



HAL
open science

Density-dependent network structuring within and across wild animal systems

Gregory Albery, Daniel Becker, Josh Firth, Matthew Silk, Amy Sweeny, Eric Vander Wal, Quinn Webber, Bryony Allen, Simon Babayan, Sahas Barve, et al.

► **To cite this version:**

Gregory Albery, Daniel Becker, Josh Firth, Matthew Silk, Amy Sweeny, et al.. Density-dependent network structuring within and across wild animal systems. 2025. hal-04735267

HAL Id: hal-04735267

<https://hal.science/hal-04735267v1>

Preprint submitted on 6 Jan 2025

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NoDerivatives 4.0 International License

1 Density-dependent network structuring within and 2 across wild animal systems

3 Gregory F Albery^{*1,2}, Daniel J Becker³, Josh A Firth^{4,5}, Matthew Silk^{6,7}, Amy R Sweeny^{8,9},
4 Eric Vander Wal¹⁰, Quinn Webber¹¹, Bryony Allen^{12,13}, Simon A Babayan¹⁴, Sahas Barve^{15,16},
5 Mike Begon¹², Richard J Birtles¹⁷, Theadora A Block^{18,19}, Barbara A Block²⁰, Janette E
6 Bradley²¹, Sarah Budischak²², Cfhristina Buesching^{23,24}, Sarah J Burthe²⁵, Aaron B Carlisle²⁶,
7 Jennifer E Caselle²⁷, Ciro Cattuto²⁸, Alexis S Chaine²⁹, Taylor Chapple³⁰, Barbara J
8 Cheney³¹, Timothy Clutton-Brock³², Melissa Collier¹, David J Curnick³³, Richard J Delahay³⁴,
9 Damien R Farine^{35,36,37,38}, Andy Fenton¹², Francesco Ferretti³⁹, Helen Fielding^{40,41}, Vivienne
10 Foroughirad^{1,42}, Celine Frere⁴³, Michael G Gardner⁴⁴, Eli Geffen⁴⁵, Stephanie S Godfrey⁴⁶,
11 Andrea L Graham⁴⁷, Phil S Hammond⁴⁸, Maik Henrich⁴⁹, Marco Heurich^{49,50,51}, Paul
12 Hopwood⁷, Amiyaal Ilany⁵², Joseph A Jackson¹⁷, Nicola Jackson⁴³, David Jacoby⁵³, Ann-
13 Marie Jacoby⁵⁴, Miloš Ježek⁵⁵, Lucinda Kirkpatrick⁵⁶, Alisa Klamm⁵⁷, James A Klarevas-
14 Irby^{35,36,58,59}, Sarah Knowles⁴, Lee Koren⁵², Ewa Krzyszczak⁶⁰, Jillian M Kusch^{61,62}, Xavier
15 Lambin⁶³, Jeffrey E Lane⁶², Herwig Leirs⁵⁶, Stephan T Leu⁶⁴, Bruce E Lyon¹⁸, David W
16 MacDonald²³, Anastasia E Madsen^{65,66}, Janet Mann¹, Marta Manser⁶⁷, Joachim Mariën⁵⁶,
17 Apia Massawe⁶⁸, Robbie A McDonald⁴¹, Kevin Morelle^{55,69}, Johann Mourier^{70,71,72}, Chris
18 Newman²³, Kenneth Nussear⁷³, Brendah Nyaguthii^{37,38,58,74}, Mina Ogino^{35,36,58}, Laura
19 Ozella⁷⁵, Yannis Papastamatiou⁷⁶, Steve Paterson⁷⁷, Eric Payne⁷⁸, Amy B Pedersen⁹,
20 Josephine M Pemberton⁹, Noa Pinter-Wollman⁷⁹, Serge Planes^{71,72}, Aura Raulo⁴, Rolando
21 Rodríguez-Muñoz⁷, Christopher Sabuni⁶⁸, Pratha Sah¹, Robbie J Schallert⁸⁰, Ben C
22 Sheldon⁴, Daizaburo Shizuka⁸¹, Andrew Sih⁷⁸, David L Sinn⁸², Vincent Sluydts⁵⁶, Orr
23 Spiegel⁴⁵, Sandra Telfer⁶³, Courtney A Thomason^{39,83}, David M Tickler⁸⁴, Tom Tregenza⁷,
24 Kimberley VanderWaal⁸⁵, Eric L Walters¹⁵, Klara M Wanelik^{77,86}, Elodie Wielgus⁴⁹, Jared
25 Wilson-Aggarwal^{7,41}, Caroline Wohlfeil⁴⁴, Shweta Bansal¹

26 *Corresponding author: gfalbery@gmail.com. Affiliations are at the end of the document.

27 Abstract

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

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

44 Introduction

45 The number of individuals occupying a given space – i.e., population density – is a central
46 factor governing social systems. At higher densities, individuals are expected to more
47 frequently share space, associate, and interact, producing more-connected spatial and
48 social networks and thereby influencing downstream processes such as mating, learning,
49 and competition. In particular, density-driven increases in network connectedness should
50 provide more opportunities for parasites to spread between hosts [1–5]. Despite the
51 fundamental nature of such density-dependent processes, evidence is relatively limited that
52 individuals inhabiting higher-density areas have more spatial and social connections.
53 Furthermore, density's effects should differ for asynchronous space sharing (e.g. home
54 range overlap) *versus* social associations (e.g. den sharing or grouping) or interactions (e.g.
55 mating or fighting). While several studies have compared animal populations at different
56 densities to demonstrate variation in social association rates among populations (e.g., [6,7])
57 or groups (e.g., [8–10]), attempts to identify such density effects *within* continuous
58 populations of individuals are rarer (but see [11–14]), and their findings have never been
59 synthesised or compared. We therefore have an incomplete understanding of how density,
60 as a fundamental ecological parameter, determines socio-spatial dynamics within and
61 across systems. This inhibits our ability to identify and predict how changes in density – e.g.
62 through culling, natural mortality, dispersal, or population booms – influence downstream
63 processes that depend on shared space and social interactions.

64 The rate at which an individual interacts with conspecifics depends on its spatial and social
65 behaviour within the context of the surrounding environment and population. Adding more
66 individuals into the same space should cause them to more frequently spatially overlap and
67 socially associate or interact (Figure 1). Often, individuals are modelled as randomly moving
68 and interacting molecules (“mass action” or “mean field”). In this conceptualisation, direct
69 contact between two molecules is analogous to a social interaction or association; rates of
70 such interactions are often assumed to increase with density (“density-dependent”; e.g.,
71 [15]), and/or to be homogenous in space (e.g., [10]). In reality individuals are unlikely to
72 behave and interact randomly in space, and instead will be influenced by spatially varying
73 factors including local density [16]. Changes in density may cause individuals to alter their
74 foraging behaviour [17–19], dispersal [20,21], social preference or avoidance [13,22], mating
75 behaviour [23], or preferred group size [7]; in some cases, interaction rates may change to
76 remain constant in the face of changing densities [24]. These and related processes might
77 produce strong nonlinearities in density-interaction relationships, which can complicate the
78 predictions of density dependence models of pathogen transmission, for example [2,4,5].
79 Nevertheless, these nonlinearities are poorly understood and rarely considered.

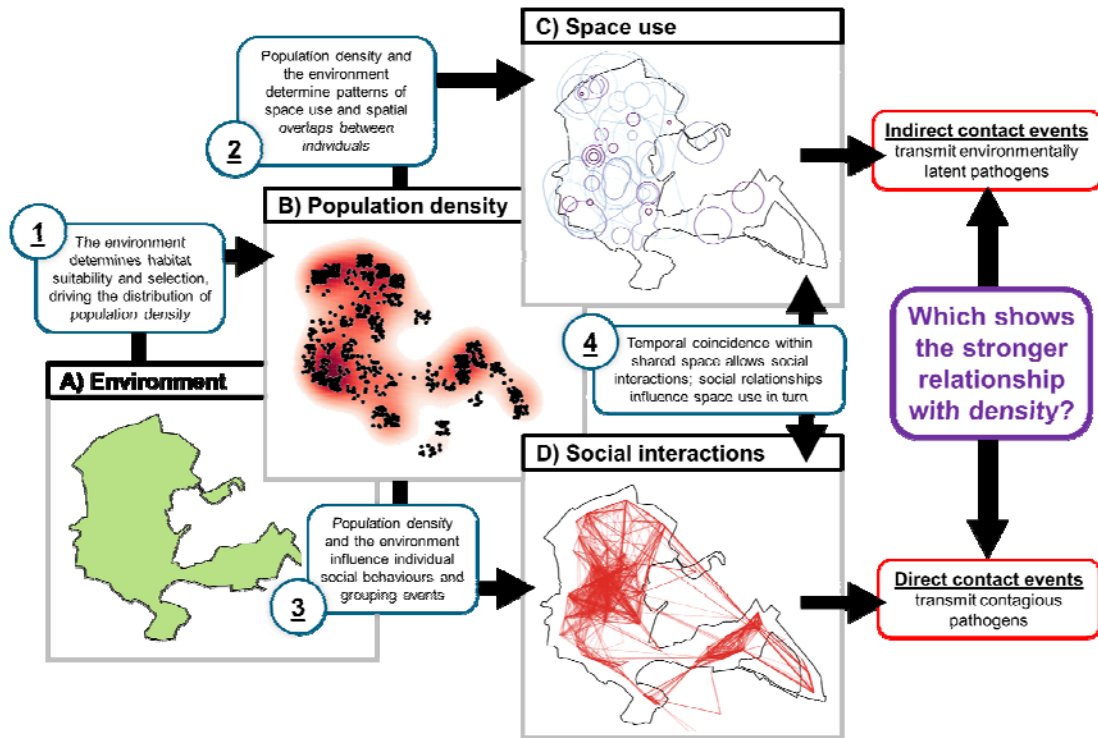
80 Several wild animal studies have suggested saturating nonlinear relationships between
81 density and social association rates [8–10,13]. Such relationships imply that association
82 rates do not increase passively with density, and that behavioural or demographic processes
83 likely change as density increases, with the ultimate consequence of slowing association
84 rates. However, these nonlinearities are difficult to examine between populations or between
85 species because they introduce a range of confounders and have few replicates along the

86 density axis [2]. Characterising gradients of density across individuals within a population
87 offers a workaround to this problem, and facilitates an appreciation of the fact that
88 interactions occur between individuals rather than at the population level. Examining
89 between-individual variation is one reason that social network analysis – which allows
90 characterisation and analysis of individual-level social traits, amongst other things – has
91 become so popular in animal ecology in recent years [25–29]. Additionally, recent years
92 have seen a substantial growth in understanding of socio-spatial behaviours, including
93 harmonising the concepts of spatial and social density [2,16,30]. Applying network analyses
94 coupled with this socio-spatial understanding of density could provide an individual-level
95 picture of density's effects on spatial and social connectedness, offering far higher resolution
96 and statistical power and greater ability to detect nonlinearities and between-system
97 differences [2]. By providing new understanding of the correlates and emergent
98 consequences of variation in density, this expansion could help to identify general rules
99 underlying social structuring and network scaling in space.

100 Critically, different types of interactions or associations should show different relationships
101 with density: for example, the need to compete for food at higher densities could drive a
102 disproportionate increase in aggression [31], but this is unlikely to be true of mating
103 interactions. This rationale is well-understood in disease ecology, as differences in density-
104 contact relationships are thought to drive differences in density dependence of infection –
105 where “contact” is defined as an interaction or association that could spread a pathogen
106 (Figure 1). “Contacts” then form the basis of spatial and social networks used to investigate
107 pathogen transmission dynamics, which should likewise diverge with density just as contacts
108 do. For example, density should drive greater transmission of respiratory pathogens but not
109 sexually transmitted pathogens [1,32]. Establishing these density-contact relationships is
110 integral to understanding disease dynamics and developing control measures [1,33], but we
111 still have a poor understanding of how different interactions (and therefore contact events for
112 different pathogens) are driven by density. This direct/indirect interaction dichotomy is most
113 fundamental to disease ecology [30], but given building interest in the spatial-social interface
114 and relationships between spatial and social networks in behavioural ecology [16], the
115 framework is readily related to other fields. Established density-interaction relationships are
116 diverse and include feral dog bites [11], ant antennations [34] and trophallaxis [24], ungulate
117 group memberships [12,17], rodent co-trapping [8,35], and agamid association patterns
118 [13,14], but no study has yet synthesised how the rates of multiple interaction types relate to
119 density, within or across systems.

120 Identifying the general rules underlying density dependence requires quantifying density's
121 relationship with proxies of interaction rates at fine scales across a diversity of systems, then
122 identifying the factors determining their slope and shape. To this end, we collate a meta-
123 dataset of over 55,000 individual animals across 34 wildlife systems globally to ask how
124 within-population variation in density determines between-individual interaction rates based
125 on connectedness in spatial and social networks. We fit multiple linear and nonlinear
126 relationships to identify the slope and shape of density effects within each system, and we
127 use meta-analyses to investigate general rules determining their slope and shape across
128 systems. In particular, we focus on comparing space sharing with social interactions and
129 associations as a cross-system case study. Ultimately, we present a *de novo* cross-system
130 analysis of individuals' social and spatial behaviour that traverses fields of behavioural,

131 population, and disease ecology, which could help to inform general rules governing the
132 structure of social systems.

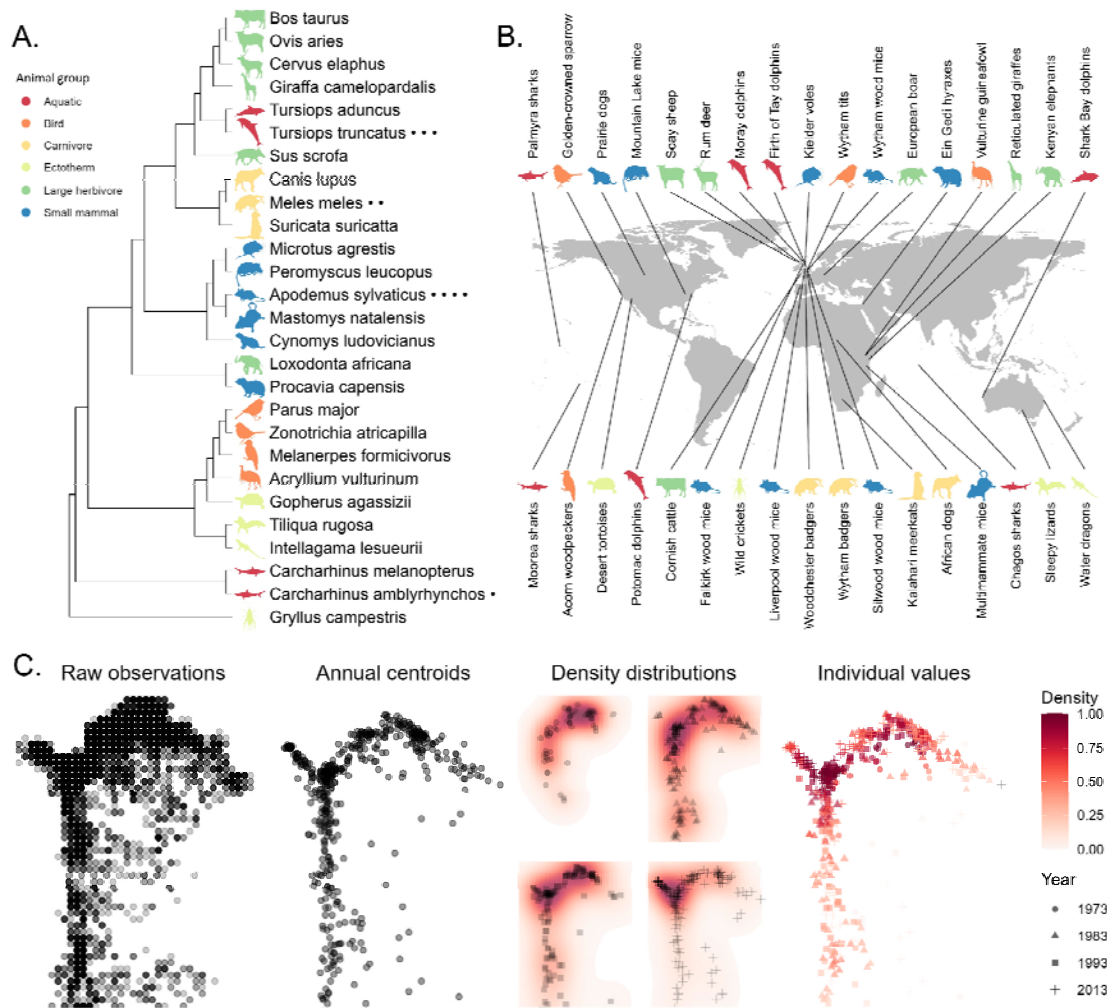


133

134 *Figure 1: Schematic detailing the rationale underlying this study, outlining how population density*
135 *drives the formation of spatial and social networks. This depiction uses the Wytham Wood great tits*
136 *as an example. Ultimately, we aim to ask whether spatial or social connections generally show a*
137 *stronger relationship with density, partly functioning as a proxy for indirect and direct contact events*
138 *with the potential to transmit pathogens. This framework moves between concepts of network and*
139 *contact formation traversing behavioural ecology, spatial and social network ecology, and disease*
140 *ecology.*

141

142



143

144 *Figure 2: The phylogenetic (A) and geographic (B) distribution of our 34 examined datasets of spatial*
 145 *and social behaviour, with (C) schematic depicting the methodology for deriving local density values,*
 146 *using the Isle of Rum red deer data as an example. The X and Y axes are bivariate spatial*
 147 *coordinates. The panels within (C) show raw observations of individuals in space that we then*
 148 *average at the individual level to make centroids; we use the centroids to generate annual density*
 149 *distributions, which are then assigned to individuals in the form of local density measures. Animal*
 150 *silhouettes are from phylopic.org; a list of attributions is in the supplement. NB the Potomac dolphins*
 151 *are now defined as Tursiops erebennus; they are currently incorporated in Panel A as T. truncatus,*
 152 *following the Open Tree of Life nomenclature.*

153 Methods

154 Data standardisation and behavioural pipeline

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

160 reptiles, and one insect (Figure 2). In one case (The Firth of Tay and Moray Dolphins) we
161 used two distinct replicates despite being composed of overlapping groups of individuals,
162 because of their distinct spatial distributions, which made it difficult to fit a coherent density
163 distribution.

164 To standardise the timescale across studies, all systems were analysed as annual replicates
165 – i.e., social and spatial networks were summarised within each year. Our analyses used 60
166 system-behaviour replicates, listed in Supplementary Table 1, and totalled 151,507 unique
167 system-individual-year-behaviour data points.

168 All spatial coordinates were converted to the scale of kilometres or metres to allow
169 comparison across systems. To provide an approximation of local density, following prior
170 methodology [12,37], we took each individual's average location across the year (their
171 centroid) and created a spatial density kernel using the `adehabitatr` package [38], which
172 provides a probabilistic distribution of population density across each study system based on
173 the local frequencies of observed individuals. Each individual was assigned an annual
174 estimate of local density based on their centroid's location within this spatial density
175 distribution. We made these density distributions as comparable as possible between
176 systems by incorporating the density raster using metre squares; however, there were large
177 differences in density across populations that were difficult to resolve and put on the same
178 scale (e.g. interactions per individual/km² unit of density). Consequently, we scaled and
179 centred density to have a mean of zero and a standard deviation of one within each
180 population, which allowed us to focus on differences in relative slope and shape across
181 systems.

182 To provide a measure of asynchronous space sharing, we constructed home range overlap
183 (HRO) networks based on proportional overlap of two individuals' minimum convex polygon
184 (MCP; i.e., the bounding polygon around all observations of each individual in a given year).
185 These HRO networks were restricted to only individuals with five or more observations in a
186 given year to allow us to create convex polygons effectively; 10/34 (29%) systems did not
187 have sufficient sampling for this analysis. We also repeated our analyses with a series of
188 higher sampling requirements for observation numbers to ensure that our findings were
189 robust to this assumption. The MCP approach is relatively low-resolution, and assumes
190 uniform space use across an individual's home range; however, this approach is less data
191 intensive – and less sensitive to assumptions – than density kernel-based approaches that
192 would estimate variation in space use across the home range, allowing us to apply the
193 models across more systems, more generalisably, and more conservatively.

194 To provide a measure of social connectedness, we built social networks using various
195 approaches as defined by the original studies: direct observations of dyadic interactions (e.g.
196 fighting or mating); gambit of the group (GoG; i.e. membership of the same group) [39]; co-
197 trapping (i.e. trapped together or in adjacent traps within a given number of trapping
198 sessions); or direct contact measured by proximity sensors (defined by a certain distance-
199 based detection threshold). Notably some analyses use indirect interactions – i.e., spatial
200 overlap – to *approximate* direct interactions, which requires spatiotemporal coincidence,
201 which we caution against particularly when modelling pathogen transmission [30,40]. While
202 the two do often correlate, here we are not using HRO to approximate direct interaction

203 rates, but rather as a measure of indirect interactions (e.g., indicative of transmission of
204 environmental parasites).

205 For each social network, we scaled connection strength relative to the number of
206 observations of each individual in a dyad (i.e., simple ratio index [41]). Our response variable
207 therefore took the form of strength centrality, scaled to between 0-1 for each dyad, for each
208 social and spatial network. We focus on comparing density effects on social interactions and
209 associations with density's effects on space sharing.

210 Density-connectedness models: what forms do density effects 211 take?

212 We developed a novel workflow to allow us to derive and compare density's effects on
213 connectedness – and their drivers – in a standardised way across our wild animal systems.
214 These took three forms: linear models fitted to the whole dataset, nonlinear models fitted to
215 the whole dataset, and linear models fitted separately to low- and high-density subsets of
216 each dataset.

217 **Linear models:** For each system-behaviour replicate, we first fitted a linear model using the
218 ``lm`` function in R, fitting scaled density as an explanatory variable to estimate linear density
219 effect slopes.

220 **Generalised additive models (GAMs):** We fitted GAMs in the ``mgcv`` package [42] to
221 identify whether each density effect was better described by a linear or nonlinear
222 relationship, and to identify the shape of these nonlinear relationships. For each model, we
223 fitted a default thin plate spline with $k=4$ knots. This knot number was selected to reduce
224 overfitting in our models, which formed several fits to the data that were difficult to reconcile
225 with functional formats. To assess whether nonlinear models fit better than linear models, we
226 used Akaike Information Criterion (AIC), with a contrast of $2\Delta AIC$ designated to distinguish
227 between models. See Supplementary Figure 1 for a schematic depicting our analytical
228 workflow.

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

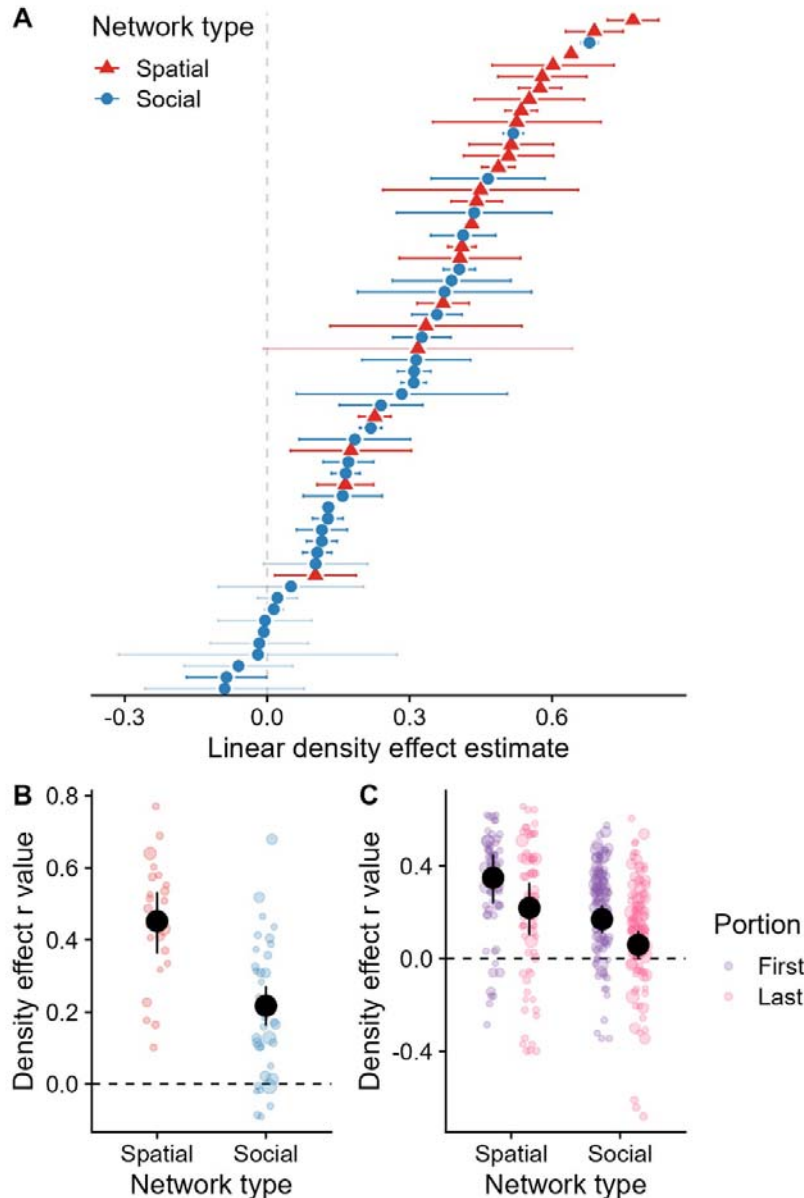
243 Meta-analysis: what factors determine the slope of density- 244 connectedness relationships?

245 To characterise the typical relative slope of density effects across systems and identify the
246 factors influencing their variation, we fitted hierarchical meta-analytical models using the
247 ``metafor`` package in R. The response variable was the standardised slope of the linear
248 density effect; because both individual network strength and density were scaled to have
249 mean of zero and standard deviation of one in the linear regression, this is equivalent to the
250 correlation coefficient (r) [43]. We converted all correlation coefficients into Fisher's Z (Z_i)
251 and computed associated sampling variance. We then used an initial model that nested
252 observations within a system-level random effect to account for within- and between-system
253 heterogeneity [44], as 24/34 systems had more than one density effect. We used a random
254 effect for species to account for repeat observations per animal species.

255 We then added a separate random effect for animal phylogeny [45]. This used a
256 phylogenetic correlation matrix of our 28 animal species derived from the Open Tree of Life
257 via the ``rotl`` package [46], with the ``ape`` package used to resolve multichotomies and
258 provide branch lengths [47]. We fitted the model using the ``rma.mv()`` function with restricted
259 maximum likelihood (REML), weighted by inverse sampling variance, and used variance
260 components to quantify R^2 , the contribution of true heterogeneity to the total variance in effect
261 size.

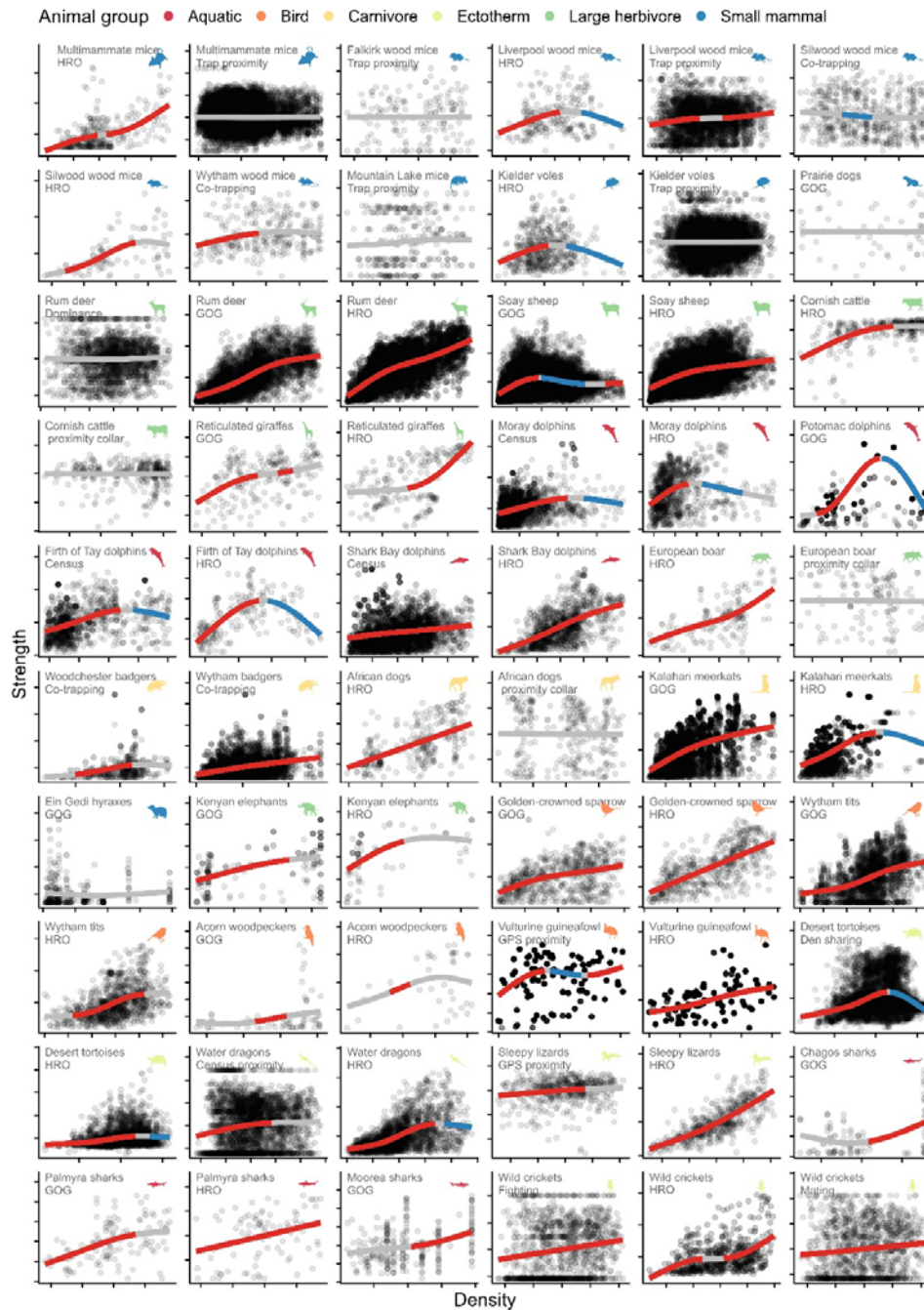
262 We next fitted models with the same random effects structure that included explanatory
263 variables. To detect whether some animals were more likely to experience density effects,
264 we fitted **Animal group** as a factor with six categories, representing a combination of
265 species' taxonomy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

274 We ran several different versions of these meta-analyses: first, we fitted meta-analytical
275 models to the **overall linear models** of spatial and social interaction types separately, and
276 then together, to investigate differences between the spatial and social networks in terms of
277 their mean density slope. Next, we fitted duplicated versions of these models, but with the
278 **saturation models**. These models were identical, but each system replicate had two linear
279 estimates: one taken from the first 50% of the data (up to the median), and one to the latter
280 50%. By fitting a binary fixed effect of "data portion" to the meta-analytical models, this
281 model would tell us whether the slopes were generally higher in the first portion of the data
282 than the last (and therefore showed generally saturating shapes). We were unable to fit
283 meta-analytical models to our GAMMs, as methods capable of meta-analysing nonlinear
284 estimates are not yet well defined.



285

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



300

301 *Figure 4: Relationships between density and network connectedness varied substantially across*
 302 *animal systems. Density in individuals per area is on the x axis; network connectedness (strength*
 303 *centrality) is on the y axis. Both values have been standardised to have a mean of zero and a*
 304 *standard deviation of 1 within each system; the axis ticks are in units of 1 standard deviation. Each*
 305 *point represents an individual-year-behaviour replicate; the lines portray the model fit from our GAMs.*

306 *Red lengths of the smooth=significantly positive; grey=not significantly different from zero;*
 307 *blue=significantly negative. Points are semi-transparent to enhance visibility. Panels are arranged*
 308 *phylogenetically following the tree displayed in Figure 2A; GOG=gambit of the group; HRO=home*
 309 *range overlap. Supplementary Figure 2 shows a version of this plot with variable smoothing*
 310 *parameters to show variation in the possible shape of the curves. Animal silhouettes are from*
 311 *phylopic.org; a set of links and attributions are in the Supplement.*

312 Results and Discussion

313 We compiled an unprecedented comparative meta-dataset of over ten million observations
314 of individual animals' spatial and social behaviour, across an expansive range of ecological
315 systems. We then ran a standardised pipeline to align their spatial and social observations,
316 identifying strong and predictable relationships between local density and network
317 connectedness at the individual level.

318 We observed strong positive relationships between individuals' local population density and
319 their connectedness in spatial and social networks across a wide range of wild animals: of
320 our 60 replicates, 48 (80%) were significantly positive when analysed using linear models
321 (Figure 3A; Supplementary Table 1). Meta-analyses identified a highly significant positive
322 mean correlation between density and connectedness, both for social networks (Estimate
323 0.22; 95% CI 0.16, 0.27) and spatial networks (0.45; 0.36, 0.53; Figure 3B). Our study
324 therefore provides fundamental evidence that high local population density broadly drives
325 greater connectedness within ecological systems, at the individual level. Slopes were highly
326 variable across systems for both spatial and social networks (Figure 3A; Q-test of
327 heterogeneity across systems: $Q_{35} = 5744.83$ and $Q_{23} = 1559.08$, both $P < 0.0001$), indicating
328 that quantifying these slopes within and between multiple systems and comparing them is
329 important for understanding animal socio-spatial structure. That is, relationships between
330 density and individual connectedness differ substantially between populations, and the
331 biological mechanisms underlying these divergent trends are likely important. As well as
332 adding resolution and allowing comparisons of density effects across systems, our
333 methodology facilitated fitting of nonlinear relationships. This approach has only rarely been
334 applied before, and then at much coarser resolution (see [8,9,11]). As such, this study fills an
335 important empirical gap by providing insights into the slope and shape of density-
336 connectedness relationships for a variety of animal groups and their social and spatial
337 behaviours (Figure 4). Nevertheless, we were able to identify several further general trends
338 in our data.

339 Remarkably, density's effect more than doubled in size for spatial compared to social
340 networks (Figure 3B; $r=0.45$ versus 0.22); there was a difference of 0.28 (CI 0.17, 0.38,
341 $P < 0.0001$) for this effect when we meta-analysed the two contact types together. This finding
342 indicates that as density increases, wild animals are more likely to share space with each
343 other, but that social connections increase at a much slower rate. Similarly, we discovered
344 that saturating shapes were extremely common: as density increased, its effect on
345 connectedness decreased, such that 44/60 systems (73%) had a steeper slope at low
346 density values than at high ones. This effect was strong for social networks (effect on $r =$
347 0.11; CI -0.20, -0.03; $P = 0.01$) and similar in size but marginally insignificant for spatial
348 networks (-0.14; -0.29, 0.01; $P = 0.058$); due to the greater overall effect for space sharing,
349 the latter half of the density-spatial connections effect was still higher than the first half of the
350 density-social connections effect (Figure 3C). In fact, the second half of the social effect
351 overlapped with zero (Figure 3C; lower CI = -0.0119): that is, considering only the upper half
352 of density values would not have uncovered a significant effect of density on individuals'
353 connectedness in social networks. Together, these observations suggest that density-
354 dependent processes act to limit the increase in social connectedness with density, but
355 without limiting spatial overlaps to the same extent. Consequently, higher-density areas are
356 characterised disproportionately by individuals asynchronously sharing space rather than

357 socially associating, while in lower-density areas individuals are disproportionately more
358 socially connected proportional to their shared space.

359 There are many possible social reasons for saturating nonlinearity in density-dependent
360 network structuring: for example, individuals in higher density areas may begin to avoid each
361 other, seeking to avoid competition or aggression [31] or exposure to infectious disease [48].
362 Eastern water dragons (*Intellagama lesueurii*) show greater avoidance at higher densities
363 [13], supporting this mechanism. Alternatively, in species with high social cognition or stable
364 bonds, saturation could reflect lower social effort or ability to keep track of social affiliates at
365 higher densities [49]. In general, individuals likely have a preferred social interaction rate or
366 group size – a preference that they may increasingly exert at higher densities [7]. It remains
367 to be seen how this preference varies among individuals, and whether individuals vary in
368 their preferred social network position given a certain density. Given that individuals vary in
369 their movement and spatial phenotypes [50–52], and social phenotypes [52–54] in ways that
370 should manifest for density-dependent behaviours specifically [16], it seems likely that these
371 slopes could vary between individuals as they do between populations. Future analyses
372 might fit variable density-connectedness slopes between individuals to identify socio-spatial
373 syndromes across systems, as has been done previously in single systems including caribou
374 (*Rangifer tarandus*) [55] and red squirrels (*Tamiasciurus hudsonicus*) [56].

375 We considered spatial behaviours might explain these trends: for example, density could
376 create greater competition over resources and therefore reduce energy to roam (and contact
377 others). Individuals may partition their niches [57], or reduce their territory or home range
378 sizes [56,58,59], potentially driven by years of plentiful resources supporting higher densities
379 alongside smaller home ranges which could drive lower association rates. However, our
380 findings do not seem to support explanations related to small home ranges, because such
381 explanations should produce an equivalent or stronger reduction in (relative) spatial
382 connectedness. In contrast, we observed that density drove individuals to become spatially
383 connected faster than socially, such that the underlying mechanisms likely involve
384 behaviours and demographic processes that specifically affect social collocation in space
385 and time. Testing the precise underlying mechanism might require finer-scale behavioural
386 observations, as described below. Regardless of mechanism, these saturating density-
387 connectedness relationships strongly support the idea that examining density effects at the
388 individual level – rather than between populations – is highly informative. For many systems,
389 “mean field” expectations of homogenous interactions under increasing density likely
390 produce an inaccurate (i.e., inflated) picture of density’s effects.

391 The fact that spatial networks show stronger and more linear density dependence than
392 social networks is likely to have important implications for the ecology of wild animal
393 systems. For example, indirectly transmitted (i.e., environmentally latent) parasites may
394 exhibit greater density dependence than directly transmitted ones, given that individuals
395 likely experience disproportionately more indirect contact at higher densities. This
396 observation contrasts with orthodoxy that contagious parasites are most likely to be density
397 dependent [60], and supports the value of investigating nonlinear changes in socio-spatial
398 behaviour and grouping patterns in response to density when considering density
399 dependence. Saturating density-connectedness functions further have implications for
400 disease modelling and control. Rather than assuming constant behavioural mixing at higher
401 densities, epidemiological models could benefit from incorporating density-dependent shifts

402 in behaviours and demography that influence direct and indirect interaction frequencies, as
403 previously suggested empirically and by epidemiological theory [15]. These relationships
404 could influence our targets for culling or vaccination coverage [61]. Given that animals at
405 high density seem likely to have a relatively shallow relationship between density and
406 contact rates, reducing population density – for example via culling – might not be effective
407 at reducing pathogen transmission initially, particularly when considering socially transmitted
408 pathogens, where contact rates are particularly likely to have saturated (Figure 3C). Similar
409 problems with culling have already been acknowledged in specific systems – e.g. in canine
410 rabies [33,62,63] – but our study implies that shallow nonlinear density-contact trends could
411 be more general than previously thought and could be driven by flexible density-dependent
412 changes in behaviour and demographic processes.

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

423 Beyond these general trends, our GAMs revealed that 46/60 density effects on network
424 connectedness (77%) were significantly nonlinear ($\Delta AIC > 2$); these relationships took a wide
425 variety of shapes, representing a range of nonlinear functions that are hard to generalise
426 (Figure 4; Supplementary Table 2). Notably, while many GAM smooths were eventually
427 significantly negative (Figure 4), the vast majority of linear models fitted to the second half of
428 the data were positive (Figure 3C); this result is likely an artefact of restricted model fitting,
429 rather than true downturns in connectedness with density. Nonlinearity did not cluster
430 according to connection type definitions, or according to host group. These observations
431 were largely corroborated by our meta-analytical models, which found no factors influencing
432 the slope and shape of density effects ($P > 0.05$). This observation speaks to the complexity
433 of these relationships within and across systems, while accentuating that simple functional
434 relationships are often likely to be complicated by contravening ecological factors like habitat
435 selection [67,68], parasite avoidance [69], and demographic structuring [70]. While we were
436 unable to identify specific between-system predictors of nonlinearity of density-
437 connectedness relationships, the finding that most such relationships are strongly nonlinear
438 is an important consideration for future work.

439 We acknowledge several limitations of our study, which we nevertheless believe could be
440 remedied in the future. First, many of our social networks were formed of general
441 spatiotemporal associations, and relatively few from specific social interactions – particularly
442 those involving direct physical contact. Our current dataset could therefore benefit from
443 supplementation with a broader range of direct interactions, particularly involving antagonism
444 or bonding. For example, datasets concerning aggression or dominance interactions (e.g.
445 [71]) or grooming alongside spatial behaviour could inform how density dependence affects
446 the transmission of certain parasites such as mycobacteria [72] or tattoo skin disease [73].

447 The meta-dataset was also unevenly distributed across animal taxa (Figure 1): there were
448 no primates or bony fishes and only one invertebrate, while rodents and ungulates were
449 over-represented. These biases likely emerge through differences in data collection
450 approaches: for example, although primate social behaviour is often studied with
451 observations of direct interactions that could augment our data as described above (e.g.
452 [74]), the spatial data required to build density distributions are rarely collected in these
453 systems. This is linked to their social structures: our workflow was best suited to studies of
454 fission-fusion societies or relatively asocial animals, rather than those with wide-ranging
455 fixed social groups that are more common in primate systems. Finally, given that our data
456 were observational, we could not account for (or estimate) bidirectional causality between
457 density and social relationships (point 4 in Figure 1): that is, as well as encountering more
458 conspecifics in areas of high density, individuals may be drawn to conspecifics, *creating*
459 areas of high density [16]. To do so might require creating in-depth, high-resolution models
460 of animal movement and group formation (e.g. [75]), potentially making use of telemetry
461 approaches and drawing from large-scale open movement repositories like Movebank [76].

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

486 Density is a universal factor underlying the dynamics of animal populations, and its linear
487 and nonlinear effects on spatial and social network structure are likely to impact myriad
488 processes in behaviour, ecology, and evolution. Similar to other studies that have reported
489 general scaling patterns in network analysis [84] and in food web ecology [85], the patterns
490 we report strongly suggest that animal systems generally become better connected spatially
491 than socially under increasing density. These might extrapolate to human networks, given
492 that other scaling patterns in animal networks do [84]. As these patterns seemingly manifest

493 regardless of animal group and interaction type, they may reflect a generalisable rule
494 governing the socio-spatial structure of ecological systems. Further refining and
495 implementing these models could facilitate prediction of network structure in novel systems.

496 Acknowledgements

497 GFA and SB were supported by NSF grant number DEB-2211287. GFA acknowledges
498 support from a College for Life Sciences Fellowship at the Wissenschaftskolleg zu Berlin and
499 WAI (C-2023-00057). DJB acknowledges support from the Edward Mallinckrodt, Jr.
500 Foundation and NSF BII 2213854. JAF acknowledges funding from BBSRC
501 (BB/S009752/1), NERC (NE/S010335/1 and NE/V013483/1), and WAI (C-2023-00057). For
502 a list of system-specific acknowledgements, please see the supplement.

503 Code availability

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

505 Affiliations

- 506 1. Department of Biology, Georgetown University, Washington, DC, USA
- 507 2. Wissenschaftskolleg zu Berlin, Berlin, Germany
- 508 3. School of Biological Sciences, University of Oklahoma, Norman, OK, USA
- 509 4. Department of Biology, University of Oxford, Oxford, UK
- 510 5. School of Biology, University of Leeds, Leeds, UK
- 511 6. CEFE, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France
- 512 7. Centre for Ecology and Conservation, University of Exeter, Penryn, UK
- 513 8. School of Biosciences, University of Sheffield, Sheffield, UK
- 514 9. Institute of Ecology and Evolution, University of Edinburgh, Edinburgh, UK
- 515 10. Department of Biology, Memorial University of Newfoundland, 45 Arctic Avenue,
516 St. John's NL
- 517 11. University of Guelph, Guelph, Canada
- 518 12. Institute of Infection, Veterinary and Ecological Sciences, University of Liverpool,
519 Liverpool, UK
- 520 13. Institute of Zoology, Zoological Society of London, Regents Park, London, UK
- 521 14. University of Glasgow, Glasgow, UK
- 522 15. Department of Biological Sciences, Old Dominion University, Norfolk, VA, USA
- 523 16. Avian Ecology Program, Archbold Biological Station, Venus, FL, USA
- 524 17. University of Salford, Salford, UK
- 525 18. Department of Ecology and Evolutionary Biology, University of California, Santa Cruz,
526 CA, USA
- 527 19. Canine Companions, 2965 Dutton Ave, Santa Rosa, CA, USA
- 528 20. Hopkins Marine Station, Stanford University, Stanford, CA, USA
- 529 21. University of Nottingham, Nottingham, UK
- 530 22. Pitzer and Scripps Colleges, Claremont, CA, USA
- 531 23. Wildlife Conservation Research Unit, The Recanati-Kaplan Centre, Department of
532 Zoology, University of Oxford, Oxford, UK
- 533 24. The University of British Columbia, Irving K. Barber Faculty of Sciences, Okanagan
534 Department of Biology, Kelowna, British Columbia, Canada

- 535 25. UK Centre for Ecology and Hydrology, Bush Estate, Midlothian, UK
- 536 26. University of Delaware, Newark, DE, USA
- 537 27. Marine Science Institute, UC Santa Barbara, Santa Barbara, CA, USA
- 538 28. ISI Foundation, Torino, Italy
- 539 29. Evolutionary Ecology Group, Station d'Ecologie Theorique et Experimentale du CNRS,
540 Moulis, France
- 541 30. Oregon State University, Corvallis, OR, USA
- 542 31. Lighthouse Field Station, School of Biological Sciences, University of Aberdeen, UK
- 543 32. Department of Zoology, University of Cambridge, Cambridge, UK
- 544 33. Institute of Zoology, Zoological Society of London, London, UK
- 545 34. National Wildlife Management Centre, Animal and Plant Health Agency, Sand Hutton,
546 York, UK
- 547 35. Department of Collective Behavior, Max Planck Institute for Animal Behavior, 78464
548 Konstanz, Germany
- 549 36. Department of Evolutionary Biology and Environmental Studies, University of Zurich,
550 8057 Zurich, Switzerland
- 551 37. Department of Ornithology, National Museum of Kenya, P.O. Box 40241-001000,
552 Nairobi, Kenya
- 553 38. Division of Ecology and Evolution, Research School of Biology, Australian National
554 University, 46 Sullivan Creek Road, Canberra, ACT 2600, Australia
- 555 39. Virginia Tech, Blacksburg, VA, USA
- 556 40. The Royal (Dick) School of Veterinary Studies, University of Edinburgh, Edinburgh, UK
- 557 41. Environment and Sustainability Institute, University of Exeter, Penryn, UK
- 558 42. Department of Marine Biology, Texas AandM University at Galveston, USA
- 559 43. School of the Environment, University of Queensland, Brisbane, Queensland, Australia
- 560 44. College of Science and Engineering, Flinders University, Adelaide, Australia
- 561 45. School of Zoology, Faculty of Life Science, Tel Aviv University, Tel Aviv, Israel
- 562 46. Department of Zoology, University of Otago, Otago, New Zealand
- 563 47. Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ,
564 USA
- 565 48. Sea Mammal Research Unit, South Oceans Institute, University of St Andrews, UK
- 566 49. Department of Visitor Management and National Park Monitoring, Bavarian Forest
567 National Park, Grafenau, Germany
- 568 50. Chair of Wildlife Ecology and Wildlife Management, Faculty of Environment and Natural
569 Resources, University of Freiburg, Freiburg, Germany
- 570 51. Department of Forestry and Wildlife Management, Faculty of Applied Ecology,
571 Agricultural Sciences and Biotechnology, Campus Evenstad, Inland Norway University of
572 Applied Sciences, Postboks 400 Vestad, 2418 Elverum, Norway
- 573 52. Faculty of Life Sciences, Bar Ilan University, Ramat Gan, Israel
- 574 53. Lancaster University, Lancaster, UK
- 575 54. Division of Marine Science and Conservation, Nicholas School of the Environment, Duke
576 University Marine Laboratory, Beaufort, NC, USA
- 577 55. Department of Game Management and Wildlife Biology, Faculty of Forestry and Wood
578 Sciences, Czech University of Life Sciences, Prague, Czech Republic
- 579 56. Evolutionary Ecology Group, EVECO, Universiteit Antwerpen, Antwerp, Belgium
- 580 57. Department of Nature Conservation and Research, Hainich National Park, Bad
581 Langensalza, Germany
- 582 58. Mpala Research Center, P.O Box 555-10400, Nanyuki, 10400, Kenya

- 583 59. Centre for the Advanced Study of Collective Behaviour, University of Konstanz, 78464
584 Konstanz, Germany
- 585 60. School of Environment and Natural Science, Bangor University, Bangor, Wales
- 586 61. Department of Biology, Memorial University of Newfoundland, St John's, NL, Canada
- 587 62. Department of Biology, University of Saskatchewan, Saskatoon, SK, Canada
- 588 63. University of Aberdeen, Aberdeen, UK
- 589 64. School of Animal and Veterinary Sciences, The University of Adelaide, Adelaide,
590 Australia
- 591 65. School of Biological Sciences, University of Nebraska-Lincoln, NE, USA
- 592 66. Department of Ecology, Behavior, and Evolution, University of California, San Diego, CA
- 593 67. Department of Evolutionary Biology and Environmental Studies, University of Zurich,
594 Zurich, Switzerland
- 595 68. Institute of Pest Management, Sokoine University of Agriculture, Morogoro, Tanzania
- 596 69. Max Planck Institute of Animal Behavior, Radolfzell, Germany
- 597 70. MARBEC, Univ Montpellier, CNRS, Ifremer, IRD, Sète, France
- 598 71. PSL Research University, Université de Perpignan, Perpignan, France
- 599 72. Laboratoire d'Excellence "CORAIL", Papetoai, Moorea, French Polynesia
- 600 73. University of Nevada, Reno, NV, USA
- 601 74. University of Eldoret, School of Natural Resource Management, Department of Wildlife,
602 1125-30100 Eldoret, Kenya
- 603 75. Department of Veterinary Sciences, University of Turin, Grugliasco (TO), Italy
- 604 76. Florida International University, FL, USA
- 605 77. University of Liverpool, Liverpool, UK
- 606 78. Department of Environmental Science and Policy, University of California Davis, Davis,
607 CA, USA
- 608 79. Department of Ecology and Evolutionary Biology, University of California, Los Angeles,
609 CA, USA
- 610 80. Stanford University, Stanford, CA, USA
- 611 81. School of Biological Sciences, University of Nebraska-Lincoln, Lincoln, NE, USA
- 612 82. Department of Wildlife, California State Polytechnic University, Humboldt, Arcata, CA,
613 USA
- 614 83. Texas Tech University, Lubbock, TX, USA
- 615 84. University of Western Australia, Crawley WA 6009, Australia
- 616 85. Department of Veterinary Population Medicine, University of Minnesota, Minneapolis, US
- 617 86. University of Surrey, Guildford, UK

618 References

- 619 1. Lloyd-Smith JO, Cross PC, Briggs CJ, Daugherty M, Getz WM, Latto J, Sanchez MS,
620 Smith AB, Swei A. 2005 Should we expect population thresholds for wildlife disease?
621 *Trends Ecol Evol* **20**, 511–519. (doi:10.1016/j.tree.2005.07.004)
- 622 2. Albery GF. 2022 Density dependence and disease dynamics: moving towards a
623 predictive framework. *EcoEvoRxiv Preprints* (doi:10.32942/OSF.IO/GAW49)
- 624 3. Hopkins SR, Fleming-Davies AE, Belden LK, Wojdak JM. 2020 Systematic review of
625 modeling assumptions and empirical evidence: does parasite transmission increase

- 626 nonlinearly with host density? *Methods Ecol Evol* **11**, 0–2. (doi:10.1111/2041-
627 210x.13361)
- 628 4. Begon M, Bennett M, Bowers RG, French NP, Hazel SM, Turner J. 2002 A
629 clarification of transmission terms in host-microparasite models: Numbers, densities
630 and areas. *Epidemiol Infect* **129**, 147–153. (doi:10.1017/S0950268802007148)
- 631 5. Ferrari MJ, Perkins SE, Pomeroy LW, Bjrnstad ON. 2011 Pathogens, social networks,
632 and the paradox of transmission scaling. *Interdiscip Perspect Infect Dis* **2011**.
633 (doi:10.1155/2011/267049)
- 634 6. Webber QMR, Vander Wal E. 2020 Heterogeneity in social network connections is
635 density-dependent: implications for disease dynamics in a gregarious ungulate. *Behav*
636 *Ecol Sociobiol* **74**, 1–13.
- 637 7. Beauchamp G. 2011 Functional relationship between group size and population
638 density in Northwest Atlantic seabirds. *Mar Ecol Prog Ser* **435**, 225–233.
639 (doi:10.3354/meps09239)
- 640 8. Borremans B, Reijnders J, Hens N, Leirs H. 2017 The shape of the contact–density
641 function matters when modelling parasite transmission in fluctuating populations. *R*
642 *Soc Open Sci* **4**. (doi:10.1098/rsos.171308)
- 643 9. Davis S, Abbasi B, Shah S, Telfer S, Begon M. 2015 Spatial analyses of wildlife
644 contact networks. *J R Soc Interface* **12**. (doi:10.1098/rsif.2014.1004)
- 645 10. Carson BD, Orians CM, Crone EE. 2023 When does spatial clustering in caterpillars
646 influence the relationship between population density and contact rates?
647 (doi:10.21203/rs.3.rs-2842538/v1)
- 648 11. Mancy R *et al.* 2022 Rabies shows how scale of transmission can enable acute
649 infections to persist at low prevalence. *Science (1979)* **376**, 512–516.
- 650 12. Albery GF, Morris A, Morris S, Pemberton JM, Clutton-Brock TH, Nussey DH, Firth
651 JA. 2021 Multiple spatial behaviours govern social network positions in a wild
652 ungulate. *Ecol Lett* **24**, 676–686. (doi:10.1101/2020.06.04.135467)
- 653 13. Strickland K, Patterson EM, Frère CH. 2018 Eastern water dragons use alternative
654 social tactics at different local densities. *Behav Ecol Sociobiol* **72**.
655 (doi:10.1007/s00265-018-2563-x)
- 656 14. Strickland K, Frère CH. 2019 Individual Variation in the Social Plasticity of Water
657 Dragons. *Am Nat* **194**, 194–206. (doi:10.5061/dryad.5j5gh63)
- 658 15. Hu H, Nigmatulina K, Eckhoff P. 2013 The scaling of contact rates with population
659 density for the infectious disease models. *Math Biosci* **244**, 125–134.
660 (doi:10.1016/j.mbs.2013.04.013)

- 661 16. Webber QMR, Albery GF, Farine DR, Pinter-wollman N, Sharma N, Vander Wal E,
662 Manlove K. 2023 Behavioural ecology at the spatial-social interface. *Biological*
663 *Reviews*, 1–40.
- 664 17. Albon SD, Staines HJ, Guinness FE, Clutton-Brock TH. 1992 Density-Dependent
665 Changes in the Spacing Behaviour of Female Kin in Red Deer. *Source: Journal of*
666 *Animal Ecology*. **61**.
- 667 18. Vas J, Andersen IL. 2015 Density-dependent spacing behaviour and activity budget in
668 pregnant, domestic goats (*Capra hircus*). *PLoS One* **10**.
669 (doi:10.1371/journal.pone.0144583)
- 670 19. Connor EF, Cargain MJ. 1994 Density-related foraging behaviour in *Closterocerus*
671 *tricinctus*, a parasitoid of the leaf-mining moth, *Cameraria hamadryadella*. *Ecol*
672 *Entomol* **19**, 327–334. (doi:10.1111/J.1365-2311.1994.TB00249.X)
- 673 20. Matthysen E. 2005 Density-dependent dispersal in birds and mammals. *Ecography*
674 **28**, 403–416. (doi:10.1111/j.0906-7590.2005.04073.x)
- 675 21. Avgar T, Betini GS, Fryxell JM. 2020 Habitat selection patterns are density dependent
676 under the ideal free distribution. *Journal of Animal Ecology* **89**, 2777–2787.
677 (doi:10.1111/1365-2656.13352)
- 678 22. Vander Wal E, Laforge MP, Mcloughlin PD, Wal E Vander, Laforge MP, Mcloughlin
679 PD, Vander Wal E, Laforge MP, Mcloughlin PD. 2014 Density dependence in social
680 behaviour: Home range overlap and density interacts to affect conspecific encounter
681 rates in a gregarious ungulate. *Behav Ecol Sociobiol* **68**, 383–390.
682 (doi:10.1007/s00265-013-1652-0)
- 683 23. Kokko H, Rankin DJ. 2006 Lonely hearts or sex in the city? Density-dependent effects
684 in mating systems. In *Philosophical Transactions of the Royal Society B: Biological*
685 *Sciences*, pp. 319–334. Royal Society. (doi:10.1098/rstb.2005.1784)
- 686 24. Modlmeier AP, Colman E, Hanks EM, Bringenberg R, Bansal S, Hughes DP. 2019
687 Ant colonies maintain social homeostasis in the face of decreased density. *Elife* **8**, 1–
688 17. (doi:10.7554/eLife.38473)
- 689 25. Farine DR, Whitehead H. 2015 Constructing, conducting and interpreting animal
690 social network analysis. *Journal of Animal Ecology* **84**, 1144–1163.
691 (doi:10.1111/1365-2656.12418)
- 692 26. Farine DR. 2024 Modelling animal social networks: New solutions and future
693 directions. *Journal of Animal Ecology* (doi:10.1111/1365-2656.14049)
- 694 27. Webber QMR, Vander Wal E. 2019 Trends and perspectives on the use of animal
695 social network analysis in behavioural ecology: a bibliometric approach. *Anim Behav*
696 **149**, 77–87. (doi:10.1016/j.anbehav.2019.01.010)

- 697 28. Pinter-Wollman N *et al.* 2014 The dynamics of animal social networks: Analytical,
698 conceptual, and theoretical advances. *Behavioral Ecology* **25**, 242–255.
699 (doi:10.1093/beheco/art047)
- 700 29. Sah P, Mann J, Bansal S. 2018 Disease implications of animal social network
701 structure: A synthesis across social systems. *Journal of Animal Ecology* **87**, 546–558.
702 (doi:10.1111/1365-2656.12786)
- 703 30. Albery GF, Kirkpatrick L, Firth JA, Bansal S. 2021 Unifying spatial and social network
704 analysis in disease ecology. *Journal of Animal Ecology* **90**, 1–17. (doi:10.1111/1365-
705 2656.13356)
- 706 31. Cubaynes S, Macnulty DR, Stahler DR, Quimby KA, Smith DW, Coulson T. 2014
707 Density-dependent intraspecific aggression regulates survival in northern Yellowstone
708 wolves (*Canis lupus*). *Journal of Animal Ecology* **83**, 1344–1356. (doi:10.1111/1365-
709 2656.12238)
- 710 32. Lloyd-Smith JO, Getz WM, Westerhoff H V. 2004 Frequency-dependent incidence in
711 models of sexually transmitted diseases: Portrayal of pair-based transmission and
712 effects of illness on contact behaviour. *Proceedings of the Royal Society B: Biological*
713 *Sciences* **271**, 625–634. (doi:10.1098/rspb.2003.2632)
- 714 33. Morters MK, Restif O, Hampson K, Cleaveland S, Wood JLN, Conlan AJK. 2013
715 Evidence-based control of canine rabies: A critical review of population density
716 reduction. *Journal of Animal Ecology* **82**, 6–14. (doi:10.1111/j.1365-
717 2656.2012.02033.x)
- 718 34. Gordon DM, Paul RE, Thorpe K. 1993 What is the function of encounter patterns in
719 ant colonies? *Anim Behav* **45**, 1083–1100. (doi:10.1006/ANBE.1993.1134)
- 720 35. Davis S, Abbasi B, Shah S, Telfer S, Begon M, Davis S. 2015 Spatial analyses of
721 wildlife contact networks. *Journal of the Royal Society, Interface / the Royal Society*
722 **12**, 20141004. (doi:10.1098/rsif.2014.1004)
- 723 36. R Development Core Team R. 2011 R: A Language and Environment for Statistical
724 Computing. *R Foundation for Statistical Computing*, **1**, 409. (doi:10.1007/978-3-540-
725 74686-7)
- 726 37. Albery GF, Newman C, Bright Ross J, Macdonald DW, Bansal S, Buesching CD.
727 2020 Negative density-dependent parasitism in a group-living carnivore. *Proceedings*
728 *of the Royal Society B: Biological Sciences* **287**, 20202655.
729 (doi:10.1101/2020.06.15.153726)
- 730 38. Calenge C. 2011 Home range estimation in R: the adehabitatHR package. See
731 <https://cran.r-project.org/web/packages/adehabitatHR/index.html> (accessed on 10
732 March 2020).
- 733 39. Franks DW, Ruxton GD, James R. 2010 Sampling animal association networks with
734 the gambit of the group. *Behav Ecol Sociobiol* **64**, 493–503. (doi:10.1007/s00265-009-
735 0865-8)

- 736 40. Wanelik KM, Farine DR. 2022 A new method for characterising shared space use
737 networks using animal trapping data. *Behav Ecol Sociobiol* **76**. (doi:10.1007/s00265-
738 022-03222-5)
- 739 41. Cairns SJ, Schwager SJ. 1987 A comparison of association indices. *Anim Behav* **35**,
740 1454–1469. (doi:10.1016/S0003-3472(87)80018-0)
- 741 42. Wood SN. 2011 Fast stable restricted maximum likelihood and marginal likelihood
742 estimation of semiparametric generalized linear models. *J R Stat Soc Series B Stat*
743 *Methodol* **73**, 3–36. (doi:10.1111/j.1467-9868.2010.00749.x)
- 744 43. Koricheva J, Gurevitch J, Mengersen KL. 2013 Handbook of meta-analysis in ecology
745 and evolution. , 498.
- 746 44. Konstantopoulos S. 2011 Fixed effects and variance components estimation in three-
747 level meta-analysis. *Res Synth Methods* **2**, 61–76. (doi:10.1002/jrsm.35)
- 748 45. Cinar O, Nakagawa S, Viechtbauer W. 2022 Phylogenetic multilevel meta-analysis: A
749 simulation study on the importance of modelling the phylogeny. *Methods Ecol Evol*
750 **13**, 383–395. (doi:10.1111/2041-210X.13760)
- 751 46. Michonneau F, Brown JW, Winter DJ. 2016 rotl: an R package to interact with the
752 Open Tree of Life data. *Methods Ecol Evol* **7**, 1476–1481. (doi:10.1111/2041-
753 210X.12593)
- 754 47. Paradis E, Schliep K. 2019 ape 5.0: an environment for modern phylogenetics and
755 evolutionary analyses in R. *Bioinformatics* **35**, 526–528.
756 (doi:10.1093/BIOINFORMATICS/BTY633)
- 757 48. Gibson AK, Amoroso CR. 2022 Evolution and Ecology of Parasite Avoidance. , 1–21.
- 758 49. Colman E, Colizza V, Hanks EM, Hughes DP, Bansal S. 2021 Social fluidity mobilizes
759 contagion in human and animal populations. *Elife* **10**. (doi:10.7554/ELIFE.62177)
- 760 50. Michelangeli M, Payne E, Spiegel O, Sinn D, Leu ST, Gardner M, Sih A. 2021
761 *Personality, spatiotemporal ecological variation, and resident/explorer movement*
762 *syndromes in the sleepy lizard*. (doi:10.1111/1365-2656.13616)
- 763 51. Spiegel O, Leu ST, Bull CM, Sih A. 2017 What's your move? Movement as a link
764 between personality and spatial dynamics in animal populations. *Ecol Lett* **20**, 3–18.
765 (doi:10.1111/ele.12708)
- 766 52. Aplin LM, Farine DR, Mann RP, Sheldon BC. 2014 Individual-level personality
767 influences social foraging and collective behaviour in wild birds. *Proceedings of the*
768 *Royal Society of London B* **281**, 20141016. (doi:10.1098/rspb.2014.1016)
- 769 53. Hunt ER, Mi B, Fernandez C, Wong BM, Pruitt JN, Pinter-Wollman N. 2018 Social
770 interactions shape individual and collective personality in social spiders. *Proceedings*
771 *of the Royal Society B: Biological Sciences* **285**, 20181366.
772 (doi:10.1098/rspb.2018.1366)

- 773 54. Firth JA, Cole EF, Ioannou CC, Quinn JL, Aplin LM, Culina A, McMahon K, Sheldon
774 BC. 2018 Personality shapes pair bonding in a wild bird social system. *Nat Ecol Evol*
775 **2**, 1696–1699. (doi:10.1038/s41559-018-0670-8)
- 776 55. Webber Q, Laforge M, Bonar M, Wal E Vander. 2022 The adaptive value of density-
777 dependent habitat specialization and social network centrality. *Authorea Preprints*
778 (doi:10.22541/AU.165210484.46672609/V1)
- 779 56. Webber QMR, Dantzer B, Lane JE, Boutin S, McAdam AG. 2023 Density-dependent
780 plasticity in territoriality revealed using social network analysis. *Journal of Animal*
781 *Ecology* **92**, 207–221. (doi:10.1111/1365-2656.13846)
- 782 57. Sheppard CE, Inger R, McDonald RA, Barker S, Jackson AL, Thompson FJ,
783 Vitikainen EIK, Cant MA, Marshall HH. 2018 Intragroup competition predicts individual
784 foraging specialisation in a group-living mammal. *Ecol Lett* **21**, 665–673.
785 (doi:10.1111/ELE.12933)
- 786 58. Sanchez JN, Hudgens BR. 2015 Interactions between density, home range
787 behaviors, and contact rates in the Channel Island fox (*Urocyon littoralis*). *Ecol Evol* **5**,
788 2466–2477. (doi:10.1002/ece3.1533)
- 789 59. Wilkin TA, Garant D, Gosler AG, Sheldon BC. 2006 Density effects on life-history
790 traits in a wild population of the great tit *Parus major*: Analyses of long-term data with
791 GIS techniques. *Journal of Animal Ecology* **75**, 604–615. (doi:10.1111/j.1365-
792 2656.2006.01078.x)
- 793 60. Cote IM, Poulin R. 1995 Parasitism and group size in social animals: a meta-analysis.
794 *Behavioral Ecology* **6**, 159–165. (doi:10.1093/beheco/6.2.159)
- 795 61. McCallum H, Barlow N, Hone J. 2001 How should pathogen transmission be
796 modelled? *Trends Ecol Evol* **16**, 295–300. (doi:10.1016/S0169-5347(01)02144-9)
- 797 62. Rajeev M, Metcalf CJE, Hampson K. 2020 Modeling canine rabies virus transmission
798 dynamics. In *Rabies*, pp. 655–670. Elsevier. (doi:10.1016/b978-0-12-818705-
799 0.00020-0)
- 800 63. Townsend SE *et al.* 2013 Designing Programs for Eliminating Canine Rabies from
801 Islands: Bali, Indonesia as a Case Study. *PLoS Negl Trop Dis* **7**.
802 (doi:10.1371/JOURNAL.PNTD.0002372)
- 803 64. Macdonald DW, Newman C. 2022 *The Badgers of Wytham Woods: a model for*
804 *behaviour, ecology, and evolution*. Oxford University Press.
- 805 65. Clutton-Brock TH, Guinness FE, Albon SD. 1982 *Red Deer: Behavior and Ecology of*
806 *Two Sexes*. Chicago, IL: University of Chicago Press. See
807 https://books.google.co.uk/books/about/Red_Deer.html?id=x4SGuA3t-NoC&pgis=1.
- 808 66. Clutton-Brock TH, Pemberton JM. 2004 *Soay sheep: population dynamics and*
809 *selection on St. Kilda*. Cambridge, UK: Cambridge University Press.

- 810 67. Tardy O, Massé A, Pelletier F, Mainguy J, Fortin D. 2014 Density-dependent
811 functional responses in habitat selection by two hosts of the raccoon rabies virus
812 variant. *Ecosphere* **5**, 1–16. (doi:10.1890/ES14-00197.1)
- 813 68. Wilber MQ, Yang A, Boughton R, Manlove KR, Miller RS, Pepin KM, Wittemyer G.
814 2022 A model for leveraging animal movement to understand spatio-temporal disease
815 dynamics. *Ecol Lett* , 1–15. (doi:10.1111/ele.13986)
- 816 69. Buck JC, Weinstein SB, Young HS. 2018 Ecological and Evolutionary Consequences
817 of Parasite Avoidance. *Trends Ecol Evol* **33**, 619–632.
818 (doi:10.1016/j.tree.2018.05.001)
- 819 70. Lion S, Boots M. 2010 Are parasites “prudent” in space? *Ecol Lett* **13**, 1245–1255.
820 (doi:10.1111/j.1461-0248.2010.01516.x)
- 821 71. Strauss ED, Decasien AR, Galindo G, Hobson EA, Shizuka D, Curley JP. 2022
822 DomArchive: a century of published dominance data. *Philosophical Transactions of*
823 *the Royal Society B* **377**. (doi:10.1098/RSTB.2020.0436)
- 824 72. Drewe JA. 2010 Who infects whom? Social networks and tuberculosis transmission in
825 wild meerkats. *Proceedings. Biological sciences / The Royal Society* **277**, 633–42.
826 (doi:10.1098/rspb.2009.1775)
- 827 73. Powell SN, Wallen MM, Miketa ML, Krzyszczyk E, Foroughirad V, Bansal S, Mann J.
828 2021 Sociality and tattoo skin disease among bottlenose dolphins in Shark Bay,
829 Australia. *Behavioral Ecology* **31**, 459–466. (doi:10.1093/BEHECO/ARZ207)
- 830 74. Testard C *et al.* 2020 Rhesus Macaques Build New Social Connections after a Natural
831 Disaster. *Current Biology* , 1–11. (doi:10.2139/ssrn.3741230)
- 832 75. Spiegel O, Leu ST, Sih A, Bull CM. 2016 Socially interacting or indifferent
833 neighbours? Randomization of movement paths to tease apart social preference
834 and spatial constraints. *Methods Ecol Evol* , 971–979. (doi:10.1111/2041-
835 210X.12553)
- 836 76. Kays R *et al.* 2021 The Movebank system for studying global animal movement and
837 demography. *Methods Ecol Evol* **2021**, 1–13. (doi:10.1111/2041-210X.13767)
- 838 77. Batsuren E, Zhang X, Song M, Wan X, Li G, Liu J, Huang S, Zhang Z. 2022 Density-
839 dependent changes of mating system and family structure in Brandt's voles
840 (*Lasiopodomys brandtii*). *Ecol Evol* , 1–16. (doi:10.1002/ece3.9199)
- 841 78. Vander Wal E, van Beest FM, Brook RK. 2013 Density-Dependent Effects on Group
842 Size Are Sex-Specific in a Gregarious Ungulate. *PLoS One* **8**, e53777.
843 (doi:10.1371/JOURNAL.PONE.0053777)
- 844 79. Ashby B, Bruns E. 2018 The evolution of juvenile susceptibility to infectious disease.
845 *Proceedings of the Royal Society B: Biological Sciences* **285**, 20180844.
846 (doi:10.1098/rspb.2018.0844)

- 847 80. Albery GF, Sweeny AR, Webber Q. In press. How behavioural ageing affects
848 infectious disease.
- 849 81. Zuk M. 2009 The sicker sex. *PLoS Pathog* **5**, 1–3. (doi:10.1371/journal.ppat.1000267)
- 850 82. Arneberg P, Skorping A, Grenfell B, Read AF. 1998 Host densities as determinants of
851 abundance in parasite communities. *Proceedings of the Royal Society B: Biological*
852 *Sciences* **265**, 1283–1289. (doi:10.1098/rspb.1998.0431)
- 853 83. Arneberg P. 2001 An ecological law and its macroecological consequences as
854 revealed by studies of relationships between host densities and parasite prevalence.
855 *Ecography* **24**, 352–358. (doi:10.1111/j.1600-0587.2001.tb00208.x)
- 856 84. Rocha LEC, Ryckebusch J, Schoors K, Smith M. 2021 Scaling of social interactions
857 across animal species. *Sci Rep* **11**, 12584.
- 858 85. Lafferty KD, DeLeo G, Briggs CJ, Dobson AP, Gross T, Kuris AM. 2015 A general
859 consumer-resource population model. *Science (1979)* **349**, 854–857.
860 (doi:10.1126/SCIENCE.AAA6224/SUPPL_FILE/LAFFERTY.SM.PDF)
- 861