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Density-dependent network structuring within and across wild animal systems

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Abstract

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

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

Introduction

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

187 changes in density – e.g. through culling, natural mortality, dispersal, or population booms –
188 influence downstream processes that depend on shared space and social interactions.

189 The rate at which an individual interacts with conspecifics depends on its spatial and social
190 behaviour within the context of the surrounding environment and population. Adding more
191 individuals into the same space should cause them to more frequently spatially overlap and
192 socially associate or interact (Figure 1). Often, individuals are modelled as randomly moving
193 and interacting molecules ("mass action" or "mean field"). In this conceptualisation, direct
194 contact between two molecules is analogous to a social interaction or association; rates of
195 such interactions are often assumed to increase with density ("density-dependent"; e.g., [17]),
196 and/or to be homogenous in space (e.g., [12]). In reality individuals are unlikely to behave and
197 interact randomly in space, and instead will be influenced by spatially varying factors including
198 local density [18] and competition for resources [9]. Changes in density may cause individuals
199 to alter their foraging behaviour [19–21], dispersal [22,23], social preference or avoidance
200 [15,24], mating behaviour [25], or preferred group size [8]. In some cases, density may have
201 no effect on interaction rates, because individual animals alter their behaviour in a density-
202 dependent manner to maintain a desired interaction rate [26]. These and related processes
203 might produce strong nonlinearities in density-interaction relationships, which can complicate
204 the predictions of density dependence models of pathogen transmission, for example [2,4,5].
205 For example, individuals or groups can learn to avoid where competitors might go, resulting in
206 greater spatial partitioning under higher densities [27]. Nevertheless, nonlinearities such as
207 these are poorly understood and rarely considered.

208 Several wild animal studies have suggested relationships between density and social
209 association rates are often nonlinear and saturating [9–12,15]. Such relationships imply that
210 association rates do not increase passively with density, but rather that behavioural or
211 demographic processes likely change as density increases, with the ultimate consequence of
212 slowing association rates. However, these nonlinearities are difficult to examine between
213 populations or between species because they introduce a range of confounders and have few
214 replicates along the density axis [2]. On the other end, lower densities may provide less ability
215 to exert social preferences, but low-density populations may be harder to study due to (for
216 example) low return on sampling investment; alternatively, the failure to achieve sufficient
217 interaction rates may result in Allee effects and ultimately drive populations toward decline
218 [28,29].

219 Characterising gradients of density across individuals within a population offers a workaround
220 to these problems, and facilitates an appreciation of the fact that interactions occur between
221 individuals rather than at the population level. Examining between-individual variation is one
222 reason that social network analysis – which allows characterisation and analysis of individual-
223 level social traits, amongst other things – has become so popular in animal ecology in recent
224 years [30–34]. Additionally, recent years have seen a substantial growth in understanding of
225 socio-spatial behaviours, including harmonising the concepts of spatial and social density
226 [2,18,35]. Applying network analyses coupled with this socio-spatial understanding of density
227 could provide an individual-level picture of density's effects on spatial and social
228 connectedness, offering far higher resolution and statistical power and greater ability to detect
229 within-system nonlinearities and between-system differences [2]. By providing new
230 understanding of the correlates and emergent consequences of variation in density, this

231 expansion could help to identify general rules underlying social structuring and network scaling
232 in space.

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

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

270

271 Results and Discussion

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

277 We observed strong positive relationships between individuals' local population density and
278 their connectedness in spatial and social networks across a wide range of wild animals: of our
279 64 replicates, 51 (78%) were significantly positive when analysed using linear models (Figure
280 3A). Meta-analyses identified a highly significant positive mean correlation between density
281 and connectedness, both for social networks (Estimate 0.22; 95% CI 0.17, 0.27) and spatial
282 networks (0.45; 0.36, 0.53; Figure 3B). Our study therefore provides fundamental evidence
283 that high local population density broadly drives greater connectedness within ecological
284 systems, at the individual level. Slopes were highly variable across systems for both spatial
285 and social networks (Figure 3A; Q-test of heterogeneity across systems: $Q_{37} = 5627.33$ and
286 $Q_{25} = 1281.83$, both P<0.0001), indicating that quantifying these slopes within and between
287 multiple systems and comparing them is important for understanding animal socio-spatial
288 structure. That is, relationships between density and individual connectedness differ
289 substantially between populations, and the biological mechanisms underlying these divergent
290 trends are likely important. As well as adding resolution and allowing comparisons of density
291 effects across systems, our methodology facilitated fitting of nonlinear relationships (using
292 generalised additive models (GAMs); see below). This approach has only rarely been applied
293 before, and then at much coarser resolution (see [10,11,13]). As such, this study fills an
294 important empirical gap by providing insights into the slope and shape of density-
295 connectedness relationships for a diverse variety of animal groups and their social and spatial
296 behaviours (Figure 4). Nevertheless, despite this diversity, we were able to identify several
297 further general trends in our data.

298 Remarkably, density's effect more than doubled in size for spatial compared to social networks
299 (Figure 3B; r=0.45 *versus* 0.22); there was a difference of 0.26 (CI 0.16, 0.36, P<0.0001) for
300 this effect when we meta-analysed the two contact types together. This finding indicates that
301 as density increases, wild animals are more likely to share space with each other, but that
302 social connections increase at a much slower rate. Similarly, we discovered that saturating
303 shapes were extremely common: as density increased, its effect on connectedness
304 decreased, such that 48/64 systems (75%) had a steeper slope at low density values than at
305 high ones. This effect was strong for both social networks (effect on r= -0.11; CI -0.19, -0.03;
306 P=0.01) and for spatial networks, with substantial overlap between their estimates (-0.22; -
307 0.37, -0.07; P=0.0042). Due to the greater overall effect for space sharing, the latter half of
308 density's spatial effect was still higher than the first half of its social effect (Figure 3C).
309 Together, these observations suggest that density-dependent processes act to limit the
310 increase in social connectedness with density, but without limiting spatial overlaps to the same
311 extent. Consequently, higher-density areas are characterised disproportionately by individuals
312 asynchronously sharing space rather than socially associating, while in lower-density areas
313 individuals are disproportionately more socially connected proportional to their shared space.

314 There are many possible social reasons for saturating nonlinearity in density-dependent
315 network structuring: for example, individuals in higher density areas may begin to avoid each
316 other, seeking to avoid competition or aggression [36] or exposure to infectious disease [44].
317 For instance, Eastern water dragons (*Intellagama lesueurii*) show greater avoidance at higher
318 densities [15], supporting avoidance-related mechanisms. Alternatively, in species with high
319 social cognition or stable bonds, saturation could reflect lower social effort or ability to keep
320 track of social affiliates at higher densities [45]. In general, individuals likely have a preferred
321 social interaction rate or group size – a preference that they may increasingly exert at higher
322 densities [8]. It remains to be seen how this preference varies among individuals, and whether
323 individuals vary in their preferred social network position given a certain density. Given that
324 individuals vary in their movement and spatial phenotypes [46–48], and social phenotypes
325 [48–50] in ways that should manifest for density-dependent behaviours specifically [18], it
326 seems likely that these slopes could vary between individuals as they do between populations.
327 Future analyses might fit variable density-connectedness slopes among individuals to identify
328 socio-spatial syndromes across systems, as has been done previously in single systems
329 including caribou (*Rangifer tarandus*) [51] and American red squirrels (*Tamiasciurus*
330 *hudsonicus*) [52]. Additionally, we could dissect the social network and its relationship to the
331 spatial network to identify levels of attraction [53,54] or avoidance [55] and how they depend
332 on density.

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

359   The fact that spatial networks show stronger and more linear density dependence than social
360   networks could heavily influence the ecology of animal systems. For example, indirectly
361   transmitted (i.e., environmentally latent) parasites may exhibit greater density dependence
362   than directly transmitted ones, given that individuals likely experience disproportionately more
363   indirect contact at higher densities. This observation contrasts with orthodoxy that directly
364   transmitted parasites are most likely to be density dependent [60], and supports the value of
365   investigating nonlinear changes in socio-spatial behaviour and grouping patterns in response
366   to density when considering density dependence. Saturating density-connectedness functions
367   further have implications for disease modelling and control. Specifically, our findings lend
368   behavioural support to the growing consensus that many diseases are density-dependent at
369   lower densities, but not at higher densities (i.e., that the slope flattens with density) [17,61].
370   Rather than assuming constant behavioural mixing at higher densities, epidemiological
371   models could benefit from incorporating density-dependent shifts in behaviours and
372   demography that influence direct and indirect interaction frequencies, as previously suggested
373   empirically and by epidemiological theory [17]. These relationships could influence our targets
374   for culling or vaccination coverage [62]. Given that animals at high density seem likely to have
375   a relatively shallow relationship between density and contact rates, reducing population
376   density – for example by culling – might therefore be ineffective at reducing pathogen
377   transmission initially, particularly when considering socially transmitted pathogens, where
378   contact rates are particularly likely to have become saturated (Figure 3C). Similar problems
379   with culling have already been acknowledged in specific systems – e.g. in canine rabies
380   [39,63,64] – but our study implies that shallow nonlinear density-contact trends could be more
381   general than previously thought and could be driven by flexible density-dependent changes in
382   behaviour and demography. Conversely, culling could be disproportionately effective at
383   intermediate densities and identifying the inflection points of the curve might help to design
384   optimal management strategies. Future studies should investigate whether the divergence in
385   spatial and social connectedness with density drives a concurrent divergence in the
386   prevalence of directly and indirectly transmitted parasites, as well as addressing several other
387   biases in our selection of systems (e.g. [65]; see Supplementary Discussion).

388   Beyond these general trends, we ran generalised additive models (GAMs) that revealed that
389   52/64 density effects on network connectedness (81%) were significantly nonlinear (ΔAIC>2);
390   these relationships took a wide variety of shapes, representing a range of nonlinear functions
391   that are hard to generalise (Figure 4). Notably, while many GAM smooths were eventually
392   significantly negative (Figure 4), the vast majority of linear models fitted to the second half of
393   the data were positive (Figure 3C); this result is likely an artefact of restricted model fitting,
394   rather than true downturns in connectedness with density. Nonlinearity did not cluster
395   according to connection type definitions, or according to animal group. These observations
396   were largely corroborated by our meta-analytical models, which found no factors influencing
397   the slope and shape of density effects overall (P>0.05; Supplementary Table 3), including no
398   clear phylogenetic signal (ΔAIC=2.71). This observation speaks to the complexity of these
399   relationships within and across systems, while accentuating that simple functional
400   relationships are often likely to be complicated by contravening ecological factors like habitat
401   selection [66,67], group formation [9], parasite avoidance [68], and demographic structuring
402   [69]. While we were unable to identify specific between-system predictors of nonlinearity of
403   density-connectedness relationships, the finding that most such relationships are strongly
404   nonlinear is an important consideration for future work.

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

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

Methods

Data standardisation and behavioural pipeline

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

446 To standardise the timescale across studies, all systems were analysed as annual replicates
447 – i.e., social and spatial networks were summarised within each year. Our analyses used 64

448 system-behaviour replicates, listed in Supplementary Table 1, and totalled 151,835 unique
449 system-individual-year-behaviour data points.

450 All spatial coordinates were converted to the scale of kilometres or metres to allow comparison
451 across systems. To provide an approximation of local density, following prior methodology
452 [14,77], we took each individual's average location across the year (their centroid) and created
453 a spatial density kernel using the `adehabitathr` package [78], which provides a probabilistic
454 distribution of population density across each study system based on the local frequencies of
455 observed individuals. Each individual was assigned an annual estimate of local density based
456 on their centroid's location within this spatial density distribution. We made these density
457 distributions as comparable as possible between systems by incorporating the density raster
458 using metre squares; however, there were large differences in density across populations that
459 were difficult to resolve and put on the same scale (e.g. interactions per individual/km^2 unit of
460 density). Consequently, we scaled and centred density to have a mean of zero and a standard
461 deviation of one within each population, which allowed us to focus on differences in relative
462 slope and shape across systems.

463 To validate the local density measures estimated using the kernel density approach, we also
464 estimated local density for individuals across all populations based on the locations of
465 individual annual centroids within a designated area. To do so, we first estimated the area of
466 the minimum bounding box (MBB) within which all individuals were censused during the study
467 period based on their annual centroids. For each individuals mean location, we then estimated
468 a circular boundary of radius r=1/20 * area of MBB. We then calculated the number of
469 individuals present within this boundary as an individual's local density measure. We
470 estimated the Pearson correlation coefficients between the local density measures derived
471 using the KDE approach and the proportional area - based approach (Supplementary Figure
472 1).

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

485 To provide a measure of social connectedness, we built social networks using various
486 approaches as defined by the original studies: direct observations of dyadic interactions (e.g.
487 fighting or mating); gambit of the group (GoG; i.e., membership of the same group) [59]; co-
488 trapping (i.e., trapped together or in adjacent traps within a given number of trapping
489 sessions); or direct contact measured by proximity sensors (defined by a certain distance-
490 based detection threshold). Notably some analyses use indirect interactions – i.e., spatial
491 overlap – to *approximate* direct interactions, which requires spatiotemporal coincidence, which

492 we caution against particularly when modelling pathogen transmission [35,79]. While the two
493 do often correlate, here we are not using HRO to approximate direct interaction rates, but
494 rather as a measure of indirect interactions (e.g., indicative of transmission of environmental
495 parasites).

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

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

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

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

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

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

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

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

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

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

564 For our hierarchical meta-analysis models, we used an initial model that nested observations
565 within a system-level random effect to account for within- and between-system heterogeneity
566 [83], as 26/36 systems had more than one density effect. We used another random effect for
567 species to account for repeat observations per animal species.

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

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

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

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

588 We ran several different versions of these meta-analyses: first, we fitted meta-analytical
589 models to the **overall linear models** of spatial and social interaction types separately, and
590 then together, to investigate differences between the spatial and social networks in terms of
591 their mean density slope. Next, we fitted duplicated versions of these models, but with the
592 **saturation models**. These models were identical, but each system replicate had two linear
593 estimates: one taken from the first 50% of the data (up to the median), and one from the latter
594 50%. By fitting a binary fixed effect of "data portion" to the meta-analytical models, this model
595 would tell us whether the slopes were generally higher in the first portion of the data than the
596 last (and therefore showed generally saturating shapes). We were unable to fit meta-analytical
597 models to our GAMMs, as methods for the meta-analysis of nonlinear estimates are not yet
598 well defined.

599 Data availability

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

604 Code availability

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

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Author contributions

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

Competing interests

The authors declare no competing interests.

Figure legends

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

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

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

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

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

672

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