

Density-dependent network structuring within and across wild animal systems

Received: 23 June 2024

Accepted: 16 July 2025

Published online: 04 September 2025

 Check for updates

A list of authors and their affiliations appears at the end of the paper

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 gap 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 that probably emerge as a result of demographic and behavioural processes that counteract density's effects. These are stronger and less saturating in spatial compared with social networks, as individuals become disproportionately spatially connected rather than socially connected at higher densities. Consequently, ecological processes that depend on spatial connections are probably more density dependent than those involving social interactions. These findings suggest fundamental scaling rules governing animal social dynamics, which could help to predict network structures in novel systems.

The number of individuals occupying a given space (that is, 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 information⁶ to spread between hosts^{1–4,7}. 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 (for example, home range overlap (HRO)) versus social associations (for example, den sharing or grouping) or interactions (for example, mating or fighting). Although several studies have compared animal populations at different densities to demonstrate variation in social association rates among populations (for example, refs. 7–9) or groups (for example, refs. 10–12),

attempts to identify such density effects within continuous populations of individuals have been less common (but see refs. 7,13–16) and their findings have never been synthesized 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 (for example, 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 (Fig. 1). Often, individuals are modelled as randomly moving and interacting molecules (using mass action or mean field theory). In this conceptualization, direct contact between

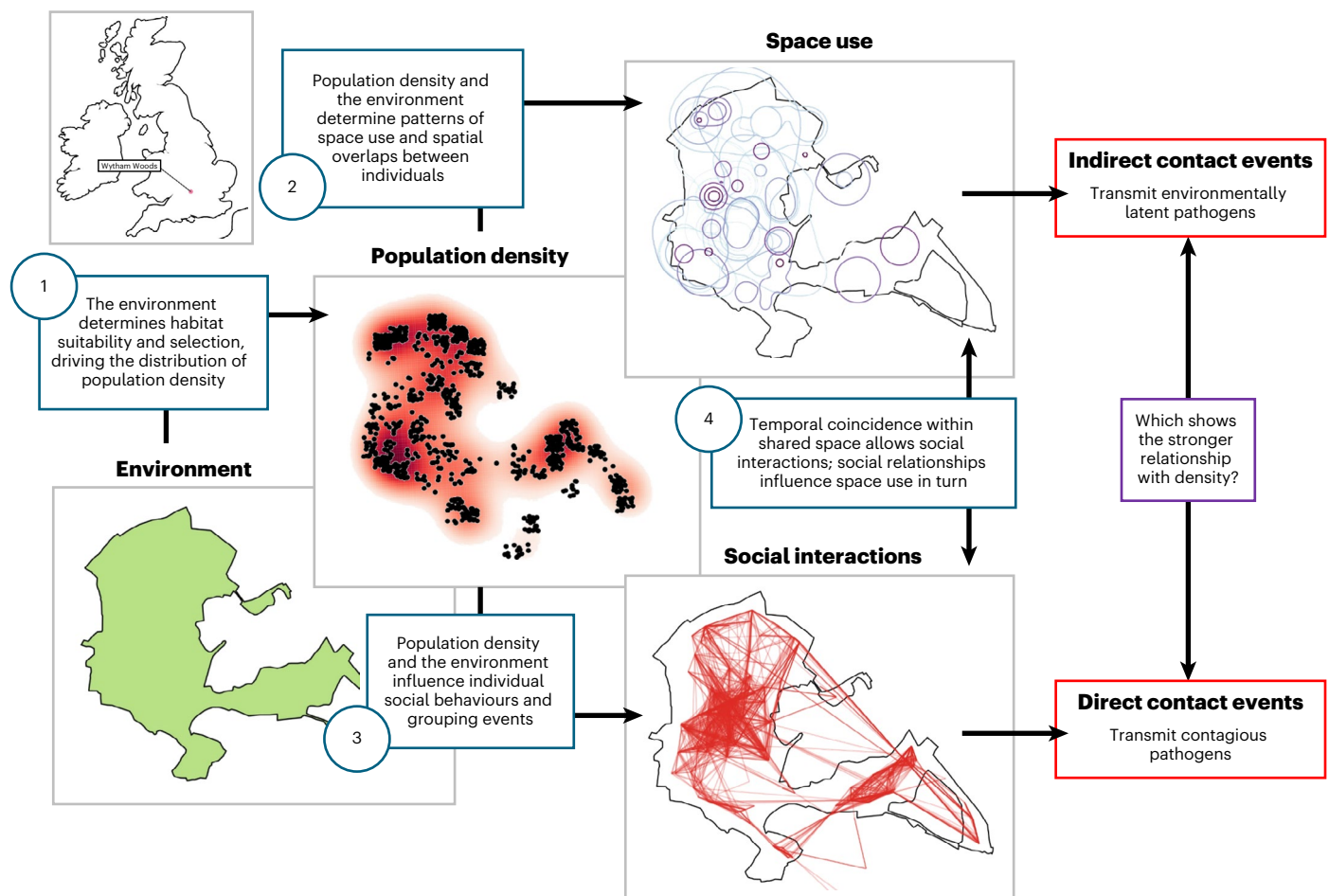


Fig. 1 | Outline of how population density drives the formation of spatial and social networks. The schematic details the rationale underlying this study, using Wytham Wood great tits as an example. In this case, the environment is represented by an outline of the woods. Under population density, the points represent the locations of individual birds, with some jittering added, and the red shading represents local population density. For space use, the different purple shades correspond to the home ranges of different individuals. Finally, for social

interactions, the 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.

two molecules is analogous to a social interaction or association; rates of such interactions are often assumed to increase with density (thus, they are density dependent; for example, ref. 17) and/or to be homogeneous in space (for example, ref. 12). In reality, individuals are unlikely to behave and interact randomly in space, and instead will be influenced by spatially varying factors including local density¹⁸ and competition for resources⁷. Changes in density may cause individuals to alter their foraging behaviour^{19–21}, dispersal^{22,23}, social preference or avoidance^{15,24}, mating behaviour²⁵ or preferred group size⁹. 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 rate²⁶. These and related processes might produce strong nonlinearities in density–interaction relationships, which can complicate the predictions of density dependence models of pathogen transmission^{2,4,5}. For example, individuals or groups may learn to avoid where competitors might go, resulting in greater spatial partitioning under higher densities²⁷. Nevertheless, nonlinearities such as these are poorly understood and rarely considered.

Several wild animal studies have suggested that relationships between density and social association rates are often nonlinear and saturating^{7,10–12,15}. Such relationships imply that association rates do not increase passively with density, but rather that behavioural or

demographic processes probably change as the density increases, with the ultimate consequence of slowing association rates. However, these nonlinearities are difficult to examine between populations or species because they introduce a range of confounders and have few replicates along the density axis². In contrast, lower densities may provide less ability to exert social preferences, but low-density populations may be more difficult to study due to (for example) low return on sampling investment; alternatively, failure to achieve sufficient interaction rates may result in Allee effects and ultimately drive populations towards decline^{28,29}.

Characterizing 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 characterization and analysis of individual-level social traits among other things, has become so popular in animal ecology in recent years^{30–34}. Additionally, recent years have seen substantial growth in our understanding of socio-spatial behaviours, including harmonizing 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 differences². 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 aggression³⁶, 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 the spatial network³⁷. This rationale is well understood in disease ecology, as differences in density–contact relationships are thought to drive differences in the density dependence of infection, where contact is defined as an interaction or association that could spread a pathogen (Fig. 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 ecology¹⁸, the framework is readily related to other fields (for example, direct versus indirect cues that can lead to social learning⁴¹). Previously established density–interaction relationships are diverse and include feral dog bites¹³, ant antennations⁴² and trophallaxis²⁶, ungulate group memberships^{14,19}, rodent co-trapping^{10,43} and agamid association patterns^{15,16}, but no study has yet synthesized 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 collated a meta-dataset of over 58,000 individual animals across 36 wildlife systems globally (Fig. 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 used meta-analyses to investigate general rules determining their slope and shape across systems. In particular, we focused 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 58,667 individual animals' spatial and social behaviour, across a wide range of ecological systems and taxonomic groups of animals. We then ran a standardized 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 (Fig. 3a). Meta-analyses identified a highly significant positive mean correlation between density and connectedness, both for social networks (estimated $r = 0.22$; 95% confidence interval (CI) = 0.17 to 0.27) and spatial networks ($r = 0.45$; CI = 0.36 and 0.53; Fig. 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 (Fig. 3a; Q -test of heterogeneity across systems: $Q_{37} = 5,627.33$ and $Q_{25} = 1,281.83$; 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 probably important. As well as adding resolution and allowing comparisons of density effects across systems, our methodology facilitated the fitting of nonlinear relationships (using generalized additive models (GAMs); see below). This approach has only rarely been applied before, and then at much coarser resolution (see refs. 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 (Fig. 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 with social networks (Fig. 3b; $r = 0.45$ versus 0.22). There was a difference of 0.26 (CI = 0.16 to 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 out of 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 to -0.03 ; $P = 0.01$) and for spatial networks, with substantial overlap between their estimates ($r = -0.22$; CI = -0.37 to -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 (Fig. 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 characterized disproportionately by individuals asynchronously sharing space rather than socially associating, whereas 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 aggression³⁶ or exposure to infectious disease⁴⁴. Eastern water dragons (*Intellagama lesueurii*) show greater avoidance at higher densities¹⁵, supporting avoidance-related mechanisms. Alternatively, in species with high social cognition or stable bonds, saturation could reflect lower social effort or inability to keep track of social affiliates at higher densities⁴⁵. In general, individuals probably have a preferred social interaction rate or group size—a preference that they may increasingly exert at higher densities⁹. 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 specifically¹⁸, it seems likely that these slopes could vary between individuals as they do between populations. Future analyses might fit variable density–connectedness

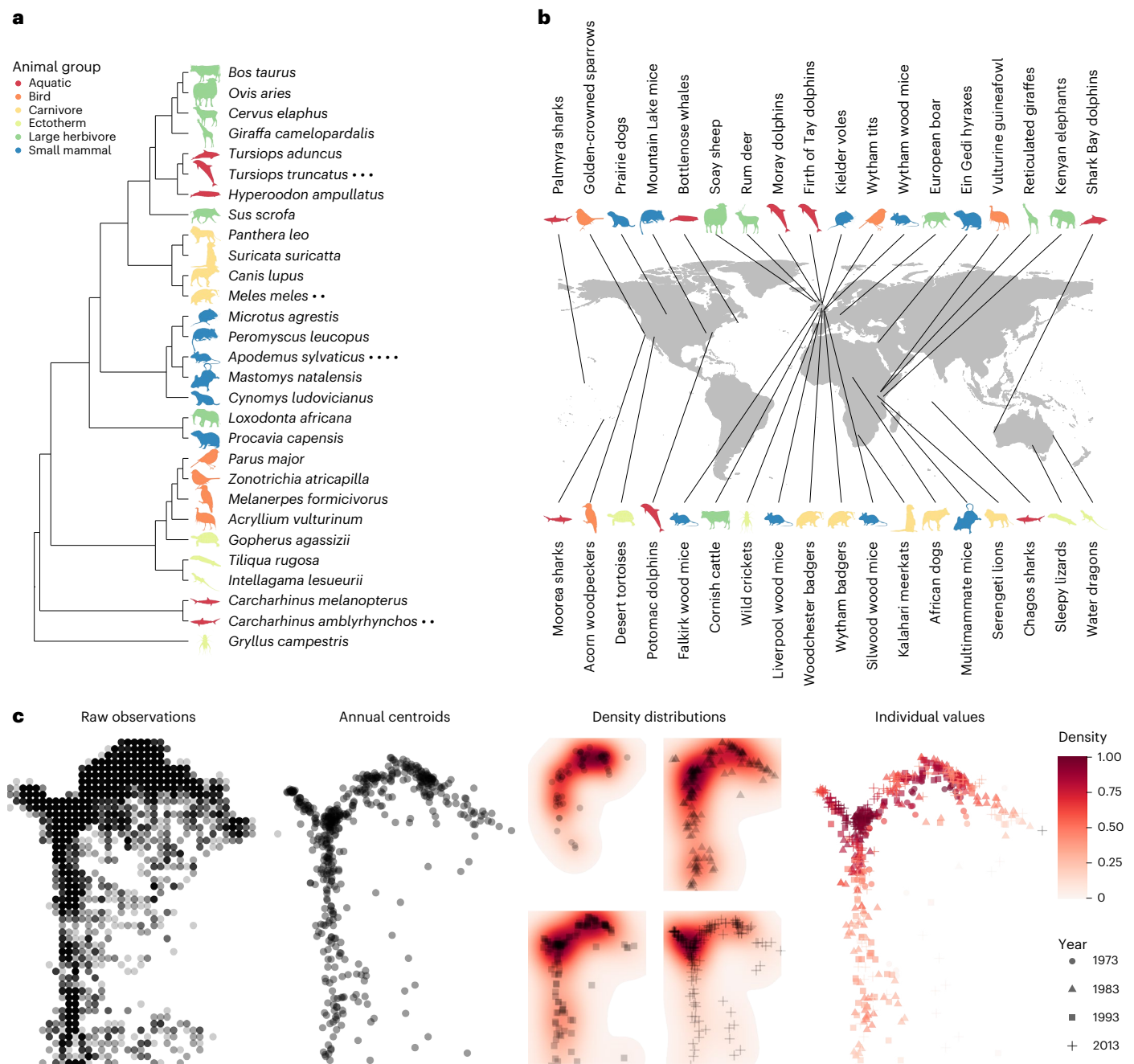


Fig. 2 | Phylogenetic and geographic distributions of the examined datasets of spatial and social behaviour and schematic. a, b. Phylogenetic (a) and geographic (b) distributions of our 36 examined datasets on spatial and social behaviour. The points next to the species' names in a denote where we had more than one population of that species. Note that the Potomac dolphins listed as *Tursiops truncatus* in a following Open Tree of Life nomenclature have since been reclassified as *Tursiops erebennus*. 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 represent bivariate spatial coordinates. Shown are raw observations of individuals in space that we then averaged at the individual level to make centroids; we used the centroids to generate annual density distributions, which were then assigned to individuals in the form of local density measures. Animal silhouettes from [phylopic.org](https://www.phylopic.org/); details on attribution appear in Supplementary Table 2.

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 with the spatial network to identify levels of attraction^{53,54} or avoidance⁵⁵ 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 niches⁵⁶

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 drives individuals to become spatially connected faster than they become socially connected, such that the underlying mechanisms probably involve behaviours and demographic processes

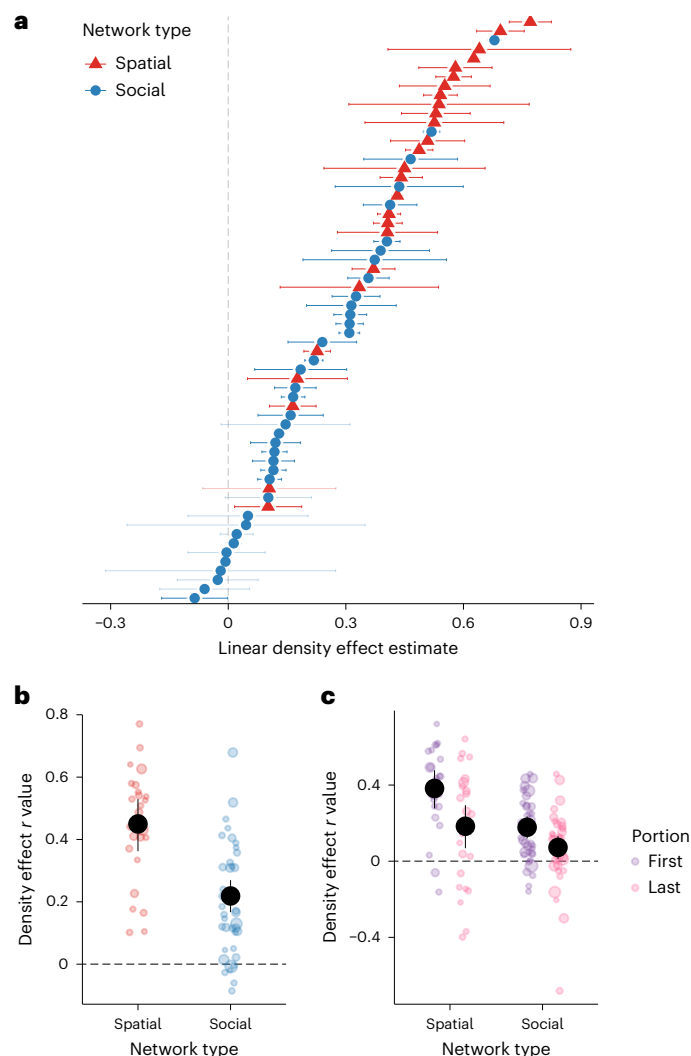


Fig. 3 | Drivers of variation in linear density effects on individual network connectedness. The results are based on a meta-analysis of $n = 36$ systems comprising $n = 64$ system-behaviour replicates. **a**, Our fitted linear model estimates of density effects on network strength. Each point represents the mean estimate from a given system and the error bars denote 95% CIs. Opaque error bars represent statistical significance (that is, they do not overlap with 0). The estimates are in units of standard deviation 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**, Centrality in spatial networks (that is, HRO; red points) had a significantly steeper relationship with density than that of 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 last (pink points) were generally less positive than those for first (purple points), implying a general saturation shape. In **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% CIs.

that specifically affect social collocation in space and time. Testing the precise underlying mechanism will probably require finer-scale behavioural observations, as described below. Regardless of the 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 probably produce an inaccurate (that

is, inflated) picture of density's effects. Importantly, our study included many examples of proximity-based social networks—most notably gambit-of-the-group measures⁵⁹—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 HRO). 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 behaviour¹⁴; 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 (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 (that is, environmentally latent) parasites may exhibit greater density dependence than directly transmitted ones, given that individuals probably experience disproportionately more indirect contact at higher densities. This observation contrasts with orthodoxy that directly transmitted parasites are most likely to be density dependent⁶⁰, 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 (that is, 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 was previously suggested empirically and by epidemiological theory¹⁷. These relationships could influence our targets for culling or vaccination coverage⁶². Given that animals at high density seem likely to have a relatively shallow relationship between density and contact rates, reducing the population's 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 (Fig. 3c). Similar problems with culling have already been acknowledged in specific systems (for example, in canine rabies^{39,63,64}), but our study implies that shallow nonlinear density-contact trends could be more general than was previously thought and could be driven by flexible density-dependent changes in behaviour and demography. Conversely, culling could be disproportionately effective at intermediate densities, such that identifying the inflection points of the curve might facilitate the design of 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 (for example, ref. 65; see Supplementary Discussion).

Beyond these general trends, we ran GAMs that revealed that 52 out of 64 density effects on network connectedness (81%) were significantly nonlinear (change in the Akaike information criterion (ΔAIC) > 2); these relationships took a wide variety of shapes, representing a range of nonlinear functions that are difficult to generalize (Fig. 4). Notably, although many GAM smooths were eventually significantly negative (Fig. 4), the vast majority of linear models fitted to the second half of the data were positive (Fig. 3c); this result is probably 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

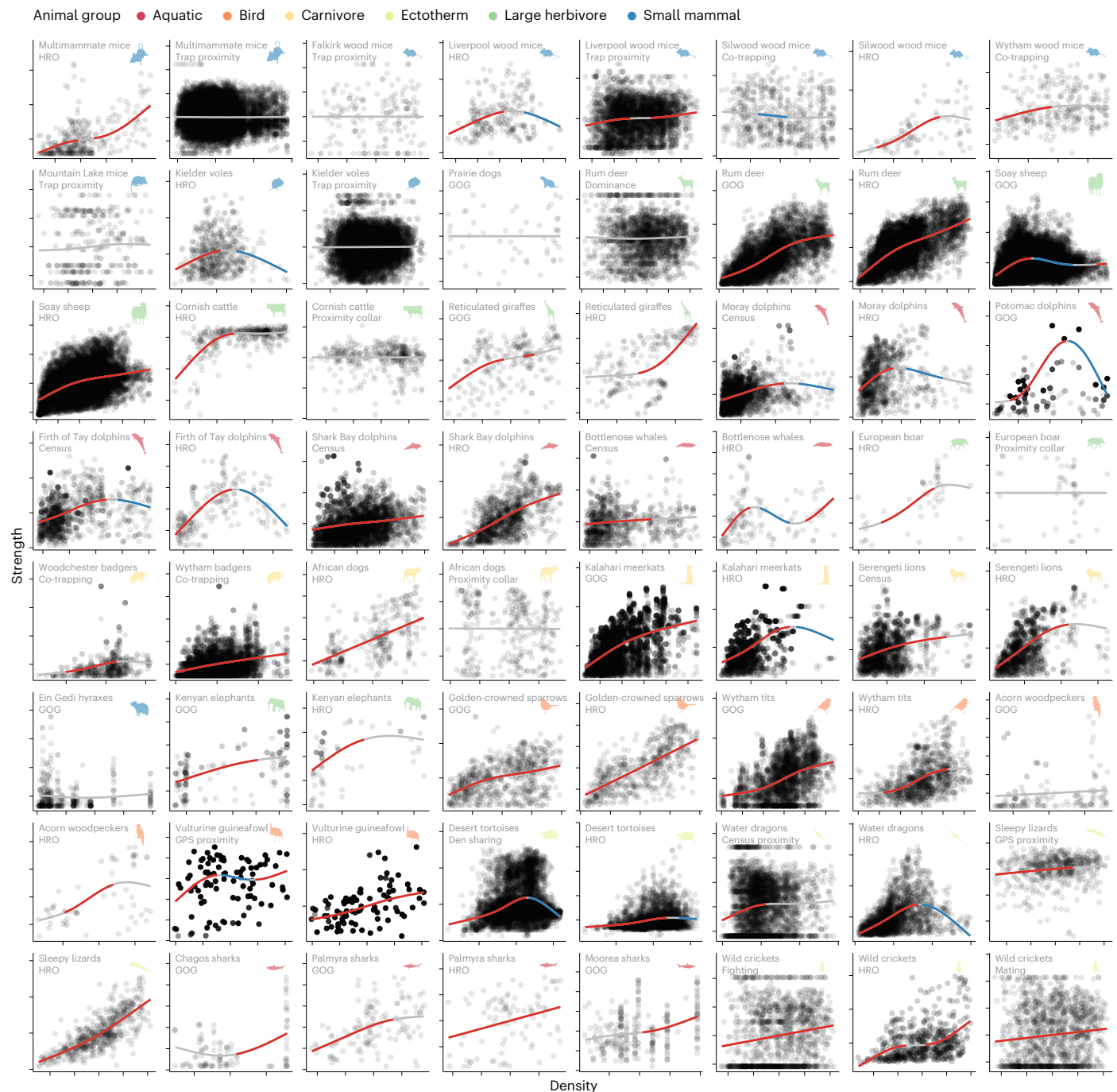


Fig. 4 | Relationships between density and network connectedness. Graphs of the relationships between density and network connectedness across $n = 64$ animal systems comprising $n = 151,835$ individual animals, showing substantial variation. The x and y axes represent density (in individuals per area) and network connectedness (strength centrality), respectively. The values have been standardized to have a mean of 0 and a standard deviation of 1 within each system. The axis ticks are in units of 1 standard deviation, so are self-referential within each panel, and hence we have left the axis tick values

unlabelled to improve clarity. Each point represents an individual-year-behaviour replicate. The lines portray model fits from our GAMs. Red, grey and blue represent a positive statistically significant relationship, no statistical significance or a negative statistically significant relationship, respectively. The points are semi-transparent to enhance visibility. The panels are arranged phylogenetically following the tree displayed in Fig. 2a. GOG, gambit of the group. Animal silhouettes from [phylopic.org](https://www.phylopic.org/); details on attribution appear in Supplementary Table 2.

($P > 0.05$; Supplementary Table 3), including no clear phylogenetic signal ($\Delta AIC = 2.71$). 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 such as habitat selection^{66,67}, group formation⁷, parasite avoidance⁶⁸ and demographic structuring⁶⁹. Although we were unable to identify specific between-system

predictors of the 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 analysis⁷⁰ and food web ecology⁷¹, 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 do⁷⁰. As these patterns seemingly manifest regardless of animal group and interaction type, they may reflect a generalizable rule governing the socio-spatial structure of ecological systems. Further refinement and implementation of these models could facilitate the prediction of network structure in new systems.

Finally, this study is relatively unique in that it comprises 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 ecology⁷², but they often revolve around analysing whole networks rather than individuals⁷³ and (to our knowledge) are never performed 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, capitalizing on the wide range of methodological approaches to behavioural data collection (for example, censuses, trapping and 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 ungulates⁷⁵. As well as being diverse, our meta-dataset contained 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 interface¹⁸.

Methods

Data standardization and behavioural pipeline

Data were manipulated and analysed using R version 4.2.3 (ref. 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 (Fig. 2). In one case (the Firth of Tay and Moray dolphins), we used two distinct replicates despite the data relating to overlapping groups of individuals, because of their distinct spatial distributions, which made it difficult to fit a coherent density distribution.

To standardize the timescale across studies, all systems were analysed as annual replicates (that is, social and spatial networks were summarized 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 previous methodology^{14,77}, we took each individual's average location across the year (their centroid) and created a spatial density kernel using the *adehabitat* package⁷⁸, which provided 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 (for example, interactions per individual per km² 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 within which all individuals were censused during the study period based on their annual centroids. For each individual's mean location, we then estimated a circular boundary of radius = 1/20 multiplied by the area of the minimum bounding box. 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 kernel density estimation approach and the proportional area-based approach (Supplementary Fig. 1).

To provide a measure of asynchronous space sharing, we constructed HRO networks based on the proportional overlap of two individuals' minimum convex polygon (that is, 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; ten out of 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 minimum convex polygon 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 generalizably and more conservatively.

To provide a measure of social connectedness, we built social networks using the following approaches, as defined by the original studies: direct observations of dyadic interactions (for example, fighting or mating); gambit-of-the-group measures (that is, assessing which animals are members of the same group)⁵⁹; co-trapping (that is, analysing which animals are trapped together or in adjacent traps within a given number of trapping sessions); or using proximity sensors to determine the incidence of direct contact (defined by a certain distance-based detection threshold). Notably, some analyses use indirect interactions (that is, spatial overlap) to approximate direct interactions. This requires spatiotemporal coincidence, which we caution against, particularly when modelling pathogen transmission^{35,79}. Although the two often correlate, here we do not use HRO to approximate direct interaction rates, but rather as a measure of indirect interactions (for example, as an indication of the transmission of environmental parasites).

For each social network, we scaled connection strength relative to the number of observations of each individual in a dyad (that is, the simple ratio index⁸⁰). Our response variable therefore took the form of summed strength centrality, scaled to between 0 and 1 for each dyad, for each social and spatial network. We focused on comparing density effects on social interactions and associations with density's effects on space sharing.

Density–connectedness models

We developed a workflow to allow us to derive and compare density's effects on connectedness—and their drivers—in a standardized way across our animal systems. We fitted models with three main forms: linear models fitted to the entire dataset; nonlinear generalized additive

models fitted to the entire 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 and residuals are displayed in Supplementary Figs. 2 and 3, respectively.

GAMs. We fitted GAMs in the `mgcv` package⁸¹ to identify whether each density effect was better described by a linear or nonlinear relationship and to identify the shapes 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 AIC, with a contrast of $2\Delta\text{AIC}$ designated to distinguish between models.

Saturation models. To quantify whether density effects were generally saturating (that is, 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 of our systems using a range of other methods (for example, comparing specific functional relationships with nonlinear least squares), but found that they were generally incapable of fitting well to the data in a standardized way across the many datasets (that is, there was non-convergence of nonlinear least squares using semi-automated starting estimates across systems). As such, this approach represented a tradeoff between tractable, generalizable 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 (1) the skew in residuals, (2) a saturating relationship and (3) heteroskedasticity impact whether we may under- or overestimate the slope of an assumed linear relationship between density and strength (Supplementary Methods section '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, nor were the second portions of the data more heteroskedastic, which would be expected if this was driving the saturating effect (Supplementary Fig. 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 Fig. 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 the resilience of our findings to uneven data distributions.

Meta-analysis

To characterize 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 standardized slope of the linear density effect; because both individual network strength and density were scaled to have a mean of 0 and a standard deviation of 1 in the linear regression, this was equivalent to the correlation coefficient (r)⁸². We converted all correlation coefficients into Fisher's $Z(Z_r)$ and computed the 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 heterogeneity⁸³, as 26 of 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 phylogeny⁸⁴. This effect used a phylogenetic correlation matrix of our 30 animal species derived from the Open Tree of Life via the `rotl` package⁸⁵, with the `ape` package used to resolve multichotomies and provide branch lengths⁸⁶.

We then fitted intercept-only models using the `rma.mv()` function with restricted maximum likelihood, 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 (that is, 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 taken 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 GAMs, as methods for the meta-analysis of nonlinear estimates are not yet well defined.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

The data required to run the meta-analysis models are available from Zenodo at <https://doi.org/10.5281/zenodo.15847435> (ref. 87) and

GitHub at <https://github.com/gfalbery/DensityMetaAnalysis>. The 36 behavioural datasets for each study system can be requested from the data collectors; requests via the corresponding author will be relayed to them.

Code availability

All of the code is available from Zenodo at <https://doi.org/10.5281/zenodo.15847435> (ref. 87) and GitHub at <https://github.com/gfalbery/DensityMetaAnalysis>.

References

- Lloyd-Smith, J. O. et al. Should we expect population thresholds for wildlife disease? *Trends Ecol. Evol.* **20**, 511–519 (2005).
- Albery, G. F. Density dependence and disease dynamics: moving towards a predictive framework. Preprint at *EcoEvoRxiv* <https://doi.org/10.32942/osf.io/gaw49> (2022).
- Hopkins, S. R., Fleming-Davies, A. E., Belden, L. K. & Wojdak, J. M. Systematic review of modeling assumptions and empirical evidence: does parasite transmission increase nonlinearly with host density? *Methods Ecol. Evol.* **11**, 476–486 (2020).
- Begon, M. et al. A clarification of transmission terms in host–microparasite models: numbers, densities and areas. *Epidemiol. Infect.* **129**, 147–153 (2002).
- Ferrari, M. J., Perkins, S. E., Pomeroy, L. W. & Bjørnstad, O. N. Pathogens, social networks, and the paradox of transmission scaling. *Interdiscip. Perspect. Infect. Dis.* **2011**, 267049 (2011).
- Cantor, M. et al. Social network architecture and the tempo of cumulative cultural evolution. *Proc. R. Soc. B Biol. Sci.* **288**, 20203107 (2021).
- Rouhbachsh, A., Wright, A. N. & Ferguson, J. M. Ecological interactions drive a power-law relationship between group size and population density in social foragers. *Ecol. Lett.* **28**, 70111 (2025).
- Webber, Q. M. R. & Vander Wal, E. Heterogeneity in social network connections is density-dependent: implications for disease dynamics in a gregarious ungulate. *Behav. Ecol. Sociobiol.* **74**, 1–13 (2020).
- Beauchamp, G. Functional relationship between group size and population density in Northwest Atlantic seabirds. *Mar. Ecol. Prog. Ser.* **435**, 225–233 (2011).
- Borremans, B., Reijnders, J., Hens, N. & Leirs, H. The shape of the contact–density function matters when modelling parasite transmission in fluctuating populations. *R. Soc. Open Sci.* **4**, 171308 (2017).
- Davis, S., Abbasi, B., Shah, S., Telfer, S. & Begon, M. Spatial analyses of wildlife contact networks. *J. R. Soc. Interface* **12**, 20141004 (2015).
- Carson, B. D., Orians, C. M. & Crone, E. E. Caterpillar movement mediates spatially local interactions and determines the relationship between population density and contact. *Mov. Ecol.* **12**, 34 (2024).
- Mancy, R. et al. Rabies shows how scale of transmission can enable acute infections to persist at low prevalence. *Science* **376**, 512–516 (2022).
- Albery, G. F. et al. Multiple spatial behaviours govern social network positions in a wild ungulate. *Ecol. Lett.* **24**, 676–686 (2021).
- Strickland, K., Patterson, E. M. & Frère, C. H. Eastern water dragons use alternative social tactics at different local densities. *Behav. Ecol. Sociobiol.* **72**, 148 (2018).
- Strickland, K. & Frère, C. H. Individual variation in the social plasticity of water dragons. *Am. Nat.* **194**, 194–206 (2019).
- Hu, H., Nigmatulina, K. & Eckhoff, P. The scaling of contact rates with population density for the infectious disease models. *Math. Biosci.* **244**, 125–134 (2013).
- Webber, Q. M. R. et al. Behavioural ecology at the spatial–social interface. *Biol. Rev.* **3**, 868–886 (2023).
- Albon, S. D., Staines, H. J., Guinness, F. E. & Clutton-Brock, T. H. Density-dependent changes in the spacing behaviour of female kin in red deer. *J. Anim. Ecol.* **61**, 131–137 (1992).
- Vas, J. & Andersen, I. L. Density-dependent spacing behaviour and activity budget in pregnant, domestic goats (*Capra hircus*). *PLoS ONE* **10**, e0144583 (2015).
- Connor, E. F. & Cargain, M. J. Density-related foraging behaviour in *Closterocerus tricinatus*, a parasitoid of the leaf-mining moth, *Cameraria hamadryadella*. *Ecol. Entomol.* **19**, 327–334 (1994).
- Matthysen, E. Density-dependent dispersal in birds and mammals. *Ecography* **28**, 403–416 (2005).
- Avagar, T., Betini, G. S. & Fryxell, J. M. Habitat selection patterns are density dependent under the ideal free distribution. *J. Anim. Ecol.* **89**, 2777–2787 (2020).
- Vander Wal, E. et al. 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 (2014).
- Kokko, H. & Rankin, D. J. Lonely hearts or sex in the city? Density-dependent effects in mating systems. *Philos. Trans. R. Soc. B Biol. Sci.* **361**, 319–334 (2006).
- Modlmeier, A. P. et al. Ant colonies maintain social homeostasis in the face of decreased density. *eLife* **8**, e38473 (2019).
- Ogino, M. & Farine, D. R. Collective intelligence facilitates emergent resource partitioning through frequency-dependent learning. *Philos. Trans. R. Soc. B Biol. Sci.* **379**, 20230177 (2024).
- Stephens, P. A. & Sutherland, W. J. Consequences of the Allee effect for behaviour, ecology and conservation. *Trends Ecol. Evol.* **14**, 401–405 (1999).
- Courchamp, F., Clutton-Brock, T. & Grenfell, B. Inverse density dependence and the Allee effect. *Trends Ecol. Evol.* **14**, 405–410 (1999).
- Farine, D. R. & Whitehead, H. Constructing, conducting and interpreting animal social network analysis. *J. Anim. Ecol.* **84**, 1144–1163 (2015).
- Farine, D. R. Modelling animal social networks: new solutions and future directions. *J. Anim. Ecol.* **93**, 250–253 (2024).
- Webber, Q. M. R. & Vander Wal, E. Trends and perspectives on the use of animal social network analysis in behavioural ecology: a bibliometric approach. *Anim. Behav.* **149**, 77–87 (2019).
- Pinter-Wollman, N. et al. The dynamics of animal social networks: analytical, conceptual, and theoretical advances. *Behav. Ecol.* **25**, 242–255 (2014).
- Sah, P., Mann, J. & Bansal, S. Disease implications of animal social network structure: a synthesis across social systems. *J. Anim. Ecol.* **87**, 546–558 (2018).
- Albery, G. F., Kirkpatrick, L., Firth, J. A. & Bansal, S. Unifying spatial and social network analysis in disease ecology. *J. Anim. Ecol.* **90**, 45–61 (2021).
- Cubaynes, S. et al. Density-dependent intraspecific aggression regulates survival in northern Yellowstone wolves (*Canis lupus*). *J. Anim. Ecol.* **83**, 1344–1356 (2014).
- Jetz, W., Carbone, C., Fulford, J. & Brown, J. H. The scaling of animal space use. *Science* **306**, 266–268 (2004).
- Lloyd-Smith, J. O., Getz, W. M. & Westerhoff, H. V. Frequency-dependent incidence in models of sexually transmitted diseases: portrayal of pair-based transmission and effects of illness on contact behaviour. *Proc. R. Soc. B Biol. Sci.* **271**, 625–634 (2004).
- Morters, M. K. et al. Evidence-based control of canine rabies: a critical review of population density reduction. *J. Anim. Ecol.* **82**, 6–14 (2013).

40. Dougherty, E. R., Seidel, D. P., Carlson, C. J., Spiegel, O. & Getz, W. M. Going through the motions: incorporating movement analyses into disease research. *Ecol. Lett.* **21**, 588–604 (2018).
41. Hoppitt, W. & Laland, K. N. Chapter 3 social processes influencing learning in animals: a review of the evidence. *Adv. Study Behav.* **38**, 105–165 (2008).
42. Gordon, D. M., Paul, R. E. & Thorpe, K. What is the function of encounter patterns in ant colonies? *Anim. Behav.* **45**, 1083–1100 (1993).
43. Davis, S. et al. Spatial analyses of wildlife contact networks. *J. R. Soc. Interface* **12**, 20141004 (2015).
44. Gibson, A. K. & Amoroso, C. R. Evolution and ecology of parasite avoidance. *Annu. Rev. Ecol. Evol. Syst.* **53**, 47–67 (2022).
45. Colman, E., Colizza, V., Hanks, E. M., Hughes, D. P. & Bansal, S. Social fluidity mobilizes contagion in human and animal populations. *eLife* **10**, e62177 (2021).
46. Michelangeli, M. et al. Personality, spatiotemporal ecological variation, and resident/explorer movement syndromes in the sleepy lizard. *J. Anim. Ecol.* **91**, 210–223 (2022).
47. Spiegel, O., Leu, S. T., Bull, C. M. & Sih, A. What's your move? Movement as a link between personality and spatial dynamics in animal populations. *Ecol. Lett.* **20**, 3–18 (2017).
48. Aplin, L. M., Farine, D. R., Mann, R. P. & Sheldon, B. C. Individual-level personality influences social foraging and collective behaviour in wild birds. *Proc. R. Soc. Lond. B* **281**, 20141016 (2014).
49. Hunt, E. R. et al. Social interactions shape individual and collective personality in social spiders. *Proc. R. Soc. B Biol. Sci.* **285**, 20181366 (2018).
50. Firth, J. A. et al. Personality shapes pair bonding in a wild bird social system. *Nat. Ecol. Evol.* **2**, 1696–1699 (2018).
51. Webber, Q., Laforge, M., Bonar, M. & Vander Wal, E. The adaptive value of density-dependent habitat specialization and social network centrality. *Nat. Commun.* **15**, 4423 (2024).
52. Webber, Q. M. R., Dantzer, B., Lane, J. E., Boutin, S. & McAdam, A. G. Density-dependent plasticity in territoriality revealed using social network analysis. *J. Anim. Ecol.* **92**, 207–221 (2023).
53. Spiegel, O., Leu, S. T., Sih, A. & Bull, C. M. Socially interacting or indifferent neighbours? Randomization of movement paths to tease apart social preference and spatial constraints. *Methods Ecol. Evol.* **7**, 971–979 (2016).
54. Gahm, K. et al. A wrap-around movement path randomization method to distinguish social and spatial drivers of animal interactions. *Philos. Trans. R. Soc. B Biol. Sci.* **379**, 20220531 (2024).
55. Strickland, K. et al. A framework for the identification of long-term social avoidance in longitudinal datasets. *R. Soc. Open Sci.* **4**, 170641 (2017).
56. Sheppard, C. E. et al. Intragroup competition predicts individual foraging specialisation in a group-living mammal. *Ecol. Lett.* **21**, 665–673 (2018).
57. Sanchez, J. N. & Hudgens, B. R. Interactions between density, home range behaviors, and contact rates in the Channel Island fox (*Urocyon littoralis*). *Ecol. Evol.* **5**, 2466–2477 (2015).
58. Wilkin, T. A., Garant, D., Gosler, A. G. & Sheldon, B. C. Density effects on life-history traits in a wild population of the great tit *Parus major*: analyses of long-term data with GIS techniques. *J. Anim. Ecol.* **75**, 604–615 (2006).
59. Franks, D. W., Ruxton, G. D. & James, R. Sampling animal association networks with the gambit of the group. *Behav. Ecol. Sociobiol.* **64**, 493–503 (2010).
60. Cote, I. M. & Poulin, R. Parasitism and group size in social animals: a meta-analysis. *Behav. Ecol.* **6**, 159–165 (1995).
61. Ketwaroo, F. R., Matechou, E., Silk, M. & Delahay, R. Modeling disease dynamics from spatially explicit capture–recapture data. *Environmetrics* **36**, e2888 (2025).
62. McCallum, H., Barlow, N. & Hone, J. How should pathogen transmission be modelled? *Trends Ecol. Evol.* **16**, 295–300 (2001).
63. Rajeev, M., Metcalf, C. J. E. & Hampson, K. in *Rabies: Scientific Basis of the Disease and its Management* 4th edn (eds Fooks, A. R. & Jackson, A. C.) 655–670 (Elsevier, 2020).
64. Townsend, S. E. et al. Designing programs for eliminating canine rabies from islands: Bali, Indonesia as a case study. *PLoS Negl. Trop. Dis.* **7**, e2372 (2013).
65. Albery, G. F. et al. Local and global density have distinct and parasite-dependent effects on infection in wild sheep. *Parasitology* **1**, 1–9 (2025).
66. Tardy, O., Massé, A., Pelletier, F., Mainguy, J. & Fortin, D. Density-dependent functional responses in habitat selection by two hosts of the raccoon rabies virus variant. *Ecosphere* **5**, 1–16 (2014).
67. Wilber, M. Q. et al. A model for leveraging animal movement to understand spatio-temporal disease dynamics. *Ecol. Lett.* **25**, 1290–1304 (2022).
68. Buck, J. C., Weinstein, S. B. & Young, H. S. Ecological and evolutionary consequences of parasite avoidance. *Trends Ecol. Evol.* **33**, 619–632 (2018).
69. Lion, S. & Boots, M. Are parasites “prudent” in space? *Ecol. Lett.* **13**, 1245–1255 (2010).
70. Rocha, L. E. C., Ryckebusch, J., Schoors, K. & Smith, M. Scaling of social interactions across animal species. *Sci. Rep.* **11**, 12584 (2021).
71. Lafferty, K. D. et al. A general consumer-resource population model. *Science* **349**, 854–857 (2015).
72. Albery, G. F., Bansal, S. & Silk, M. J. Comparative approaches in social network ecology. *Ecol. Lett.* **27**, e14345 (2024).
73. Collier, M., Albery, G. F., McDonald, G. C. & Bansal, S. Pathogen transmission modes determine contact network structure, altering other pathogen characteristics. *Proc. R. Soc. B Biol. Sci.* **289**, 20221389 (2022).
74. Stuber, E. F., Carlson, B. S. & Jesmer, B. R. Spatial personalities: a meta-analysis of consistent individual differences in spatial behavior. *Behav. Ecol.* **33**, 477–486 (2022).
75. Kaur, P. et al. A protocol for assessing bias and robustness of social network metrics using GPS based radio-telemetry data. *Mov. Ecol.* **12**, 55 (2024).
76. R Development Core Team. *R: a Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, 2011).
77. Albery, G. F. et al. Negative density-dependent parasitism in a group-living carnivore. *Proc. R. Soc. B Biol. Sci.* **287**, 20202655 (2020).
78. Calenge, C. adehabitatHR: Home range estimation. R package version 0.4.22 <https://cran.r-project.org/web/packages/adehabitatHR/index.html> (2011).
79. Wanelik, K. M. & Farine, D. R. A new method for characterising shared space use networks using animal trapping data. *Behav. Ecol. Sociobiol.* **76**, 127 (2022).
80. Cairns, S. J. & Schwager, S. J. A comparison of association indices. *Anim. Behav.* **35**, 1454–1469 (1987).
81. Wood, S. N. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *J. R. Stat. Soc. Ser. B Stat. Methodol.* **73**, 3–36 (2011).
82. Koricheva, J., Gurevitch, J. & Mengersen, K. L. *Handbook of Meta-Analysis in Ecology and Evolution* (Princeton Univ. Press, 2013).

83. Konstantopoulos, S. Fixed effects and variance components estimation in three-level meta-analysis. *Res. Synth. Methods* **2**, 61–76 (2011).
84. Cinar, O., Nakagawa, S. & Viechtbauer, W. Phylogenetic multilevel meta-analysis: a simulation study on the importance of modelling the phylogeny. *Methods Ecol. Evol.* **13**, 383–395 (2022).
85. Michonneau, F., Brown, J. W. & Winter, D. J. rotl: an R package to interact with the Open Tree of Life data. *Methods Ecol. Evol.* **7**, 1476–1481 (2016).
86. Paradis, E. & Schliep, K. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics* **35**, 526–528 (2019).
87. Albery, G. F. gfalbery / DensityMetaAnalysis. Zenodo <https://github.com/gfalbery/DensityMetaAnalysis> (2025).

Acknowledgements

G.F.A. and S. Bansal were supported by National Science Foundation grant DEB-2211287. G.F.A. acknowledges support from a College for Life Sciences Fellowship at the Wissenschaftskolleg zu Berlin and Wild Animal Initiative (C-2023-00057). D.J.B. acknowledges support from the Edward Mallinckrodt, Jr. Foundation and National Science Foundation (NSF BII 2213854). J.A.F. acknowledges funding from the Biotechnology and Biological Sciences Research Council (BB/S009752/1), Natural Environment Research Council (NE/S010335/1 and NE/V013483/1) and Wild Animal Initiative (C-2023-00057). System-specific acknowledgements are provided in the Supplementary Notes.

Author contributions

G.F.A. conceived of and led the study, collated and analysed the datasets and wrote the paper, supervised by S. Bansal. A.R.S. helped to clean the data. D.J.B. helped with meta-analysis of the data. S.R. conducted an independent assessment of the density metric. J.A.F.,

D.D.M., M.S., E.V.W. and Q.W. advised throughout. All of the other authors donated data. All authors commented on drafts of the paper.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information The online version contains supplementary material available at <https://doi.org/10.1038/s41559-025-02843-z>.

Correspondence and requests for materials should be addressed to Gregory F. Albery.

Peer review information *Nature Ecology & Evolution* thanks the anonymous reviewers for their contribution to the peer review of this work.

Reprints and permissions information is available at www.nature.com/reprints.

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.

© The Author(s), under exclusive licence to Springer Nature Limited 2025

Gregory F. Albery^{1,2,3}✉, Daniel J. Becker⁴, Josh A. Firth^{5,6}, Delphine De Moor⁷, Sanjana Ravindran⁸, Matthew Silk^{8,9,10}, Amy R. Sweeny^{8,11}, Eric Vander Wal¹², Quinn Webber¹³, Bryony Allen^{14,15}, Simon A. Babayan¹⁶, Sahas Barve^{17,18}, Mike Begon¹⁴, Richard J. Birtles¹⁹, Theadora A. Block^{20,21}, Barbara A. Block²², Janette E. Bradley²³, Sarah Budischak²⁴, Christina Buesching²⁵, Sarah J. Burthe²⁶, Aaron B. Carlisle²⁷, Jennifer E. Caselle²⁸, Ciro Cattuto²⁹, Alexis S. Chaine³⁰, Taylor K. Chapple³¹, Barbara J. Cheney³², Timothy Clutton-Brock³³, Melissa Collier², David J. Curnick¹⁵, Richard J. Delahay³⁴, Damien R. Farine^{35,36,37,38}, Andy Fenton¹⁴, Francesco Ferretti³⁹, Laura Feyrer^{40,41}, Helen Fielding^{42,43}, Vivienne Foroughirad^{42,44}, Celine Frere⁴⁵, Michael G. Gardner⁴⁶, Eli Geffen⁴⁷, Stephanie S. Godfrey⁴⁸, Andrea L. Graham⁴⁹, Phil S. Hammond⁵⁰, Maik Henrich⁵¹, Marco Heurich^{51,52,53}, Paul Hopwood¹⁰, Amiyaal Ilany⁵⁴, Joseph A. Jackson¹⁹, Nicola Jackson⁴⁵, David M. P. Jacoby⁵⁵, Ann-Marie Jacoby⁵⁶, Miloš Ježek⁵⁷, Lucinda Kirkpatrick^{58,59}, Alisa Klamm⁶⁰, James A. Klarevas-Irby^{35,36,61,62}, Sarah Knowles⁵, Lee Koren⁵⁴, Ewa Krzyszczyk⁵⁹, Jillian M. Kusch^{12,63}, Xavier Lambin⁶⁴, Jeffrey E. Lane⁶³, Herwig Leirs⁵⁸, Stephan T. Leu⁶⁵, Bruce E. Lyon²⁰, David W. Macdonald⁶⁶, Anastasia E. Madsen^{67,68}, Janet Mann², Marta Manser³⁶, Joachim Mariën⁵⁸, Apia Massawe⁶⁹, Robbie A. McDonald⁴³, Kevin Morelle^{57,70}, Johann Mourier^{71,72,73}, Chris Newman⁶⁶, Kenneth Nussear⁷⁴, Brendah Nyaguthii^{37,38,61,75}, Mina Ogino^{35,36,61}, Laura Ozella⁷⁶, Craig Packer⁷⁷, Yannis P. Papastamatiou⁷⁸, Steve Paterson⁷⁹, Eric Payne⁸⁰, Amy B. Pedersen⁸, Josephine M. Pemberton⁸, Noa Pinter-Wollman⁸¹, Serge Planes^{72,73}, Aura Raulo⁵, Rolando Rodríguez-Muñoz¹⁰, Lauren Rudd⁵, Christopher Sabuni⁶⁹, Pratha Sah², Robert J. Schallert⁸², Ben C. Sheldon⁵, Daizaburo Shizuka⁶⁷, Andrew Sih⁸⁰, David L. Sinn⁸³, Vincent Sluydts⁵⁸, Orr Spiegel⁴⁷, Sandra Telfer⁶⁴, Courtney A. Thomason^{39,84}, David M. Tickler⁸⁵, Tom Tregenza¹⁰, Kimberley VanderWaal⁸⁶, Sam Walmsley⁴⁰, Eric L. Walters¹⁷, Klara M. Wanelik^{79,87}, Hal Whitehead⁴⁰, Elodie Wielgus⁵¹, Jared Wilson-Aggarwal^{10,43}, Caroline Wohlfeil⁴⁶ & Shweta Bansal²

¹School of Natural Sciences, Trinity College Dublin, Dublin, Ireland. ²Department of Biology, Georgetown University, Washington, DC, USA.

³Wissenschaftskolleg zu Berlin, Berlin, Germany. ⁴School of Biological Sciences, University of Oklahoma, Norman, OK, USA. ⁵Department of Biology, University of Oxford, Oxford, UK. ⁶School of Biology, University of Leeds, Leeds, UK. ⁷Department of Primate Behavior and Evolution, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany. ⁸Institute of Ecology and Evolution, University of Edinburgh, Edinburgh, UK. ⁹Centre d'Ecologie Fonctionnelle et Evolutive, Université de Montpellier, Centre National de la Recherche Scientifique, École Pratique des Hautes Études, Institut de

Recherche pour le Développement, Montpellier, France. ¹⁰Centre for Ecology and Conservation, University of Exeter, Penryn, UK. ¹¹School of Biosciences, University of Sheffield, Sheffield, UK. ¹²Department of Biology, Memorial University of Newfoundland, St. John's, Newfoundland and Labrador, Canada. ¹³University of Guelph, Guelph, Ontario, Canada. ¹⁴Institute of Infection, Veterinary and Ecological Sciences, University of Liverpool, Liverpool, UK. ¹⁵Institute of Zoology, Zoological Society of London, London, UK. ¹⁶University of Glasgow, Glasgow, UK. ¹⁷Department of Biological Sciences, Old Dominion University, Norfolk, VA, USA. ¹⁸Avian Ecology Program, Archbold Biological Station, Venus, FL, USA. ¹⁹University of Salford, Salford, UK. ²⁰Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, Santa Cruz, CA, USA. ²¹Canine Companions, Santa Rosa, CA, USA. ²²Hopkins Marine Station, Stanford University, Stanford, CA, USA. ²³University of Nottingham, Nottingham, UK. ²⁴Pitzer and Scripps Colleges, Claremont, CA, USA. ²⁵Okanagan Department of Biology, Irving K. Barber Faculty of Science, University of British Columbia, Kelowna, British Columbia, Canada. ²⁶UK Centre for Ecology and Hydrology, Edinburgh, UK. ²⁷University of Delaware, Newark, DE, USA. ²⁸Marine Science Institute, University of California, Santa Barbara, Santa Barbara, CA, USA. ²⁹ISI Foundation, Torino, Italy. ³⁰Evolutionary Ecology Group, Station d'Écologie Théorique et Expérimentale du CNRS, Moulis, France. ³¹Oregon State University, Corvallis, OR, USA. ³²Lighthouse Field Station, School of Biological Sciences, University of Aberdeen, Aberdeen, UK. ³³Department of Zoology, University of Cambridge, Cambridge, UK. ³⁴National Wildlife Management Centre, Animal and Plant Health Agency, York, UK. ³⁵Department of Collective Behavior, Max Planck Institute for Animal Behavior, Konstanz, Germany. ³⁶Department of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich, Switzerland. ³⁷Department of Ornithology, National Museum of Kenya, Nairobi, Kenya. ³⁸Division of Ecology and Evolution, Research School of Biology, Australian National University, Canberra, Australian Capital Territory, Australia. ³⁹Virginia Tech, Blacksburg, VA, USA. ⁴⁰Department of Biology, Dalhousie University, Halifax, Nova Scotia, Canada. ⁴¹Department of Fisheries and Oceans, Bedford Institute of Oceanography, Dartmouth, Nova Scotia, Canada. ⁴²The Royal (Dick) School of Veterinary Studies, University of Edinburgh, Edinburgh, UK. ⁴³Environment and Sustainability Institute, University of Exeter, Penryn, UK. ⁴⁴Department of Marine Biology, Texas A&M University at Galveston, Galveston, TX, USA. ⁴⁵School of the Environment, University of Queensland, Brisbane, Queensland, Australia. ⁴⁶College of Science and Engineering, Flinders University, Adelaide, South Australia, Australia. ⁴⁷School of Zoology, Faculty of Life Science, Tel Aviv University, Tel Aviv, Israel. ⁴⁸Department of Zoology, University of Otago, Otago, New Zealand. ⁴⁹Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ, USA. ⁵⁰Sea Mammal Research Unit, South Oceans Institute, University of St Andrews, St Andrews, UK. ⁵¹Department of Visitor Management and National Park Monitoring, Bavarian Forest National Park, Grafenau, Germany. ⁵²Chair of Wildlife Ecology and Wildlife Management, Faculty of Environment and Natural Resources, University of Freiburg, Freiburg, Germany. ⁵³Department of Forestry and Wildlife Management, Faculty of Applied Ecology, Agricultural Sciences and Biotechnology, Inland Norway University of Applied Sciences, Elverum, Norway. ⁵⁴Faculty of Life Sciences, Bar Ilan University, Ramat Gan, Israel. ⁵⁵Lancaster University, Lancaster, UK. ⁵⁶Division of Marine Science and Conservation, Nicholas School of the Environment, Duke University Marine Laboratory, Beaufort, NC, USA. ⁵⁷Department of Game Management and Wildlife Biology, Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, Prague, Czech Republic. ⁵⁸Evolutionary Ecology Group—EVECO, Universiteit Antwerpen, Antwerp, Belgium. ⁵⁹School of Environment and Natural Science, Bangor University, Bangor, Wales. ⁶⁰Department of Nature Conservation and Research, Hainich National Park, Bad Langensalza, Germany. ⁶¹Mpala Research Center, Nanyuki, Kenya. ⁶²Centre for the Advanced Study of Collective Behaviour, University of Konstanz, Konstanz, Germany. ⁶³Department of Biology, University of Saskatchewan, Saskatoon, Saskatchewan, Canada. ⁶⁴University of Aberdeen, Aberdeen, UK. ⁶⁵School of Animal and Veterinary Sciences, University of Adelaide, Adelaide, South Australia, Australia. ⁶⁶Wildlife Conservation Research Unit, The Recanati-Kaplan Centre, Department of Zoology, University of Oxford, Oxford, UK. ⁶⁷School of Biological Sciences, University of Nebraska–Lincoln, Lincoln, NE, USA. ⁶⁸Department of Ecology, Behavior, and Evolution, University of California, San Diego, San Diego, CA, USA. ⁶⁹Institute of Pest Management, Sokoine University of Agriculture, Morogoro, Tanzania. ⁷⁰Max Planck Institute of Animal Behavior, Radolfzell, Germany. ⁷¹Biodiversité Marine, Exploitation et Conservation, Université de Montpellier, Centre National de la Recherche Scientifique, Institut Français de Recherche pour l'Exploitation de la Mer, Institut de Recherche pour le Développement, Sète, France. ⁷²PSL Research University, Université de Perpignan, Perpignan, France. ⁷³Laboratoire d'Excellence CORAIL, Papetoai, French Polynesia. ⁷⁴University of Nevada, Reno, NV, USA. ⁷⁵Department of Wildlife, School of Natural Resource Management, University of Eldoret, Eldoret, Kenya. ⁷⁶Department of Veterinary Sciences, University of Turin, Grugliasco, Italy. ⁷⁷Department of Ecology, Evolution and Behavior, University of Minnesota, Saint Paul, MN, USA. ⁷⁸Florida International University, Florida, FL, USA. ⁷⁹University of Liverpool, Liverpool, UK. ⁸⁰Department of Environmental Science and Policy, University of California, Davis, Davis, CA, USA. ⁸¹Department of Ecology and Evolutionary Biology, University of California, Los Angeles, Los Angeles, CA, USA. ⁸²Stanford University, Stanford, CA, USA. ⁸³Department of Wildlife, California State Polytechnic University, Arcata, CA, USA. ⁸⁴Texas Tech University, Lubbock, TX, USA. ⁸⁵University of Western Australia, Perth, Western Australia, Australia. ⁸⁶Department of Veterinary Population Medicine, University of Minnesota, Minneapolis, MN, USA. ⁸⁷University of Surrey, Guildford, UK. ✉e-mail: gfalbery@gmail.com

Reporting Summary

Nature Portfolio wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Portfolio policies, see our [Editorial Policies](#) and the [Editorial Policy Checklist](#).

Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a	Confirmed
☐	☒ The exact sample size (<i>n</i>) for each experimental group/condition, given as a discrete number and unit of measurement
☒	☐ A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☐	☒ The statistical test(s) used AND whether they are one- or two-sided <i>Only common tests should be described solely by name; describe more complex techniques in the Methods section.</i>
☐	☒ A description of all covariates tested
☐	☒ A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
☐	☒ A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☐	☒ For null hypothesis testing, the test statistic (e.g. <i>F</i> , <i>t</i> , <i>r</i>) with confidence intervals, effect sizes, degrees of freedom and <i>P</i> value noted <i>Give P values as exact values whenever suitable.</i>
☒	☐ For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☐	☒ For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☐	☒ Estimates of effect sizes (e.g. Cohen's <i>d</i> , Pearson's <i>r</i>), indicating how they were calculated

Our web collection on [statistics for biologists](#) contains articles on many of the points above.

Software and code

Policy information about [availability of computer code](#)

Data collection	NA
Data analysis	Data were manipulated and analysed using R version 4.2.3.

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio [guidelines for submitting code & software](#) for further information.

Data

Policy information about [availability of data](#)

- All manuscripts must include a [data availability statement](#). This statement should provide the following information, where applicable:
- Accession codes, unique identifiers, or web links for publicly available datasets
 - A description of any restrictions on data availability
 - For clinical datasets or third party data, please ensure that the statement adheres to our [policy](#)

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.

Research involving human participants, their data, or biological material

Policy information about studies with [human participants or human data](#). See also policy information about [sex, gender \(identity/presentation\), and sexual orientation](#) and [race, ethnicity and racism](#).

Reporting on sex and gender

NA

Reporting on race, ethnicity, or other socially relevant groupings

NA

Population characteristics

NA

Recruitment

NA

Ethics oversight

NA

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences

☐ Behavioural & social sciences

☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description

We aggregated 36 animal study systems donated by a series of collaborators. In each system, we built density distributions and social and spatial networks, with which we derived individual-level measures of density and connection strength. For each system we built linear and non-linear models examining the relationships between density and connectedness, which we then meta-analysed.

Research sample

The samples described as much data as researchers were willing and able to share. We contacted any researchers we knew had access to spatial and social behavioural datasets, with regular updating when we encountered a new publication with available apparently suitable data. Nobody we contacted did not agree to participate.

Sampling strategy

NA

Data collection

NA

Timing and spatial scale

The study systems were globally distributed and variably over the course of the last four decades, as detailed in the figures in the main text.

Data exclusions

We eliminated individuals that did not have at least 5 observations from the home range overlap analyses, and removed study systems with insufficient replication.

Reproducibility

NA

Randomization

NA

Blinding

NA

Did the study involve field work?

☐ Yes

☒ No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involvement in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology and archaeology
☒	☐ Animals and other organisms
☒	☐ Clinical data
☒	☐ Dual use research of concern
☒	☐ Plants

Methods

n/a	Involvement in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging

Plants

Seed stocks	None
Novel plant genotypes	None
Authentication	None