wojdak JM. 2020 Systematic review of modeling assumptions and empirical evidence: does parasite transmission increase nonlinearly with host density? *Methods Ecol Evol* **11**, 0–2. (doi:10.1111/2041-210x.13361)

4. Begon M, Bennett M, Bowers RG, French NP, Hazel SM, Turner J. 2002 A clarification of transmission terms in host-microparasite models: Numbers, densities and areas. *Epidemiol Infect* **129**, 147–153. (doi:10.1017/S0950268802007148)

5. Ferrari MJ, Perkins SE, Pomeroy LW, Bjrnstad ON. 2011 Pathogens, social networks, and the paradox of transmission scaling. *Interdiscip Perspect Infect Dis* **2011**. (doi:10.1155/2011/267049)

6. Cantor M, Chimento M, Smeele SQ, He P, Papageorgiou D, Aplin LM, Farine DR. 2021 Social network architecture and the tempo of cumulative cultural evolution. *Proceedings of the Royal Society B: Biological Sciences* **288**. (doi:10.1098/rspb.2020.3107)

7. Webber QMR, Vander Wal E. 2020 Heterogeneity in social network connections is density-dependent: implications for disease dynamics in a gregarious ungulate. *Behav Ecol Sociobiol* **74**, 1–13.

8. Beauchamp G. 2011 Functional relationship between group size and population density in Northwest Atlantic seabirds. *Mar Ecol Prog Ser* **435**, 225–233. (doi:10.3354/meps09239)

9. Rouhbakhsh A, Wright AN, Ferguson JM. 2025 Ecological Interactions Drive a Power-Law Relationship Between Group Size and Population Density in Social Foragers. *Ecol Lett* **28**, 70111. (doi:10.1111/ele.70111)

10. Borremans B, Reijniers J, Hens N, Leirs H. 2017 The shape of the contact–density function matters when modelling parasite transmission in fluctuating populations. *R Soc Open Sci* **4**. (doi:10.1098/rsos.171308)

11. Davis S, Abbasi B, Shah S, Telfer S, Begon M. 2015 Spatial analyses of wildlife contact networks. *J R Soc Interface* **12**, 20141004. (doi:10.1098/rsif.2014.1004)

12. Carson BD, Orians CM, Crone EE. 2023 When does spatial clustering in caterpillars inuence the relationship between population density and contact rates? (doi:10.21203/rs.3.rs-2842538/v1)

13. Mancy R *et al.* 2022 Rabies shows how scale of transmission can enable acute infections to persist at low prevalence. *Science (1979)* **376**, 512–516.

14. Albery GF, Morris A, Morris S, Pemberton JM, Clutton-Brock TH, Nussey DH, Firth JA. 2021 Multiple spatial behaviours govern social network positions in a wild ungulate. *Ecol Lett* **24**, 676–686. (doi:10.1101/2020.06.04.135467)

15. Strickland K, Patterson EM, Frère CH. 2018 Eastern water dragons use alternative social tactics at different local densities. *Behav Ecol Sociobiol* **72**. (doi:10.1007/s00265-018-2563-x)

16. Strickland K, Frère CH. 2019 Individual Variation in the Social Plasticity of Water Dragons. *Am Nat* **194**, 194–206. (doi:10.5061/dryad.5j5gh63)

17. Hu H, Nigmatulina K, Eckhoff P. 2013 The scaling of contact rates with population density for the infectious disease models. *Math Biosci* **244**, 125–134. (doi:10.1016/j.mbs.2013.04.013)

18. Webber QMR, Albery GF, Farine DR, Pinter-wollman N, Sharma N, Vander Wal E, Manlove K. 2023 Behavioural ecology at the spatial-social interface. *Biological Reviews* **3**, 868–886.

19. Albon SD, Staines HJ, Guinness FE, Clutton-Brock TH. 1992 Density-Dependent Changes in the Spacing Behaviour of Female Kin in Red Deer. *Journal of Animal Ecology* **61**, 131–137.

20. Vas J, Andersen IL. 2015 Density-dependent spacing behaviour and activity budget in pregnant, domestic goats (Capra hircus). *PLoS One* **10**, e0144583. (doi:10.1371/journal.pone.0144583)

21. Connor EF, Cargain MJ. 1994 Density-related foraging behaviour in Closterocerus tricinctus, a parasitoid of the leaf-mining moth, Cameraria hamadryadella. *Ecol Entomol* **19**, 327–334. (doi:10.1111/J.1365-2311.1994.TB00249.X)

22. Matthysen E. 2005 Density-dependent dispersal in birds and mammals. *Ecography* **28**, 403–416. (doi:10.1111/j.0906-7590.2005.04073.x)

23. Avgar T, Betini GS, Fryxell JM. 2020 Habitat selection patterns are density dependent under the ideal free distribution. *Journal of Animal Ecology* **89**, 2777–2787. (doi:10.1111/1365-2656.13352)

24. Vander Wal E, Laforge MP, Mcloughlin PD, Wal E Vander, Laforge MP, Mcloughlin PD, Vander Wal E, Laforge MP, Mcloughlin PD. 2014 Density dependence in social behaviour: Home range overlap and density interacts to affect conspecific encounter rates in a gregarious ungulate. *Behav Ecol Sociobiol* **68**, 383–390. (doi:10.1007/s00265-013-1652-0)

25. Kokko H, Rankin DJ. 2006 Lonely hearts or sex in the city? Density-dependent effects in mating systems. *Philosophical Transactions of the Royal Society B: Biological Sciences* **361**, 319–334. (doi:10.1098/rstb.2005.1784)

26. Modlmeier AP, Colman E, Hanks EM, Bringenberg R, Bansal S, Hughes DP. 2019 Ant colonies maintain social homeostasis in the face of decreased density. *Elife* **8**, 1–17. (doi:10.7554/eLife.38473)

27. Ogino M, Farine DR. 2024 Collective intelligence facilitates emergent resource partitioning through frequency-dependent learning. *Philosophical Transactions of the Royal Society B: Biological Sciences* **379**. (doi:10.1098/RSTB.2023.0177;JOURNAL:JOURNAL:RSTB1887;WEBSITE:WEBSITE:RSJ-SITE;WGROUP:STRING:PUBLICATION)

28. Stephens PA, Sutherland WJ. 1999 Consequences of the Allee effect for behaviour, ecology and conservation. *Trends Ecol Evol* **14**, 401–405. (doi:10.1016/S0169-5347(99)01684-5)

29. Courchamp F, Clutton-Brock T, Grenfell B. 1999 Inverse density dependence and the Allee effect. *Trends Ecol Evol* **14**, 405–410. (doi:10.1016/S0169-5347(99)01683-3)

30. Farine DR, Whitehead H. 2015 Constructing, conducting and interpreting animal social network analysis. *Journal of Animal Ecology* **84**, 1144–1163. (doi:10.1111/1365-2656.12418)

31. Farine DR. 2024 Modelling animal social networks: New solutions and future directions. *Journal of Animal Ecology* **93**, 250–253. (doi:10.1111/1365-2656.14049)

32. Webber QMR, Vander Wal E. 2019 Trends and perspectives on the use of animal social network analysis in behavioural ecology: a bibliometric approach. *Anim Behav* **149**, 77–87. (doi:10.1016/j.anbehav.2019.01.010)

33. Pinter-Wollman N *et al.* 2014 The dynamics of animal social networks: Analytical, conceptual, and theoretical advances. *Behavioral Ecology* **25**, 242–255. (doi:10.1093/beheco/art047)

34. Sah P, Mann J, Bansal S. 2018 Disease implications of animal social network structure: A synthesis across social systems. *Journal of Animal Ecology* **87**, 546–558. (doi:10.1111/1365-2656.12786)

35. Albery GF, Kirkpatrick L, Firth JA, Bansal S. 2021 Unifying spatial and social network analysis in disease ecology. *Journal of Animal Ecology* **90**, 1–17. (doi:10.1111/1365-2656.13356)

36. Cubaynes S, Macnulty DR, Stahler DR, Quimby KA, Smith DW, Coulson T. 2014 Density-dependent intraspecific aggression regulates survival in northern Yellowstone wolves (Canis lupus). *Journal of Animal Ecology* **83**, 1344–1356. (doi:10.1111/1365-2656.12238)

37. Jetz W, Carbone C, Fulford J, Brown JH. 2004 The scaling of animal space use. *Science (1979)* **306**, 266–268. (doi:10.1126/SCIENCE.1102138/SUPPL_FILE/JETZ.SOM.PDF)

38. Lloyd-Smith JO, Getz WM, Westerhoff H V. 2004 Frequency-dependent incidence in models of sexually transmitted diseases: Portrayal of pair-based transmission and effects of illness on contact behaviour. *Proceedings of the Royal Society B: Biological Sciences* **271**, 625–634. (doi:10.1098/rspb.2003.2632)

39. Morters MK, Restif O, Hampson K, Cleaveland S, Wood JLN, Conlan AJK. 2013 Evidence-based control of canine rabies: A critical review of population density reduction. *Journal of Animal Ecology* **82**, 6–14. (doi:10.1111/j.1365-2656.2012.02033.x)

40. Dougherty ER, Seidel DP, Carlson CJ, Spiegel O, Getz WM. 2018 Going through the motions : incorporating movement analyses into disease research. *Ecol Lett* **21**, 588–604. (doi:10.1111/ele.12917)

41. Hoppitt W, Laland KN. 2008 Chapter 3 Social Processes Influencing Learning in Animals: A Review of the Evidence. *Adv Study Behav* **38**, 105–165. (doi:10.1016/S0065-3454(08)00003-X)

42. Gordon DM, Paul RE, Thorpe K. 1993 What is the function of encounter patterns in ant colonies? *Anim Behav* **45**, 1083–1100. (doi:10.1006/ANBE.1993.1134)

43. Davis S, Abbasi B, Shah S, Telfer S, Begon M, Davis S. 2015 Spatial analyses of wildlife contact networks. *Journal of the Royal Society, Interface / the Royal Society* **12**, 20141004. (doi:10.1098/rsif.2014.1004)

44. Gibson AK, Amoroso CR. 2022 Evolution and Ecology of Parasite Avoidance. *Annu Rev Ecol Evol Syst* **53**, 47–67.

45. Colman E, Colizza V, Hanks EM, Hughes DP, Bansal S. 2021 Social fluidity mobilizes contagion in human and animal populations. *Elife* **10**. (doi:10.7554/ELIFE.62177)

46. Michelangeli M, Payne E, Spiegel O, Sinn D, Leu ST, Gardner M, Sih A. 2022 Personality, spatiotemporal ecological variation, and resident/explorer movement syndromes in the sleepy lizard. *Journal of Animal Ecology* **91**, 210–223. (doi:10.1111/1365-2656.13616)

47. Spiegel O, Leu ST, Bull CM, Sih A. 2017 What's your move? Movement as a link between personality and spatial dynamics in animal populations. *Ecol Lett* **20**, 3–18. (doi:10.1111/ele.12708)

48. Aplin LM, Farine DR, Mann RP, Sheldon BC. 2014 Individual-level personality influences social foraging and collective behaviour in wild birds. *Proceedings of the Royal Society of London B* **281**, 20141016. (doi:10.1098/rspb.2014.1016)

49. Hunt ER, Mi B, Fernandez C, Wong BM, Pruitt JN, Pinter-Wollman N. 2018 Social interactions shape individual and collective personality in social spiders. *Proceedings*

of the Royal Society B: Biological Sciences **285**, 20181366. (doi:10.1098/rspb.2018.1366)

50. Firth JA, Cole EF, Ioannou CC, Quinn JL, Aplin LM, Culina A, McMahon K, Sheldon BC. 2018 Personality shapes pair bonding in a wild bird social system. *Nat Ecol Evol* **2**, 1696–1699. (doi:10.1038/s41559-018-0670-8)

51. Webber Q, Laforge M, Bonar M, Wal E Vander. 2024 The adaptive value of density-dependent habitat specialization and social network centrality. *Nat Commun* **15**, 4423. (doi:10.22541/AU.165210484.46672609/V1)

52. Webber QMR, Dantzer B, Lane JE, Boutin S, McAdam AG. 2023 Density-dependent plasticity in territoriality revealed using social network analysis. *Journal of Animal Ecology* **92**, 207–221. (doi:10.1111/1365-2656.13846)

53. Spiegel O, Leu ST, Sih A, Bull CM. 2016 Socially interacting or indifferent neighbours? Randomization of movement paths to tease apart social preference and spatial constraints. *Methods Ecol Evol* , 971–979. (doi:10.1111/2041-210X.12553)

54. Gahm K, Nguyen R, Acácio M, Anglister N, Vaadia G, Spiegel O, Pinter-Wollman N. 2024 A wrap-around movement path randomization method to distinguish social and spatial drivers of animal interactions. *Philosophical Transactions of the Royal Society B: Biological Sciences* **379**. (doi:10.1098/RSTB.2022.0531,)

55. Strickland K, Levengood A, Foroughirad V, Mann J, Krzyszczyk E, Frère CH. 2017 A framework for the identification of long-term social avoidance in longitudinal datasets. *R Soc Open Sci* **4**. (doi:10.1098/rsos.170641)

56. Sheppard CE, Inger R, McDonald RA, Barker S, Jackson AL, Thompson FJ, Vitikainen EIK, Cant MA, Marshall HH. 2018 Intragroup competition predicts individual foraging specialisation in a group-living mammal. *Ecol Lett* **21**, 665–673. (doi:10.1111/ELE.12933)

57. Sanchez JN, Hudgens BR. 2015 Interactions between density, home range behaviors, and contact rates in the Channel Island fox (Urocyon littoralis). *Ecol Evol* **5**, 2466–2477. (doi:10.1002/ece3.1533)

58. Wilkin TA, Garant D, Gosler AG, Sheldon BC. 2006 Density effects on life-history traits in a wild population of the great tit Parus major: Analyses of long-term data with GIS techniques. *Journal of Animal Ecology* **75**, 604–615. (doi:10.1111/j.1365-2656.2006.01078.x)

59. Franks DW, Ruxton GD, James R. 2010 Sampling animal association networks with the gambit of the group. *Behav Ecol Sociobiol* **64**, 493–503. (doi:10.1007/s00265-009-0865-8)

60. Cote IM, Poulin R. 1995 Parasitism and group size in social animals: a meta-analysis. *Behavioral Ecology* **6**, 159–165. (doi:10.1093/beheco/6.2.159)

61. Ketwaroo FR, Matechou E, Silk M, Delahay R. 2025 Modeling Disease Dynamics From Spatially Explicit Capture-Recapture Data. *Environmetrics* **36**, e2888. (doi:10.1002/ENV.2888)

62. McCallum H, Barlow N, Hone J. 2001 How should pathogen transmission be modelled? *Trends Ecol Evol* **16**, 295–300. (doi:10.1016/S0169-5347(01)02144-9)

63. Rajeev M, Metcalf CJE, Hampson K. 2020 Modeling canine rabies virus transmission dynamics. In *Rabies*, pp. 655–670. Elsevier. (doi:10.1016/b978-0-12-818705-0.00020-0)

64. Townsend SE *et al.* 2013 Designing Programs for Eliminating Canine Rabies from Islands: Bali, Indonesia as a Case Study. *PLoS Negl Trop Dis* **7**, e2372. (doi:10.1371/JOURNAL.PNTD.0002372)

65. Albery GF, Sweeny AR, Corripio-Miyar Y, Evans MJ, Hayward A, Pemberton JM, Pilkington JG, Nussey DH. 2024 Local and global density have distinct and parasite-dependent effects on infection in wild sheep. *bioRxiv* , 2024.04.30.591781. (doi:10.1101/2024.04.30.591781)

66. Tardy O, Massé A, Pelletier F, Mainguy J, Fortin D. 2014 Density-dependent functional responses in habitat selection by two hosts of the raccoon rabies virus variant. *Ecosphere* **5**, 1–16. (doi:10.1890/ES14-00197.1)

67. Wilber MQ, Yang A, Boughton R, Manlove KR, Miller RS, Pepin KM, Wittemyer G. 2022 A model for leveraging animal movement to understand spatio-temporal disease dynamics. *Ecol Lett* , 1–15. (doi:10.1111/ele.13986)

68. Buck JC, Weinstein SB, Young HS. 2018 Ecological and Evolutionary Consequences of Parasite Avoidance. *Trends Ecol Evol* **33**, 619–632. (doi:10.1016/j.tree.2018.05.001)

69. Lion S, Boots M. 2010 Are parasites ‘“prudent”’ in space? *Ecol Lett* **13**, 1245–1255. (doi:10.1111/j.1461-0248.2010.01516.x)

70. Rocha LEC, Ryckebusch J, Schoors K, Smith M. 2021 Scaling of social interactions across animal species. *Sci Rep* **11**, 12584.

71. Lafferty KD, DeLeo G, Briggs CJ, Dobson AP, Gross T, Kuris AM. 2015 A general consumer-resource population model. *Science (1979)* **349**, 854–857. (doi:10.1126/SCIENCE.AAA6224/SUPPL_FILE/LAFFERTY.SM.PDF)

72. Albery GF, Bansal S, Silk MJ. 2024 Comparative approaches in social network ecology. *Ecol Lett* **27**. (doi:10.1111/ele.14345)

73. Collier M, Albery GF, McDonald GC, Bansal S. 2022 Pathogen transmission modes determine contact network structure, altering other pathogen characteristics. *Proceedings of the Royal Society B* **289**. (doi:10.1098/RSPB.2022.1389)

74. Stuber EF, Carlson BS, Jesmer BR. 2022 Spatial personalities: A meta-analysis of consistent individual differences in spatial behavior. *Behavioral Ecology*. **33**, 477–486. (doi:10.1093/beheco/arab147)

75. Kaur P *et al.* 2024 A protocol for assessing bias and robustness of social network metrics using GPS based radio-telemetry data. *Mov Ecol* **12**. (doi:10.1186/s40462-024-00494-6)

76. R Development Core Team R. 2011 R: A Language and Environment for Statistical Computing. *R Foundation for Statistical Computing*. **1**, 409. (doi:10.1007/978-3-540-74686-7)

77. Albery GF, Newman C, Bright Ross J, Macdonald DW, Bansal S, Buesching CD. 2020 Negative density-dependent parasitism in a group-living carnivore. *Proceedings of the Royal Society B: Biological Sciences* **287**, 20202655. (doi:10.1101/2020.06.15.153726)

78. Calenge C. 2011 Home range estimation in R: the adehabitatHR package. See https://cran.r-project.org/web/packages/adehabitatHR/index.html (accessed on 10 March 2020).

79. Wanelik KM, Farine DR. 2022 A new method for characterising shared space use networks using animal trapping data. *Behav Ecol Sociobiol* **76**. (doi:10.1007/s00265-022-03222-5)

80. Cairns SJ, Schwager SJ. 1987 A comparison of association indices. *Anim Behav* **35**, 1454–1469. (doi:10.1016/S0003-3472(87)80018-0)

81. Wood SN. 2011 Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *J R Stat Soc Series B Stat Methodol* **73**, 3–36. (doi:10.1111/j.1467-9868.2010.00749.x)

82. Koricheva J, Gurevitch J, Mengersen KL. 2013 Handbook of meta-analysis in ecology and evolution. , 498.

83. Konstantopoulos S. 2011 Fixed effects and variance components estimation in three-level meta-analysis. *Res Synth Methods* **2**, 61–76. (doi:10.1002/jrsm.35)

84. Cinar O, Nakagawa S, Viechtbauer W. 2022 Phylogenetic multilevel meta-analysis: A simulation study on the importance of modelling the phylogeny. *Methods Ecol Evol* **13**, 383–395. (doi:10.1111/2041-210X.13760)

85. Michonneau F, Brown JW, Winter DJ. 2016 rotl: an R package to interact with the Open Tree of Life data. *Methods Ecol Evol* **7**, 1476–1481. (doi:10.1111/2041-210X.12593)

86. Paradis E, Schliep K. 2019 ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics* **35**, 526–528. (doi:10.1093/BIOINFORMATICS/BTY633)