Density-dependent network structuring within and across wild animal systems

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Abstract

High population density should drive individuals to more frequently share space and interact, producing better-connected spatial and social networks. Despite this widely-held assumption, it remains unconfirmed how local density generally drives individuals' positions within wild animal networks. We analysed 34 datasets of simultaneous spatial and social behaviour in >55,000 individual animals, spanning 28 species of fish, reptiles, birds, mammals, and insects. >80% of systems exhibited strongly positive relationships between local density and network centrality, providing broad empirical evidence that local density increases connectedness at the individual level. However, >75% of density-connectedness relationships were nonlinear, and density's importance declined at higher values in >70% of systems, signifying saturating effects. Density's effect was much stronger and less saturating for spatial than social networks, suggesting population density drives individuals to become disproportionately spatially connected rather than socially. These findings reveal fundamental trends underlying societal structuring, with widespread behavioural, ecological, and evolutionary implications.

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 to spread between hosts [1–5]. 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's 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., [6,7]) or groups (e.g., [8–10]), attempts to identify such density effects *within* continuous populations of individuals are rarer (but see [11–14]), and their findings have never been synthesised or compared. 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., [15]), and/or to be homogenous in space (e.g., [10]). In reality individuals are unlikely to behave and interact randomly in space, and instead will be influenced by spatially varying factors including local density [16]. Changes in density may cause individuals to alter their foraging behaviour [17–19], dispersal [20,21], social preference or avoidance [13,22], mating behaviour [23], or preferred group size [7]; in some cases, interaction rates may change to remain constant in the face of changing densities [24]. 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]. Nevertheless, these nonlinearities are poorly understood and rarely considered.

Several wild animal studies have suggested saturating nonlinear relationships between density and social association rates [8–10,13]. Such relationships imply that association rates do not increase passively with density, and 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]. Characterising gradients of density across individuals within a population offers a workaround to this problem, 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 [25–29]. Additionally, recent years have seen a substantial growth in understanding of socio-spatial behaviours, including harmonising the concepts of spatial and social density [2,16,30]. 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 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 [31], but this is unlikely to be true of mating interactions. 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 [1,32]. Establishing these density-contact relationships is integral to understanding disease dynamics and developing control measures [1,33], 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 [30], but given building interest in the spatial-social interface and relationships between spatial and social networks in behavioural ecology [16], the framework is readily related to other fields. Established density-interaction relationships are diverse and include feral dog bites [11], ant antennations [34] and trophallaxis [24], ungulate group memberships [12,17], rodent co-trapping [8,35], and agamid association patterns [13,14], but no study has yet synthesised how the rates of multiple interaction 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 55,000 individual animals across 34 wildlife systems globally to ask how within-population variation in density determines between-individual interaction rates based on connectedness in spatial and social networks. We fit multiple 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.

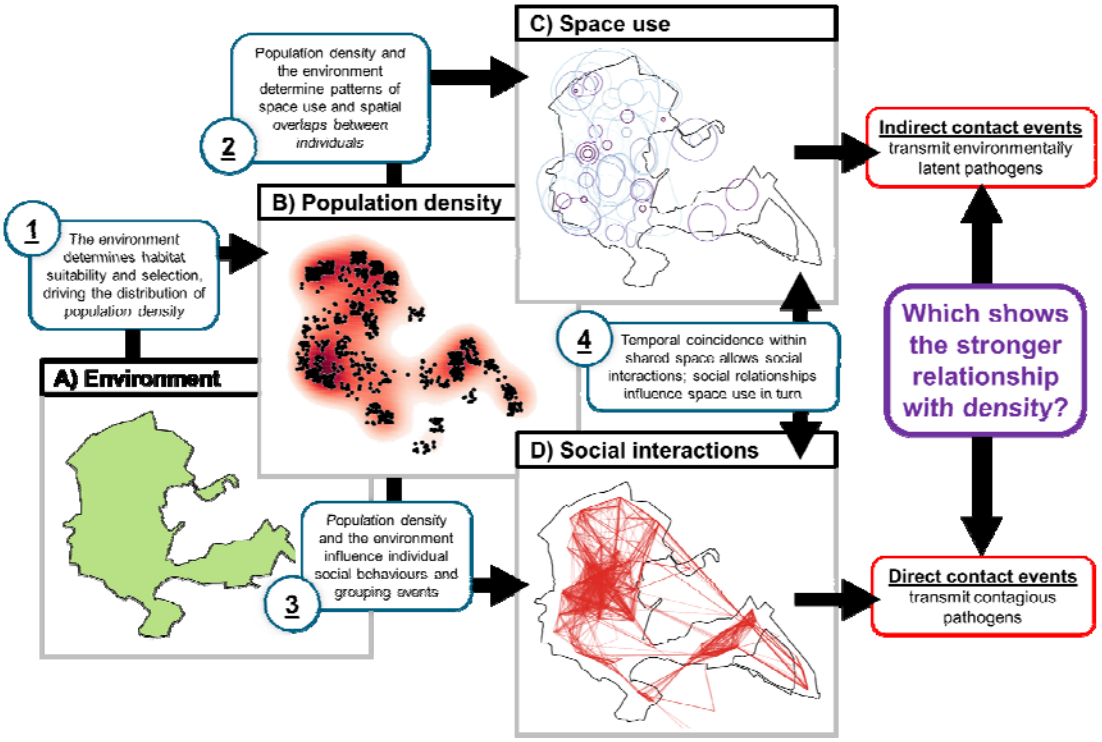

Figure 1: Schematic detailing the rationale underlying this study, outlining how population density drives the formation of spatial and social networks. This depiction uses the Wytham Wood great tits as an example. Ultimately, we aim to ask whether spatial or social connections generally show a stronger 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.

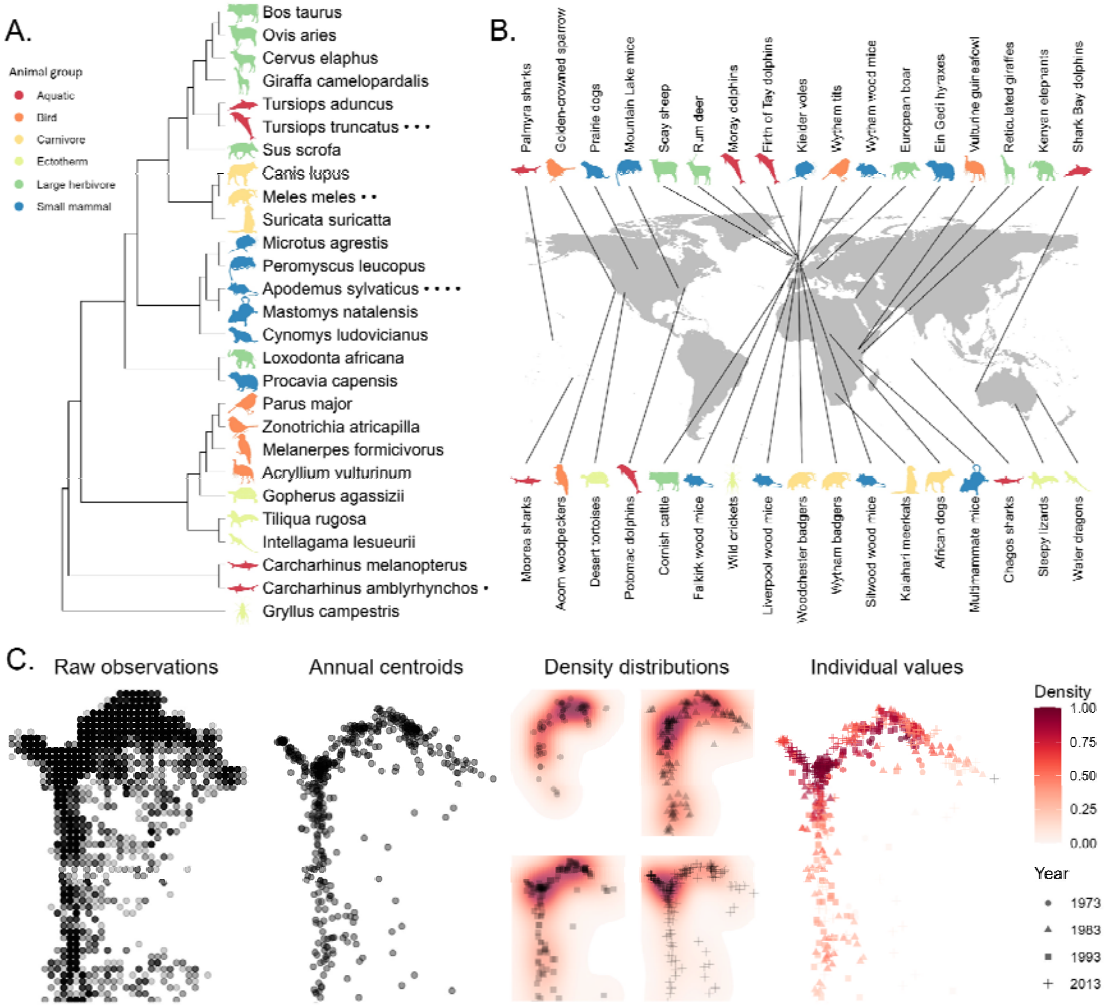

Figure 2: The phylogenetic (A) and geographic (B) distribution of our 34 examined datasets of spatial and social behaviour, with (C) schematic depicting the methodology for deriving local density values, using the Isle of Rum red deer data as an example. The X and Y axes are bivariate spatial coordinates. 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. 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.*

Methods

Data standardisation and behavioural pipeline

Data were manipulated and analysed using R version 4.2.3 [36], and all R code is available at https://github.com/gfalbery/DensityMetaAnalysis. Our 34 datasets each involved at least one continuous uninterrupted spatial distribution of observations in a single population; some datasets comprised multiple such populations. These datasets covered 28 different host species, including sharks, carnivores, cetaceans, ungulates, rodents, elephants, birds,

reptiles, and one 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 60 system-behaviour replicates, listed in Supplementary Table 1, and totalled 151,507 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 [12,37], we took each individual's average location across the year (their centroid) and created a spatial density kernel using the `adehabitathr` package [38], 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 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; 10/34 (29%) 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) [39]; 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 [30,40]. 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 [41]). 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 novel workflow to allow us to derive and compare density's effects on connectedness – and their drivers – in a standardised way across our wild animal systems. These took three forms: linear models fitted to the whole dataset, nonlinear models fitted to the whole dataset, and linear 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.

Generalised additive models (GAMs): We fitted GAMs in the `mgcv` package [42] 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 2ΔAIC designated to distinguish between models. See Supplementary Figure 1 for a schematic depicting our analytical workflow.

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.

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*) [43]. We converted all correlation coefficients into Fisher's *Z* (Z_r) and computed associated sampling variance. We then used an initial model that nested observations within a system-level random effect to account for within- and between-system heterogeneity [44], as 24/34 systems had more than one density effect. We used a random effect for species to account for repeat observations per animal species.

We then added a separate random effect for animal phylogeny [45]. This used a phylogenetic correlation matrix of our 28 animal species derived from the Open Tree of Life via the `rotl` package [46], with the `ape` package used to resolve multichotomies and provide branch lengths [47]. We fitted the model 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 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 host 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 to 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 capable of meta-analysing nonlinear estimates are not yet well defined.

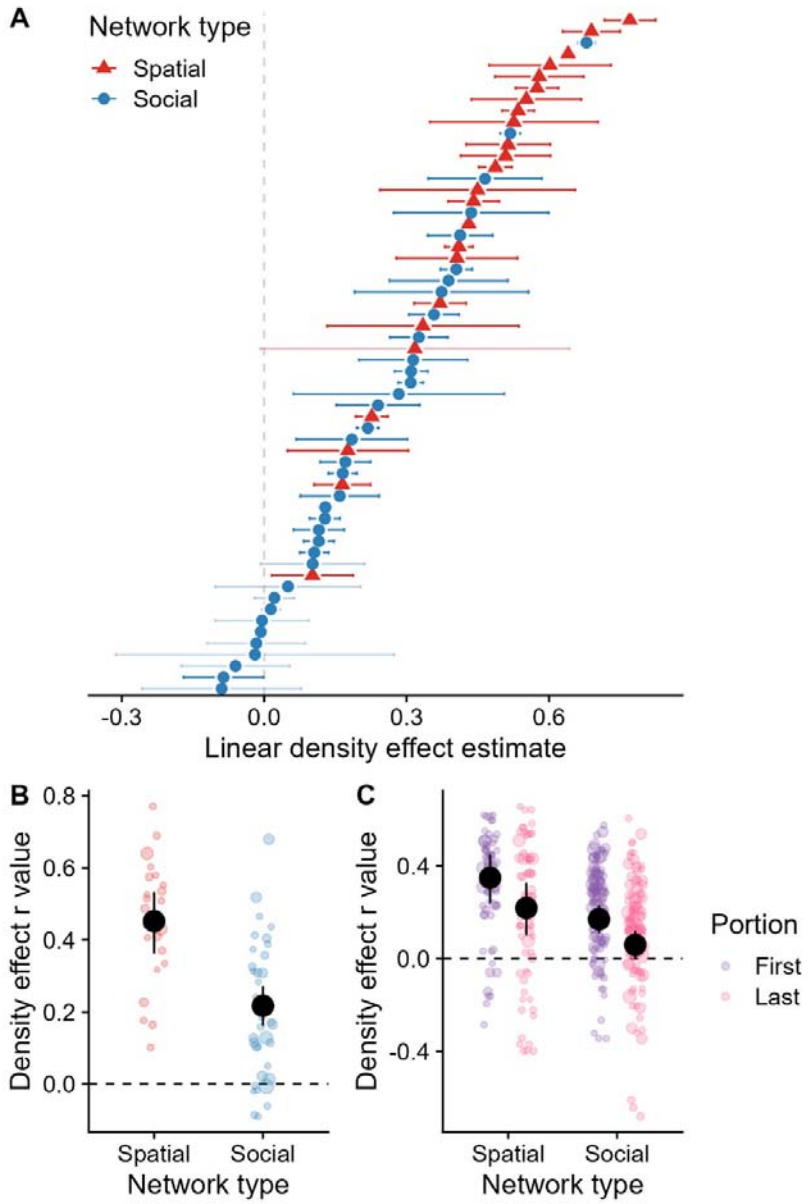

Figure 3: Meta-analysis revealed drivers of variation in linear density effects on individual network connectedness across systems. A) Our fitted linear model estimates of density effects on network strength. Each point represents the mean estimate from a given system; the error bars denote 95% confidence 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) When linear models were fitted separately to two portions of the data (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.

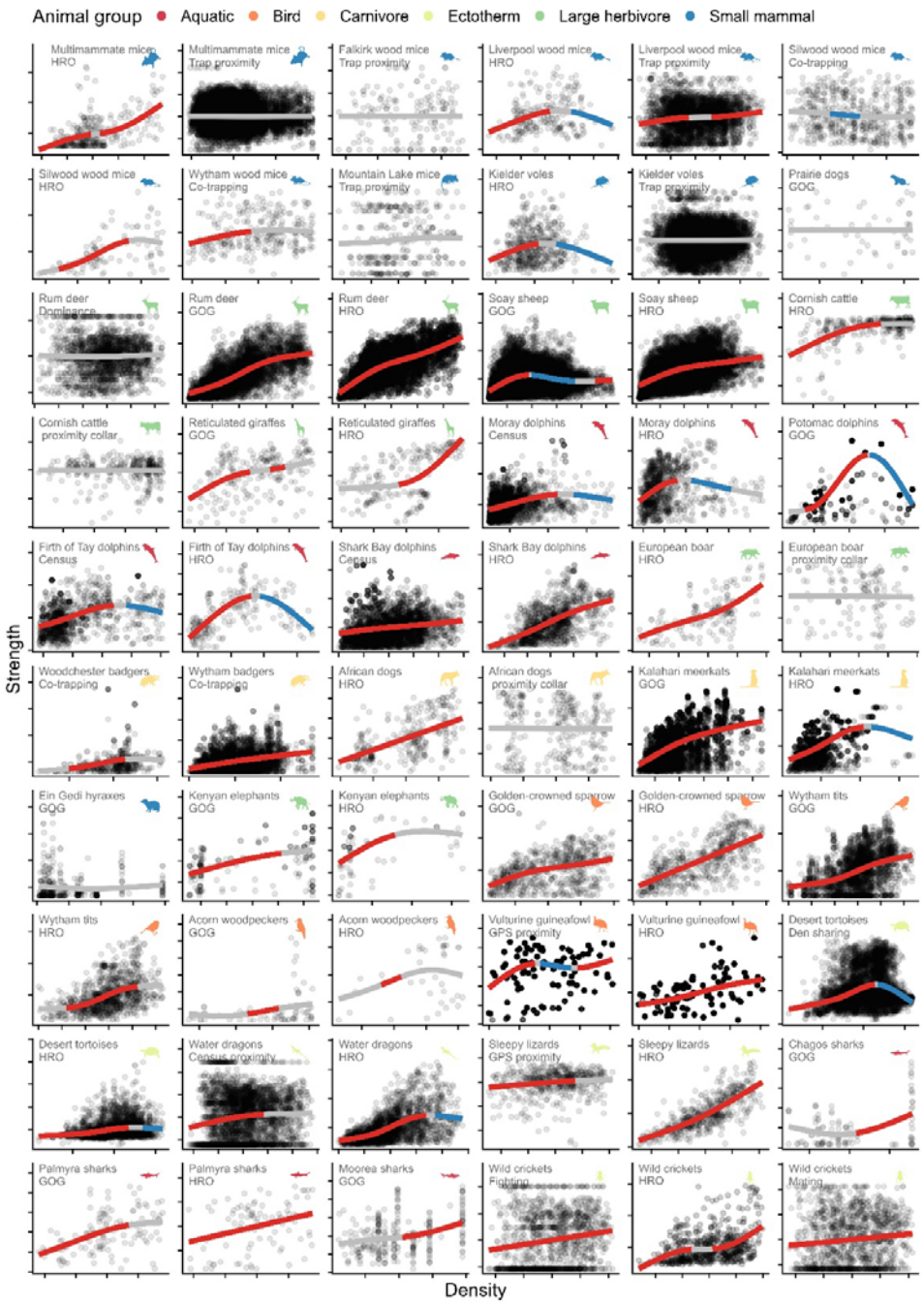

Figure 4: Relationships between density and network connectedness varied substantially across animal systems. Density in individuals per area is on the x axis; network connectedness (strength centrality) is on the y axis. Both values have been standardised to have a mean of zero and a standard deviation 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 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. Supplementary Figure 2 shows a version of this plot with variable smoothing parameters to show variation in the possible shape of the curves. Animal silhouettes are from phylopic.org; a set of links and attributions are in the Supplement.

Results and Discussion

We compiled an unprecedented comparative meta-dataset of over ten million observations of individual animals' spatial and social behaviour, across an expansive range of ecological systems. 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 60 replicates, 48 (80%) were significantly positive when analysed using linear models (Figure 3A; Supplementary Table 1). Meta-analyses identified a highly significant positive mean correlation between density and connectedness, both for social networks (Estimate 0.22; 95% CI 0.16, 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_{35} = 5744.83 and Q_{23} = 1559.08, 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. This approach has only rarely been applied before, and then at much coarser resolution (see [8,9,11]). As such, this study fills an important empirical gap by providing insights into the slope and shape of density-connectedness relationships for a variety of animal groups and their social and spatial behaviours (Figure 4). Nevertheless, 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 0.28 (CI 0.17, 0.38, 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 44/60 systems (73%) had a steeper slope at low density values than at high ones. This effect was strong for social networks (effect on r= -0.11; CI -0.20, -0.03; P=0.01) and similar in size but marginally insignificant for spatial networks (-0.14; -0.29, 0.01; P=0.058); due to the greater overall effect for space sharing, the latter half of the density-spatial connections effect was still higher than the first half of the density-social connections effect (Figure 3C). In fact, the second half of the social effect overlapped with zero (Figure 3C; lower CI=-0.0119): that is, considering only the upper half of density values would not have uncovered a significant effect of density on individuals' connectedness in social networks. 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 [31] or exposure to infectious disease [48]. Eastern water dragons (*Intellagama lesueurii*) show greater avoidance at higher densities [13], supporting this mechanism. 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 [49]. In general, individuals likely have a preferred social interaction rate or group size – a preference that they may increasingly exert at higher densities [7]. 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 [50–52], and social phenotypes [52–54] in ways that should manifest for density-dependent behaviours specifically [16], it seems likely that these slopes could vary between individuals as they do between populations. Future analyses might fit variable density-connectedness slopes between individuals to identify socio-spatial syndromes across systems, as has been done previously in single systems including caribou (*Rangifer tarandus*) [55] and red squirrels (*Tamiasciurus hudsonicus*) [56].

We considered 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 [57], or reduce their territory or home range sizes [56,58,59], potentially driven by years of plentiful resources supporting higher densities alongside smaller home ranges 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 might 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.

The fact that spatial networks show stronger and more linear density dependence than social networks is likely to have important implications for the ecology of wild 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 contagious 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. 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 [15]. These relationships could influence our targets for culling or vaccination coverage [61]. Given that animals at high density seem likely to have a relatively shallow relationship between density and contact rates, reducing population density – for example via culling – might not be effective at reducing pathogen transmission initially, particularly when considering socially transmitted pathogens, where contact rates are particularly likely to have saturated (Figure 3C). Similar problems with culling have already been acknowledged in specific systems – e.g. in canine rabies [33,62,63] – 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 demographic processes.

Operationally, the common nature of saturating density effects will impact researchers' ability to detect density dependence: that is, density dependence could be harder to observe in higher-density areas given the shallower slopes we observed. Most of the systems in this study are relatively long-term studies of known individuals; these populations tend to be in carefully selected, high-density areas that make it convenient to study the focal animal with relatively low operational costs. For example, it has previously been noted that the badgers of Wytham Wood, the red deer of the Isle of Rum, and the Soay sheep of St Kilda are all at high densities for their respective species [64–66]. As such, we may be inherently investigating the upper end of density-connectedness relationships in the wild, and it could be difficult and costly to investigate the effects of low density so widely.

Beyond these general trends, our GAMs revealed that 46/60 density effects on network connectedness (77%) were significantly nonlinear ($\Delta AIC>2$); these relationships took a wide variety of shapes, representing a range of nonlinear functions that are hard to generalise (Figure 4; Supplementary Table 2). 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 host group. These observations were largely corroborated by our meta-analytical models, which found no factors influencing the slope and shape of density effects ($P>0.05$). 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 [67,68], parasite avoidance [69], and demographic structuring [70]. 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.

We acknowledge several limitations of our study, which we nevertheless believe could be remedied in the future. First, many of our social networks were formed of general spatiotemporal associations, and relatively few from specific social interactions – particularly those involving direct physical contact. Our current dataset could therefore benefit from supplementation with a broader range of direct interactions, particularly involving antagonism or bonding. For example, datasets concerning aggression or dominance interactions (e.g. [71]) or grooming alongside spatial behaviour could inform how density dependence affects the transmission of certain parasites such as mycobacteria [72] or tattoo skin disease [73].

The meta-dataset was also unevenly distributed across animal taxa (Figure 1): there were no primates or bony fishes and only one invertebrate, while rodents and ungulates were over-represented. These biases likely emerge through differences in data collection approaches: for example, although primate social behaviour is often studied with observations of direct interactions that could augment our data as described above (e.g. [74]), the spatial data required to build density distributions are rarely collected in these systems. This is linked to their social structures: our workflow was best suited to studies of fission-fusion societies or relatively asocial animals, rather than those with wide-ranging fixed social groups that are more common in primate systems. Finally, given that our data were observational, we could not account for (or estimate) bidirectional causality between density and social relationships (point 4 in Figure 1): that is, as well as encountering more conspecifics in areas of high density, individuals may be drawn to conspecifics, *creating* areas of high density [16]. To do so might require creating in-depth, high-resolution models of animal movement and group formation (e.g. [75]), potentially making use of telemetry approaches and drawing from large-scale open movement repositories like Movebank [76].

Aside from incorporating more specific interaction types, there exist a range of potential extensions to our analysis. For example, density dependence often varies between age or sex classes (e.g. [77,78]), and age effects on infection are common and ecologically important [79,80], as are sex differences [81]. We chose not to analyse how individual animals' traits alter the shape or slope of density's effects for brevity and simplicity; however, given that many of the systems nevertheless include these data, future analyses could make use of this meta-dataset to investigate how density affects connectedness of different classes of hosts. Further, researchers could investigate other behavioural questions such as the role of observation biases; the factors influencing the correlation between spatial and social networks; and the role of environmental drivers and spatial autocorrelation in driving observed patterns of connectivity [12,16]. Finally, as our analysis approximated density-contact relationships and not host-parasite interactions specifically, important future work could investigate whether contact rates (as approximated by network connectedness) ultimately translate to greater infection risk or parasite burden. Although some previous investigations have linked density-related metrics to aspects of infection [82,83], density covaries with a range of other factors including nutrition, cooperation, and competition, all of which could complicate density-driven increases in exposure [2]. For example, in the case of ectoparasite transmission, although contact rates in general would likely increase with density, so too might grooming behaviours that remove parasites; in cases such as these, density's overall effect on ectoparasite infection may be neutral. In the future, verifying that within- and between-population variation in density-contact relationships translate to variation in infection – and whether these trends might be influenced by flexible avoidance behaviours [37] – will be a vital part of understanding and predicting density-dependent disease dynamics.

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 [84] and in food web ecology [85], the patterns we report strongly suggest that animal systems generally become better connected spatially than socially under increasing density. These might extrapolate to human networks, given that other scaling patterns in animal networks do [84]. 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.

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Code availability

All R code is available at https://github.com/gfalbery/DensityMetaAnalysis.

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