

1 Negative density-dependent parasitism 2 in a group-living carnivore

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9 Abstract

10 Animals living at high population densities commonly experience greater exposure to
11 disease, leading to increased parasite burdens. However, social animals can benefit
12 immunologically and hygienically from cooperation, and individuals may alter their socio-
13 spatial behaviour in response to infection, both of which could counteract density-related
14 increases in exposure. Consequently, the costs and benefits of sociality for disease are often
15 uncertain. Here, we use a long-term study of a wild European badger population (*Meles*
16 *meles*) to investigate how within-population variation in host density determines infection
17 with multiple parasites. Four out of five parasite taxa exhibited consistent spatial hotspots of
18 infection, which peaked among badgers living in areas of low local population density.
19 Combined movement, survival, spatial, and social network analyses revealed that parasite
20 avoidance was the likely cause of this negative density dependence, with possible roles for
21 localised mortality, encounter-dilution effects, and micronutrient-enhanced immunity. These
22 findings demonstrate that animals can organise their societies in space to minimise parasite
23 infection, with important implications for badger behavioural ecology and for the control of
24 badger-associated diseases.

25 Introduction

26 A wild animal's infectious disease burden is determined by its exposure and susceptibility to
27 infective pathogens. Typically, higher population density results in increased contact rates
28 and thus greater exposure [1,2]; however, sociality carries immunological and hygienic
29 benefits that can counteract this exposure-exacerbating effect [3,4]. For instance, cooperative
30 foraging improves nutrition, alleviating infection costs [5]; mutual grooming removes
31 ectoparasites [6–8]; and “social immune responses” maintain collective group health [9,10],
32 e.g. through extirpating sick individuals [11]. Additionally, the environmental distribution of
33 resources can influence spatial behaviour [12–14] and determine local population densities
34 [15], while altering susceptibility [16] and transmission efficiency [17]. Sociality and disease
35 may thus be confounded through shared causal origins rather than being mechanistically
36 linked [17]. Finally, individuals can minimise exposure by avoiding environmental cues
37 [18,19] or infected conspecifics [8,20], creating a population-level “landscape of disgust”
38 analogous to predatory “landscapes of fear” [21,22]. These processes could produce negative
39 density effects, sometimes depending on parasite transmission mode [1,17,23], but their role
40 in defining observed density-infection relationships is poorly understood.

41 Uncertainty concerning density-infection relationships largely arises because studies of social
42 effects are often carried out across discrete groups [1,24], between populations [25,26], or
43 between species (e.g. [1,2,24,27]). Continuous density measures are rarely linked to parasite
44 burden within one contiguous host population, and studies that do so generally use purely
45 social metrics rather than spatial density gradients (e.g. [28–30]). Continuous spatial density
46 measures are advantageous because: density is a continuous, spatially explicit variable [31–
47 33]; for the many parasites that are spread through the environment, spatial density measures
48 better represent transmission than direct (social network) metrics [17,34–36]; and between-
49 population and cross-species comparisons are fraught with confounding factors such as
50 shared environmental causality or compensatory evolutionary changes [1,3], which within-
51 population studies can more easily avoid or overcome. Furthermore, accounting for spatial
52 effects may help anticipate or test the caveats of cooperation, environmental causality, and
53 behavioural avoidance outlined above.

54 European badgers (*Meles meles*) are nocturnal, ground-dwelling mustelids with a pan-
55 European distribution, eating a varied diet composed largely of earthworms [37]. Badgers are
56 of particular interest for cattle health in the United Kingdom because of their role in

57 maintaining and spreading bovine tuberculosis [37,38]. Although intended as a control
58 measure, intense culling perturbs badger social systems, causing stressed survivors to
59 disperse, thereby spreading bovine tuberculosis to neighbouring farms [39–41].
60 Understanding badgers’ socio-spatial behaviours and their epidemiological implications is
61 therefore an important research priority (e.g. [38,42–44]). The demography, behaviour, and
62 parasitism of badgers in Wytham Woods, Oxfordshire have been studied continuously since
63 1987 [37,45]. Dens (termed “setts”) are situated dependent on soil composition and landscape
64 topography [46]. These badgers reside in cohesive mixed-sex social groups, with around 35%
65 consistent philopatry; however, these groups are also fluid: 16.4% of individuals are trapped
66 at a different social group to their previous capture history, and 19.8% away from their natal
67 group [47]. Furthermore, from genetic pedigree, 48% of cubs have extra-group paternity [48].
68 Badgers host several arthropod parasites, including badger-specific fleas (*Paraceras melis*)
69 and lice (*Trichodectes melis*) and generalist ticks (*Ixodes* sp.) [49]. They also carry two
70 gastrointestinal protozoans: *Eimeria melis* and *Isospora melis*. *E. melis* predominantly infects
71 young individuals, causing substantial mortality [50,51]. Although studies have examined
72 social grooming effects on ectoparasite burden [6,52] and roles of denning behaviour in
73 parasite transmission [49], the within-population spatial-social parasite epidemiology has yet
74 to be investigated.

75 Here, we investigate parasite burdens in the Wytham badger population and their associations
76 with spatial and social behaviour. We establish parasite distributions using spatial
77 autocorrelation models. We quantify social drivers using both spatial density gradients and
78 social network metrics, postulating that greater badger densities would drive higher parasite
79 burdens through increased exposure. Finally, we examine survival effects, investigating
80 whether parasite-linked mortality might alter spatial patterns of badger population density.
81 We consider a range of potential social/spatial covariates of parasite burden, including
82 density-related exposure changes, benefits of cohabitation, condition/susceptibility effects,
83 encounter-dilution effects, and parasite avoidance behaviours.

84 **Methods**

85 **Data collection**

86 Badgers were sampled as part of a long-term study in Wytham Woods, Oxfordshire, UK
87 (51.778°N, 1.313°W), established in 1987 and recording one of the highest local badger
88 densities ever reported [37,45]. Badgers were trapped overnight at their setts in steel-mesh

89 cages baited with peanuts, collected the next morning, transported to a handling facility and
90 sedated. Individuals were identifiable by tattoo, applied on first trapping (typically as cubs).
91 Measures were taken of head-body length (mm) and weight (to the nearest 0.1kg). We
92 calculated a standardised index of body condition dividing $\log(\text{weight})$ by $\log(\text{body length})$.
93 The population was trapped seasonally (winter: Jan/Feb/March; spring: April/May/June;
94 summer: July/Aug/Sept; autumn: Oct/Nov/Dec) in 4 quadrants, for 3 days per quadrant. Our
95 dataset included 9016 captures of 1369 badgers spanning 29 years (1990-2018).

96 The population currently comprises 23 social groups (mean group size=11; range 2-29
97 individuals), each using more than one sett, with sett/social group affiliation established using
98 baitmarking [46,53]. Badgers were assigned to groups using established residency rules [48].
99 We computed social networks based on co-trapping using a “gambit of the group” approach,
100 where individuals trapped in the same sett in the same year were assumed to have interacted
101 [54].

102 Fleas were counted during a stereotyped 20-second inspection of the badger’s full body, and
103 ticks (*Ixodes* sp.) and lice (*Trichodectes melis*) were counted within a 4x4cm square of
104 preferentially-parasitised skin near the groin (per Cox *et al.* 1999). Faecal sampling for two
105 protozoan endoparasites, *Eimeria melis* and *Isospora melis*, was carried out through 1993-
106 1997 and 2009-2017 (N=1287 counts). Endoparasite were counted using salt flotation and
107 microscopy [51,55]. Each count was duplicated, and data were reduced to a binary
108 infected/uninfected status (rather than counts) because of their highly overdispersed
109 distribution.

110 **Statistical Analysis**

111 **Covariates**

112 Statistical analysis and data manipulation used R version 3.6.0 [56]. All data and code are
113 available at <https://github.com/gfalbery/Badgeworks>. Models were constructed using the
114 `inla` package [57,58]. Response variables included counts of fleas and lice (negative
115 binomial distribution) and prevalence of ticks, *Eimeria*, and *Isospora*. Explanatory covariates
116 included: Year (continuous); Month (categorical); Age Category (categorical: cub, yearling,
117 and adult); Sex (male and female); and Body Condition (continuous). Continuous covariates
118 were standardised (mean=0; standard deviation=1). Individual Identity and Year were fitted
119 throughout as categorical random effects.

120 1. Spatial autocorrelation models

121 To identify generalised spatial patterns we first fitted models accounting for continuous
122 spatial autocorrelation across the population [33,57,58]. We fitted a base model using only
123 Year, Month, Age Category, and Sex, with individual and annual random effects. We then
124 added an SPDE random effect controlling for spatial autocorrelation in the response variable
125 in space, based on individuals' point locations. We then compared these models using
126 Deviance Information Criterion (DIC) to establish whether accounting for spatial
127 autocorrelation improved model fit; models within $2\Delta DIC$ were judged competitive.

128 2. Density models

129 We then fitted models that replaced the SPDE effects with individual measures of local
130 population density. Models included a range of social/spatial density measures, calculated
131 using various methods. Spatial density metrics represent numbers of individuals in a given
132 space, and therefore tread the line between social and spatial behavioural traits [17]. We
133 computed these by creating space use distribution kernels with the `adehabitatR` package in
134 R [59]. We rasterised the usage distribution, assigning each individual a local density based
135 on the raster value for their map location (Figure 1A-B). Measures included: 1) **Lifetime**
136 **density**: the density of individuals' centroids across the study period. 2) **Trapping density**:
137 the density of trapping events, incorporating multiple captures of the same individual per
138 year. 3) **Annual density**: the density of individuals' centroids in the sampling year,
139 calculated from annual density kernels. Only one spatial density measure was allowed in a
140 given model, as the measures correlate ($R > 0.5$) and co-fitting several measures produced
141 spurious, unexpected correlations in the opposite direction expected from data exploration.
142 We also used two social metrics based on co-trapping patterns. **Degree centrality** was the
143 number of unique badgers with whom each individual was trapped in the same sett per year.
144 **Group size** was the total number of individuals trapped in a given social group per year.
145 Following spatial autocorrelation model procedures, we conducted a model selection
146 procedure for behavioural metrics, using $2\Delta DIC$ as the cutoff, and only including the best-
147 fitting metric. We conducted these models for: the overall dataset ($N=9016$); adults only (age
148 2+, fitting age in years as a fixed covariate; $N=6159$); and juveniles only ($N=1639$). For these
149 models, we display only the best-fitting metric, and for the overall dataset if it exhibited a
150 significant trend (and a subset-only model otherwise).

151 3. Multi-response models

152 To investigate whether parasites covaried with badger density at the within- or between-
153 individual level, we constructed multi-response models in MCMCglmm with an unstructured
154 covariance matrix [60,61]. We fitted parasites and local density as response variables,
155 estimating their covariance when accounting for other fixed effects and decomposing this
156 covariance at the within- and between-individual level. A negative within-individual
157 (residual) correlation would imply that higher burden/prevalence individuals (compared to
158 their baseline) moved to lower density areas during their lives, supporting either social
159 ostracism or sickness behaviours. In contrast, negative between-individual covariance would
160 imply that individuals inhabiting lower densities generally had inherently greater parasitism.
161 We only constructed these models for parasite-host age category combinations that
162 demonstrated density effects in the INLA models.

163 4. Survival models

164 To investigate parasites' mortality effects, we fitted models with survival as a binary response
165 (1=animal seen in any subsequent year; 0 otherwise). These models included the same
166 covariates as the parasite models, plus parasite prevalence/count and badger density
167 measures. Parasite measures were either $\log(x+1)$ -transformed integers (fleas, lice) or binary
168 (ticks, *Eimeria*, and *Isospora*). We conducted another model selection procedure, adding
169 parasite metrics successively if they improved model fit. This was carried out for adults and
170 juveniles separately.

171 Results

172 INLA autocorrelation models revealed considerable spatial structuring of parasite burdens.
173 Models for 4/5 parasites were substantially improved by incorporating spatial effects
174 ($\Delta\text{DIC}>8$; Table 1). Only *Isospora*'s model was not improved by spatial autocorrelation
175 (Table 1).

176 Density models provided substantial support for negative associations between badger
177 density and parasite infection. Including at least one density measure as a covariate improved
178 the model for at least one age category for 4/5 parasites; all had significant negative slopes
179 for density effects (Figure 2; Figure SII-4; Table SII-3). Slopes were relatively shallow, but
180 extremely significant and robust (Figure 2). Flea counts were best described by Lifetime
181 Density for the overall model ($\Delta\text{DIC}=-16.31$; $P<0.0001$; Figure 2A), while lice burdens
182 decreased with Trapping Density in the juveniles-only model ($\Delta\text{DIC}=-8.77$; $P=0.0017$; Figure

183 2B). Tick prevalence was lower in areas of higher Lifetime Density ($\Delta\text{DIC}=-2.47$; $P=0.0038$;
184 Figure 2C), and *Eimeria* prevalence was lower with greater Trapping Density ($\Delta\text{DIC}=-5.83$;
185 $P=0.0053$; Figure 2D). Only one positive social effect was detected: adults with greater
186 degree had slightly more lice ($\Delta\text{DIC}=-2.39$; $P=0.027$; Figure SI2). All DIC changes
187 associated with the model addition procedure are presented in Table SI1-3.

188 MCMCgmm multi-response models revealed similar trends to INLA univariate models
189 (Figure SI1-4), and allowed us to decompose density-parasite correlations into within- and
190 between-individual changes (Figure 3B). Correlations were greater and much more
191 significant between- than within-individuals in all cases (Figure 3B). This demonstrates that
192 movement between high- and low-density areas was unlikely to produce changes in parasite
193 burden over an individual's lifetime, but rather that individuals' home ranges exhibited
194 inherently different local density-parasite relationships. Only louse infection predicted
195 survival probability; the effect was relatively small, minimally significant, and specific to
196 juveniles ($P=0.038$; Figure 3A).

197 Our models also revealed various other effects (Figures SI1-4). Briefly, in the overall models,
198 juveniles had fewer fleas, more lice, and greater *Eimeria* prevalence than did yearlings and
199 adults, and lower *Isospora* prevalence than adults (Figure SI1). Males had more lice than did
200 females, with substantial monthly variation in all parasites (Figure SI1). Additionally, body
201 condition was negatively associated with fleas, lice, and *Eimeria* infection in all age/sex
202 classes (Figure SI1). The adults-only and juveniles-only models were very similar to the
203 overall models (Figures SI1-3); notably, in adults, lice burden increased with age in years,
204 whereas *Eimeria* and *Isospora* prevalence decreased (Figure SI2).

205 Discussion

206 Using a combination of spatial and social network analysis, we uncovered negative
207 associations between local population density and multiple parasites in this wild group-living
208 carnivore. We found strong but contrasting spatial structuring of fleas, lice, ticks, and
209 *Eimeria*, and, contrary to expectations, all four were most prevalent or abundant in areas of
210 lowest badger density. Co-trapping network and grouping metrics were not predictive of
211 parasitism, implying that "direct" social behaviours, such as mutual allo-grooming, were
212 unlikely to explain the negative density effects. Additionally, badger density effects
213 manifested independent of survival and body condition effects, implying that spatial
214 structuring of the host population did not originate from: 1) localised host mortality, 2)

215 reduced susceptibility arising from co-habitation and implied cooperation benefits [3,5], or 3)
216 greater local resource availability influencing susceptibility [16,62,63]. Additionally, multi-
217 response models revealed low within-individual covariance between density and parasites,
218 providing little support for heavily-parasitised individuals becoming ostracised during the
219 course of their lives [11]. Taking spatial structuring together with setts' propensity to harbour
220 parasites [49,64], the most parsimonious interpretation is that badgers avoid infection
221 behaviourally, preferring to inhabit areas poorly disposed to parasite transmission (Table 2).
222 These individual-level avoidance behaviours amplify at the population level to produce
223 patterns of badger density inversely related to parasite distributions in the environment, as
224 expected under a "landscape of disgust" [19,21,22]. As well as providing rare evidence of
225 non-consumptive effects of parasites in a wild carnivore, these results imply that animals can
226 arrange their society in space according to parasite transmission.

227 Our study demonstrates observationally that parasites can determine a society's structure in
228 the environment, and that this phenomenon may counteract the more conventional prediction
229 that host density exacerbates parasitism through increased exposure (e.g. [1,2,65]).

230 Consequently, studies aiming to quantify social covariates of disease should explicitly seek
231 to investigate individual movement and avoidance behaviours, socio-spatial structuring, and
232 feedbacks between sociality and space use [17]. Previous studies on other mammals have
233 revealed avoidance of infected conspecifics [8] and faeces [18,66], but it remained unclear
234 whether animals avoid spatial hotspots of transmission themselves, and whether these could
235 have population-level consequences [21,22]. Badgers respond to social scent cues and may
236 use these to detect and avoid infested or infectious individuals [67]; furthermore, they move
237 between setts regularly to avoid accumulating parasites [64,68], abandoning highly infested
238 setts and chambers [49]; we posit that this behaviour has emergent population-level
239 consequences. Wytham badgers preferentially establish their setts on northwest-facing slopes
240 in areas with sandy soils [46], and variation in internal sett temperature and humidity are
241 associated with reproductive success [69,70]. Our data suggest additional selection for sett
242 traits and sites resistant to parasite infestation and transmission, which produce an emergent
243 trend for fewer setts, with fewer occupants, in more highly parasitised areas. Quantifying
244 parasites in the environment or inside setts and correlating them with badger behaviour could
245 provide support for this hypothesis. Environmental (sett chamber-based) data on parasite
246 presence would be needed to determine whether badgers avoid infection *actively* (pre-

247 infection), using environmental cues that predict parasitism, or *reflexively* (post-infection), by
248 moving away from areas of high parasitism due to irritation or sickness.

249 Four parasites exhibited negative density effects, which could impose tradeoffs on avoidance
250 behaviour. The parasites' distributions were highly contrasting, likely driven by different
251 environmental factors: for example, sett microclimates favouring flea survival will facilitate
252 their transmission [49,64]; similarly, *Eimeria* is transmitted faecal-orally, and oocysts are
253 likely acquired from warm, moist sett chambers, which may explain the gradual decline
254 moving away from the Thames river in the Northwest toward drier parts of the woods (Figure
255 1F). Ultimately, in combination with other socio-ecological factors (e.g., finding suitable
256 mates), badgers may be incapable of completely avoiding all parasites via denning decisions,
257 which could mediate co-infection and promote diverse parasite communities, giving rise to
258 local hotspots across the population. This may lead to parasite avoidance being traded off
259 against foraging, reproductive success and survival [22,71]. If badgers exhibit between-
260 individual variation in movement and foraging specialisation [72], avoidance of multiple co-
261 infecting parasites could maintain between-individual immune heterogeneity [55]. Notably,
262 only cub density was negatively associated with lice. This observation could be linked to the
263 detectable mortality effects in cubs, driving local cub mortality and/or motivating
264 reproducing females to avoid spatial hotspots of lice.

265 All of the parasites we examined employ some degree of indirect transmission, likely
266 yielding different relationships with host density than more directly transmitted parasites
267 [1,17]. Ultimately, only avoiding conspecifics can help avoid direct parasite transmission
268 (e.g. [8]), which may not be achievable through purely spatial structuring. Future studies
269 could examine sexually transmitted infections or aerosol-transmitted viruses to investigate
270 whether individuals living in areas of lower density gain any benefit in terms of direct
271 parasite transmission. This may be of particular importance for bovine tuberculosis (bTB),
272 which has a complex, nonlinear relationship with badger sociality [73–75]. Notably,
273 previous bTB studies have generally used social group size as a metric of sociality; given that
274 bTB has an environmental transmission component, particularly between badgers and cattle
275 [76], spatial density metrics, such as those employed here, could be revealing.

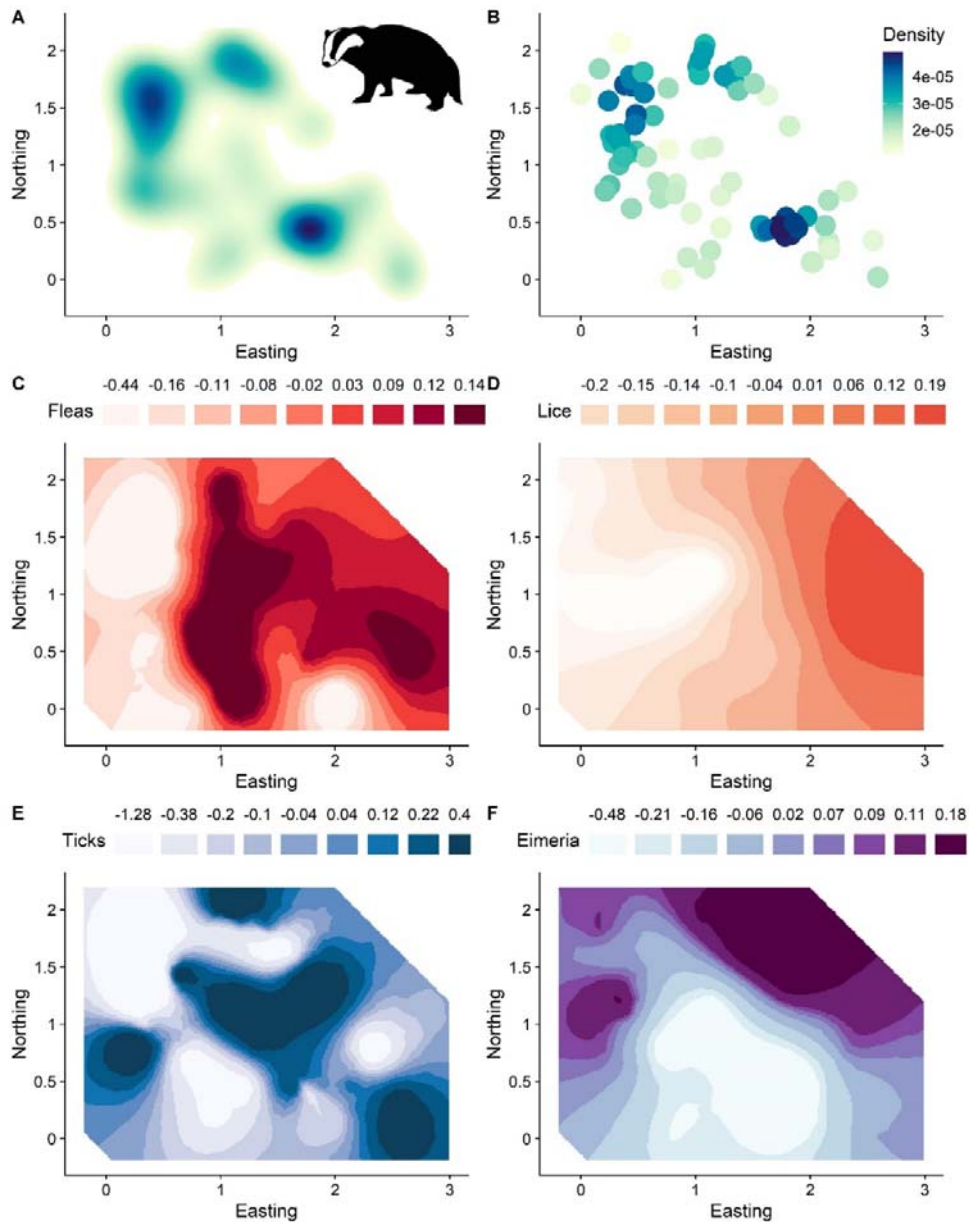
276 We note two potential sources of negative density dependence untested by our modelling
277 approach: the encounter-dilution effect [77,78] and micronutrient impacts on immunity [79].
278 For the former, where parasites exhibit a constant attack rate in space, greater host densities
279 actually drive a lower per-individual burden of disease because the same number of parasites

280 is divided among more available hosts [77,78]. Because this requires that the spatial
281 distributions of parasites are not tightly linked to the host distribution (e.g. through
282 reproducing on the host), it is unlikely to apply for any of the badger-specific parasites
283 studied here. However, non-host-specific ticks (*Ixodes* sp.) could transmit from other species
284 to badgers in a given area, producing an encounter-dilution effect; therefore, we are unable to
285 rule out this mechanism (Table 2). Regarding nutritional status, we used body condition
286 index as a coarse predictor of the ability to mount a healthy immune response. However,
287 micronutrients are essential to effective immune function [79] and would not be detected
288 from body condition indices; therefore, it is plausible that badgers might congregate in areas
289 of high micronutrient availability. If this behavioural tendency functions to combat pathogens
290 specifically, it amounts to a “landscape of disgust” acting through reduced susceptibility
291 rather than reduced exposure. This possibility could be tested in this or similar systems by
292 comparing the spatial distributions of high-resolution individual-level immune measures with
293 host density distributions.

294 Our findings have important implications for the socio-spatial dynamics of this system and its
295 resilience to pathogens and ecological change. If badger populations are organised optimally
296 to occupy areas of least parasite transmission, even small disturbances (e.g. setts lost to
297 forestry) could disrupt its socio-spatial structure and force individuals into unfavourable,
298 more highly parasitised areas, exacerbating their disease burden. Therefore, disruptive
299 anthropogenic activities such as culling-linked perturbation could have unseen consequences
300 for badger disease beyond larger-scale movement impacts (e.g. [39,40]). These findings
301 further inform our understanding of the drivers of badger spatial behaviour, offering insights
302 that may be invaluable for their conservation and disease control [38,46].

303 **Acknowledgements**

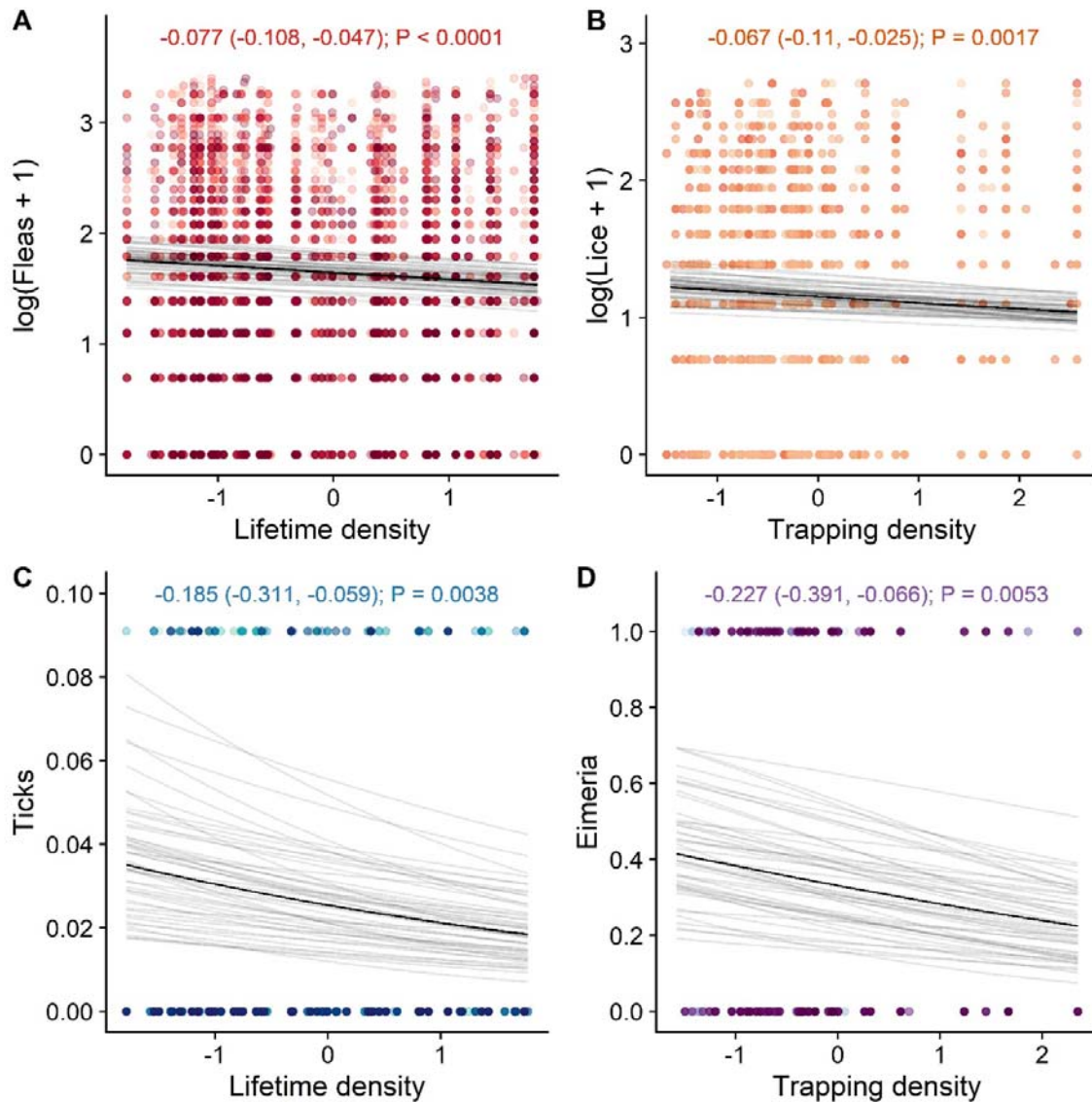
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308

309 Figure 1: Spatial distributions of badger population density and parasites in Wytham Woods,
 310 Oxfordshire, between 1989 and 2018. A: badger population density distributed across Wytham
 311 Woods, calculated based on a space use kernel for individuals' annual centroids. B: Individual
 312 badgers trapped at setts (represented by points) were assigned a local density value based on their
 313 location on the rasterised space use kernel. Darker blue colours in A and B correspond to greater
 314 population density. C-F: the spatial distribution of the four spatially distributed parasites, estimated
 315 using the INLA SPDE effect. Darker colours correspond to increased parasitism. The density values
 316 in B were fitted as covariates in linear models to explain individual parasite burdens, revealing a
 317 negative correlation between density and parasitism (see Fig. 2). All axes are in kilometres, with the
 318 0,0 point at the bottom left of the study area. We examined a fifth parasite, *Isospora melis*, but it was
 319 not significantly spatially distributed (see Table 1).

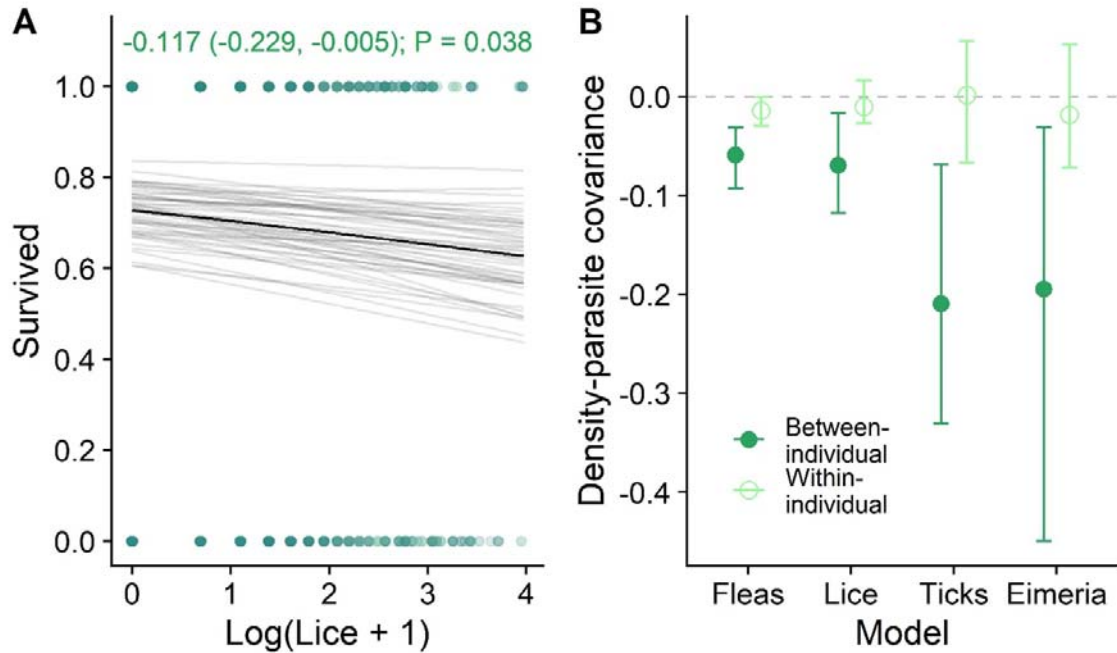
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322 Figure 2: Negative associations between population density and parasite infection. Badgers living at
323 higher densities had fewer fleas (A), fewer lice (B), lower tick prevalence (C), and lower *Eimeria*
324 *melis* prevalence (D). B represents juveniles only. Points represent individual samples, with colours
325 randomised along a colour palette for plotting clarity. Opaque black lines are derived from linear
326 model fits, taking the mean of the posterior distribution. Transparent grey lines represent 100 fits
327 drawn randomly from the posterior estimate distributions of each model, to demonstrate error in the
328 slope and intercepts. Text at the top of the Figures communicates slope estimates, with lower and
329 upper 95% credibility intervals in brackets, and P values. NB: in panel C, the y axis scale and the
330 location of the positive points have been altered for plotting clarity and to better visualise the slope,
331 due to low tick prevalence.

332



333

334 Figure 3: Associations of parasitism with survival and density-parasitism covariance partitioning. A)
 335 Louse burden was negatively associated with individual survival probability in juveniles. Opaque
 336 black line=linear model fit. Transparent grey lines=100 fits drawn randomly from the posterior
 337 estimate distribution, to demonstrate error in the slope and intercept. Text at the top of panel A
 338 communicates slope estimate, with lower and upper credibility interval in brackets and P value. B)
 339 Estimates for within- and between-individual covariance between parasitism and density, taken from
 340 MCMCglmm multivariate models. Points=posterior mean effect size estimates; error bars=95%
 341 credibility intervals.

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	Fleas	Lice	Ticks	Eimeria	Isospora
Base	153.03	36.57	49.25	8.28	0
SPDE	0	0	0	0	2.25

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Table 1: DIC changes associated with spatial autocorrelation terms for the five examined parasites. Lower numbers denote better models; best-fitting models Δ DIC=0. All models except *Isospora* were improved by addition of spatial fields (“SPDE”).

Potential mechanism	Conclusion	Reason for conclusion
Co-habitation/ cooperation benefits	No	No direct social effects or competition with body condition effects (Model Set 2; Figure SI1-3)
Allo-grooming	No	Spatial rather than direct social effects; grooming not possible for endoparasites (Model Set 2; Figure SI1-3; Table SI1-3)
Nutrition-associated immune benefits	No	No competition with body condition effects (Model Set 2; Figure SI1-3)
Social ostracism/self- isolation	No	Low within-individual covariance of density and parasitism (Model Set 3; Figure 3B)
Local host die-offs	~No	Possible for lice, in juveniles, but no other mortality effects were evident (Model Set 4; Figure 3A)
Encounter-Dilution	~No	Possible for generalist ticks, but not for the other (badger-specific, non-mobile) parasites [77,78]
Avoidance	Yes	All other possibilities eliminated; consistent with individual-level behavioural responses [64]

352

353 Table 2: Reasoning surrounding our hypothesis testing. We rejected most hypotheses for our observed
354 negative density effects other than parasite avoidance.

355

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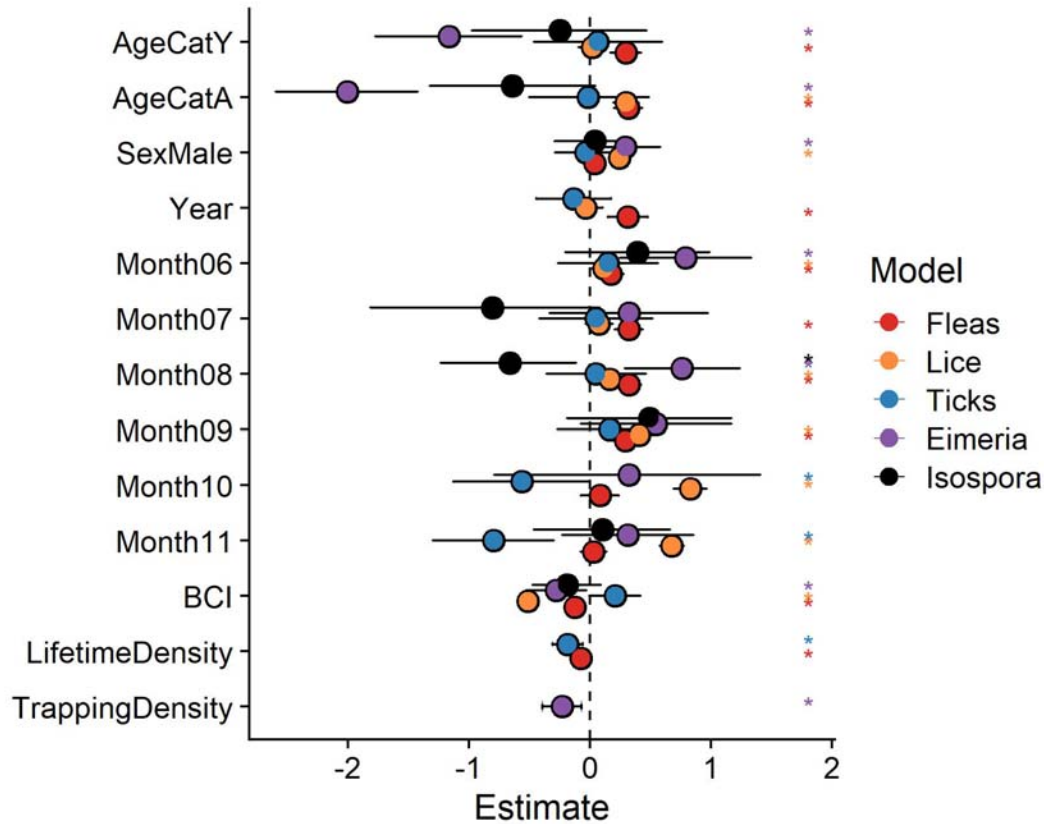
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595 **Supplementary figures and tables: Negative density-**
596 **dependent parasitism in a group-living carnivore**

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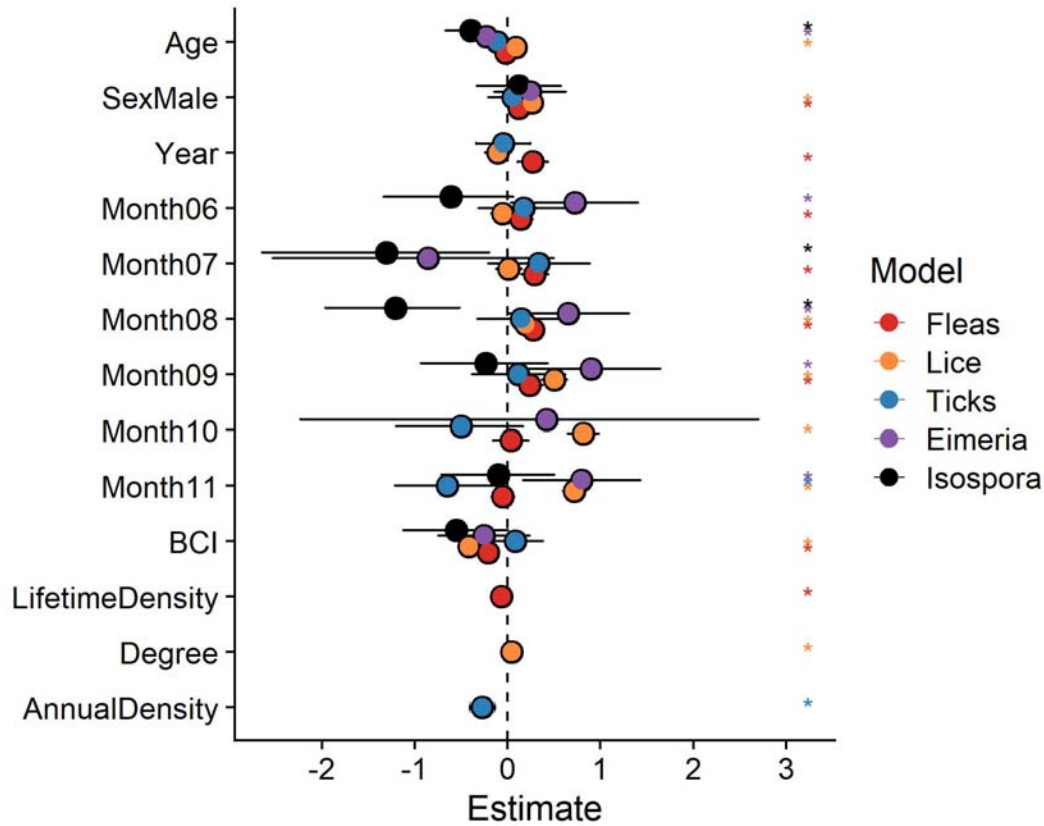
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599 Figure S11: Model effect outputs for the full dataset INLA density models. Points represent modes of
600 the posterior distribution of the effect estimates; error bars represent the 95% credibility intervals.

601 Asterisks denote significant results, whose 95% credibility intervals did not overlap with zero. Only

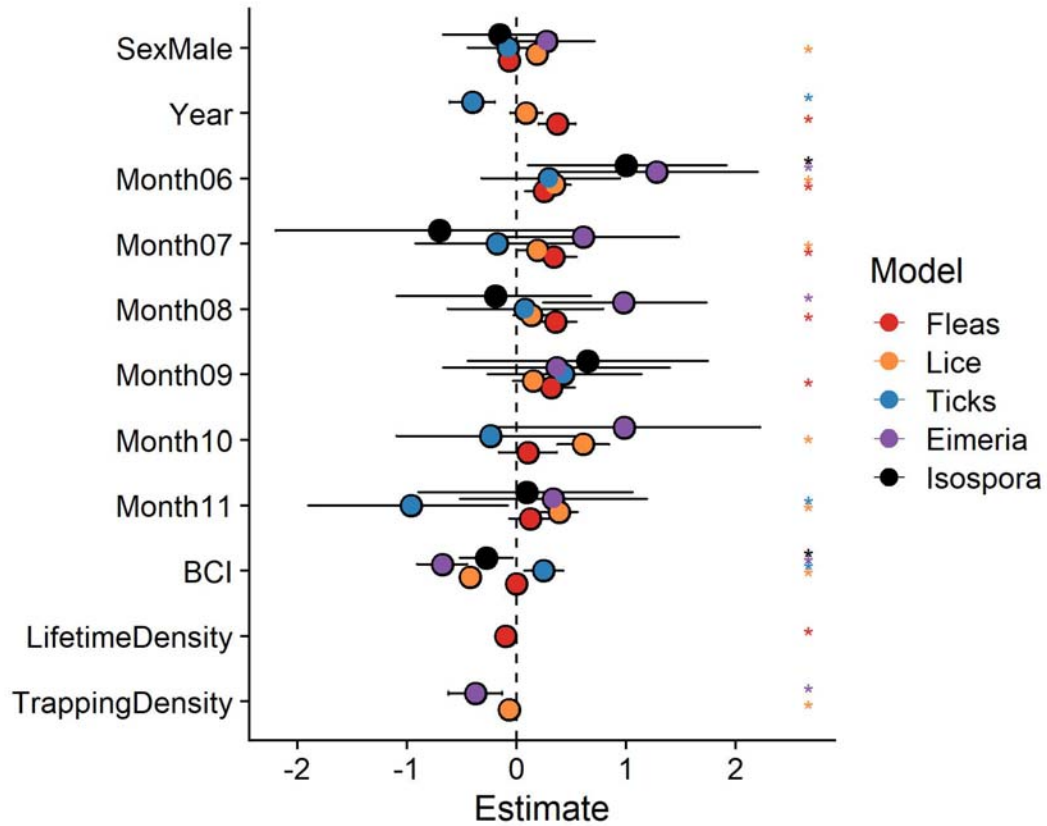
602 the behavioural traits that improved the model fit ($\Delta\text{DIC} < -2$) and were kept in the final model are

603 shown.



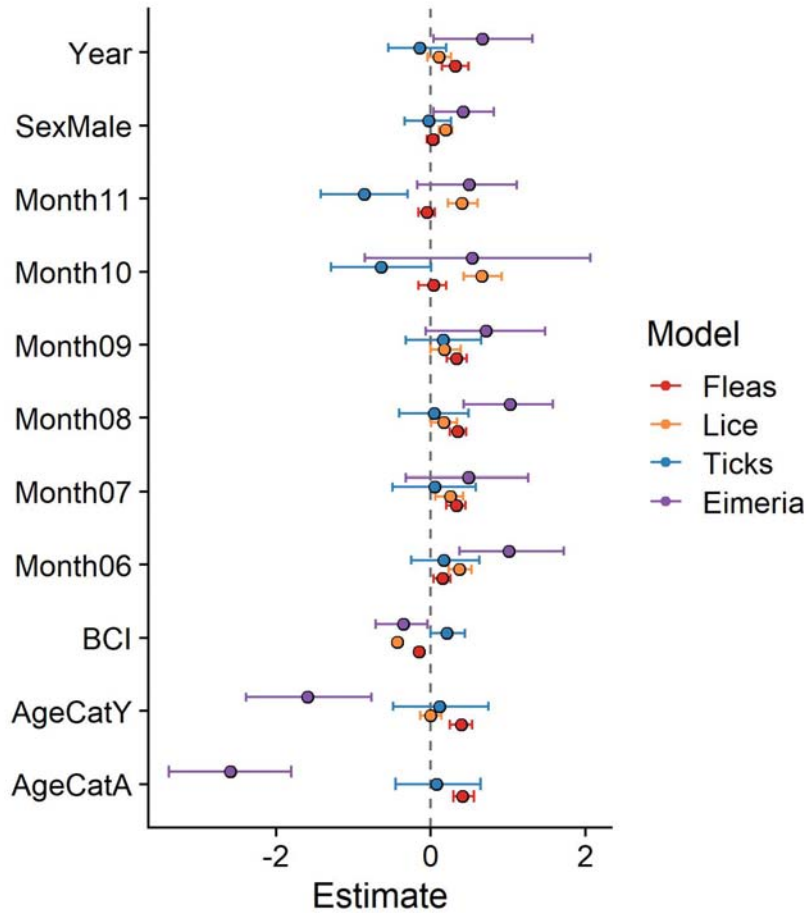
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605 Figure SI2: Model effect outputs for the adults-only dataset INLA density models. Points represent
606 modes of the posterior distribution of the effect estimates; error bars represent the 95% credibility
607 intervals. Asterisks denote significant results, whose 95% credibility intervals did not overlap with
608 zero. Only the behavioural traits that improved the model fit ($\Delta\text{DIC} < -2$) and were kept in the final
609 model are shown.



610

611 Figure SI3: Model effect outputs for the juveniles-only dataset INLA density models. Points represent
612 modes of the posterior distribution of the effect estimates; error bars represent the 95% credibility
613 intervals. Asterisks denote significant results, whose 95% credibility intervals did not overlap with
614 zero. Only the behavioural traits that improved the model fit ($\Delta\text{DIC} < -2$) and were kept in the final
615 model are shown.



616

617 Figure SI4: Model effect outputs for the multivariate MCMCglmm models closely represent the INLA
618 univariate models. Points represent modes of the posterior distribution of the effect estimates; error
619 bars represent the 95% credibility intervals. Asterisks denote significant results, whose 95%
620 credibility intervals did not overlap with zero. Only the behavioural traits that improved the model fit
621 ($\Delta\text{DIC} < -2$) and were kept in the final model are shown.

622

623

PARASITE	ROUND	VARIABLE	DELTA	KEPT
FLEAS	1	Degree	2.08	0
	1	GroupSize	2.055	0
	1	**LifetimeDensity**	-16.001	1
	1	TrappingDensity	1.115	0
	1	AnnualDensity	-6.889	0
LICE	1	Degree	1.796	0
	1	GroupSize	1.3	0
	1	LifetimeDensity	1.694	0
	1	TrappingDensity	0.166	0
	1	AnnualDensity	1.117	0
TICKS	1	Degree	0.773	0
	1	GroupSize	3.644	0
	1	**LifetimeDensity**	-2.192	1
	1	TrappingDensity	1.007	0
	1	AnnualDensity	-0.266	0
EIMERIA	1	Degree	1.134	0
	1	GroupSize	1.79	0
	1	LifetimeDensity	1.084	0
	1	**TrappingDensity**	-6.035	1
	1	AnnualDensity	1.851	0
ISOSPORA	1	Degree	1.897	0
	1	GroupSize	1.861	0

	1	LifetimeDensity	1.873	0
	1	TrappingDensity	1.507	0
	1	AnnualDensity	1.717	0

624

625 Table SII: DIC Changes (Δ DIC) associated with density measure model addition for the full
626 models. Negative Δ DIC values correspond to increased model fit. In each round, the variable
627 that increased model the most was retained, and then the process was repeated, until no
628 variables improved the model by decreasing Δ DIC by more than -2. Variables that were
629 retained in each round are highlighted by asterisks.

630

631

PARASITE	ROUND	VARIABLE	DELTA	KEPT
FLEAS	1	Degree	1.835	0
	1	GroupSize	1.251	0
	1	**LifetimeDensity**	-8.444	1
	1	TrappingDensity	1.509	0
	1	AnnualDensity	-4.549	0
LICE	1	**Degree**	-2.388	1
	1	GroupSize	1.747	0
	1	LifetimeDensity	1.332	0
	1	TrappingDensity	1.943	0
	1	AnnualDensity	0.944	0
TICKS	1	Degree	1.93	0
	1	GroupSize	-12.573	0
	1	LifetimeDensity	-5.864	0
	1	TrappingDensity	1.2	0
	1	**AnnualDensity**	-14.067	1
EIMERIA	1	Degree	14.117	0
	1	GroupSize	1.964	0
	1	LifetimeDensity	1.817	0
	1	TrappingDensity	-0.283	0
	1	AnnualDensity	1.237	0
ISOSPORA	1	Degree	1.569	0
	1	GroupSize	0.882	0

	1	LifetimeDensity	1.9	0
	1	TrappingDensity	1.65	0
	1	AnnualDensity	1.8	0

632

633 Table SI2: DIC Changes (Δ DIC) associated with density measure model addition for the
634 adults-only models. Negative Δ DIC values correspond to increased model fit. In each round,
635 the variable that increased model the most was retained, and then the process was repeated,
636 until no variables improved the model by decreasing Δ DIC by more than -2. Variables that
637 were retained in each round are highlighted by asterisks.

638

639

PARASITE	ROUND	VARIABLE	DELTA	KEPT
FLEAS	1	Degree	0.985	0
	1	GroupSize	-2.362	0
	1	**LifetimeDensity**	-15.209	1
	1	TrappingDensity	1.337	0
	1	AnnualDensity	-10.016	0
LICE	1	Degree	-2.862	0
	1	GroupSize	1.747	0
	1	LifetimeDensity	-3.907	0
	1	**TrappingDensity**	-8.087	1
	1	AnnualDensity	-2.572	0
TICKS	1	Degree	1.602	0
	1	GroupSize	0.462	0
	1	LifetimeDensity	-0.244	0
	1	TrappingDensity	0.918	0
	1	AnnualDensity	-0.459	0
EIMERIA	1	Degree	1.42	0
	1	GroupSize	1.067	0
	1	LifetimeDensity	-0.127	0
	1	**TrappingDensity**	-7.465	1
	1	AnnualDensity	-0.945	0
ISOSPORA	1	Degree	1.73	0
	1	GroupSize	1.096	0

	1	LifetimeDensity	1.775	0
	1	TrappingDensity	1.567	0
	1	AnnualDensity	1.709	0

640

641 Table SI3: DIC Changes (Δ DIC) associated with density measure model addition for the
642 juvenile-only models. Negative Δ DIC values correspond to increased model fit. In each
643 round, the variable that increased model the most was retained, and then the process was
644 repeated, until no variables improved the model by decreasing Δ DIC by more than -2.
645 Variables that were retained in each round are highlighted by asterisks.

646

647