Negative density-dependent parasitism in a group-living carnivore

Gregory F Albery*[1], Chris Newman[2], Julius G Bright Ross[2], David W Macdonald[2], Shweta Bansal[1], Christina D Buesching[2]

1. Department of Biology, Georgetown University, Washington, DC, USA
2. Wildlife Conservation Research Unit, The Recanati-Kaplan Centre, Department of Zoology, University of Oxford, Oxford, U.K.

*Corresponding author: gfalbery@gmail.com

Animals living at high population densities are expected to experience greater exposure to disease, leading to greater parasite burdens. However, social animals can accrue immunological and hygienic benefits from group living, and individuals can often minimise exposure using avoidance behaviours, so the costs and benefits of sociality for disease are often uncertain. Here, we show in wild European badgers that population density was negatively correlated with infection with three arthropod ectoparasites and one gastrointestinal protozoan, despite highly contrasting spatial distributions among parasites. Combined survival, spatial, and social network analyses suggested that parasite avoidance was the likely cause of this negative density-dependence. These findings demonstrate that animals can organise their societies in space to minimise infection, providing evidence for a "landscape of disgust".

Understanding the relationships between parasite infection and host density is fundamental to disease ecology (*1*, *2*) and can help understanding the risk factors for zoonotic spillover (*3*–*6*). In wild animals, as in humans, greater population density should produce higher contact rates, resulting in greater exposure and increased parasitism (*2*, *7*, *8*). However, several mechanisms can counteract sociality-associated disease risk. First, individuals can minimise exposure by avoiding environmental cues (*9*, *10*) or infected conspecifics (*11*), so the spatial distribution of disease may create a population-level "landscape of disgust" just as predators create a "landscape of fear" (*12*, *13*). Second, individuals can upregulate immune defence in anticipation of exposure, e.g. when in the presence of (infected) conspecifics (*14*, *15*). Third, sociality has numerous immunological and hygienic benefits, all of which can reduce the burden or prevalence of disease (*16*, *17*). These individual- and population-level processes can complicate parasites' relationships with population density. As yet, most evidence for social density effects on parasite infection is based on meta-analyses and cross-species comparisons (*2*, *7*, *8*), and empirical support for landscapes of disgust is scarce (*12*, *13*).

Here, we quantified within-population density-dependence of parasite counts in a wild population of European badgers (*Meles meles*). In this population, which has been studied continuously since 1987 (*18*, *19*), dens (termed "setts") are situated dependent on soil type and landscape topography (*20*). Badgers reside in cohesive groups, but are socially fluid, with >20% of individuals trapped at different setts between captures (*21*). Setts act as refuges for parasites (*22*), and individual badgers respond behaviourally to infection by moving between setts (*23*). Previous work has established that badger sociality has a complex, nonlinear relationship with disease (*24–26*). Wytham badgers host several arthropod parasites, including badger-specific fleas (*Paraceras melis*) and lice (*Trichodectes melis*) and generalist ticks (*Ixodes* sp.) (*22*). They also carry two badger-specific gastrointestinal protozoans: *Eimeria melis* and *Isospora melis* (*27*). All these exhibit a combination of direct (contact-driven) and indirect (environmentally latent) transmission except *I. melis*, which employs a paratenic host. Although studies have examined social grooming effects on ectoparasite burden (*28*) and role of denning behaviours in parasite transmission (*22*), the within-population socio-spatial epidemiology of the parasites remains to be investigated.

Spatial Integrated Nested Laplace Approximation (INLA) models revealed that all parasites but *I. melis* exhibited strong spatial patterns (ΔDIC<-8.2; Figure 1; Table SI1). Parasites' distributions differed substantially, implying different biotic and abiotic drivers (Figure 1); setts' variable microclimates (*29*) might alter their suitability for maintaining and transmitting parasites, producing the observed patterns. As increased exposure from sociality could also explain the spatial patterns (*2*, *7*, *8*), we tested whether parasite burdens correlated with social metrics. Contrary to expectations, all four spatially distributed parasites were negatively associated with local population density (Figure 1). Slopes were shallow but robust and significant. Higher local badger density was associated with decreased flea count (ΔDIC=-16.3; P<0.0001), tick prevalence (ΔDIC=-2.47; P=0.0038), and *E. melis* prevalence (ΔDIC=-5.83; P=0.0053) across the whole population, and with lower louse count in juveniles (ΔDIC=-8.77; P=0.0017).

We considered multiple possible explanations for this negative relationship between parasitism and density, most of which we rejected (Table 1). First, group-living animals may experience benefits of cooperation or cohabitation such as improved resource acquisition (*30*, *31*). We discounted this possibility for two reasons: because badgers forage independently and collaborate little (*18*), and because body condition was accounted for in the models (Figure SI1), so improved nutrition or generalized immune benefits were unlikely. Second, individuals may be groomed by conspecifics, reducing their parasite burdens more in high-density areas (*28*). We discounted this mechanism because "direct" social metrics such as co-trapping network centrality and social group size had no detectable effects on parasitism (Table SI2-3), so the drivers of the negative density correlations were likely more spatial than social. Allogrooming is also fundamentally unable to explain lower *Eimeria* prevalence. Finally, individuals living in highly parasitized areas may suffer increased parasite-associated mortality, reducing density in these areas (*32*). In our dataset, only lice had a (weak) detectable effect on survival (Figure 3), so localised mortality could not explain three out of four parasite-density relationships. After rejecting these mechanisms, spatial avoidance was the most parsimonious explanation for the negative relationships with density (Table 1).

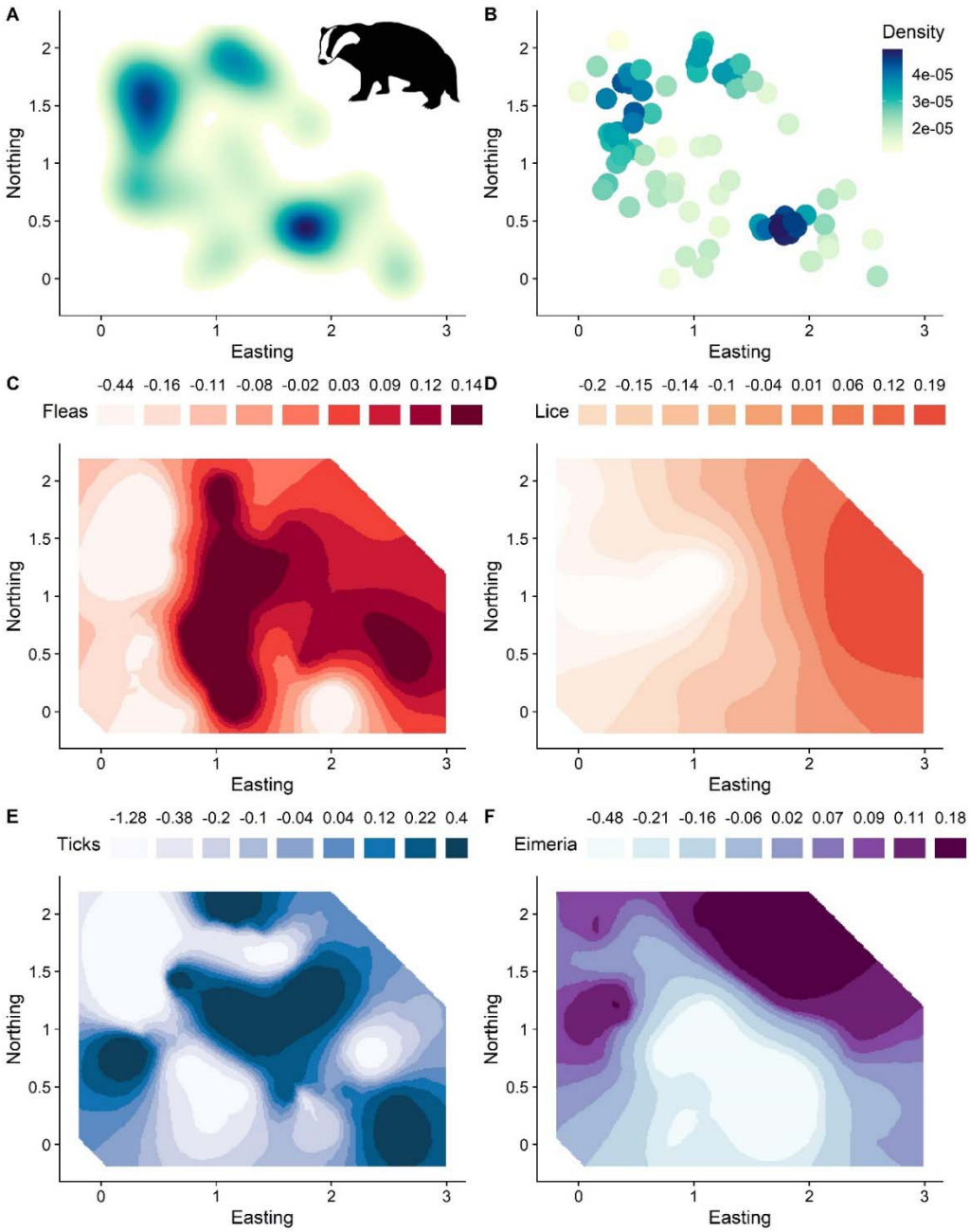

Figure 1: Spatial distributions of badger population density and parasites in Wytham Woods, Oxfordshire, between 1989 and 2018. A: badger population density distributed across Wytham Woods, calculated based on a space use kernel for individuals' annual centroids. B: Individual badgers trapped at setts (represented by points) were assigned a local density value based on their location on the rasterised space use kernel. Darker blue colours in A and B correspond to greater population density. C-F: the spatial distribution of the four spatially distributed parasites, estimated using the INLA SPDE effect. Darker colours correspond to increased parasitism. The density values in B were fitted as covariates in linear models to explain individual parasite burdens, revealing a negative correlation between density and parasitism (see Figure 2). All axes are in kilometres.

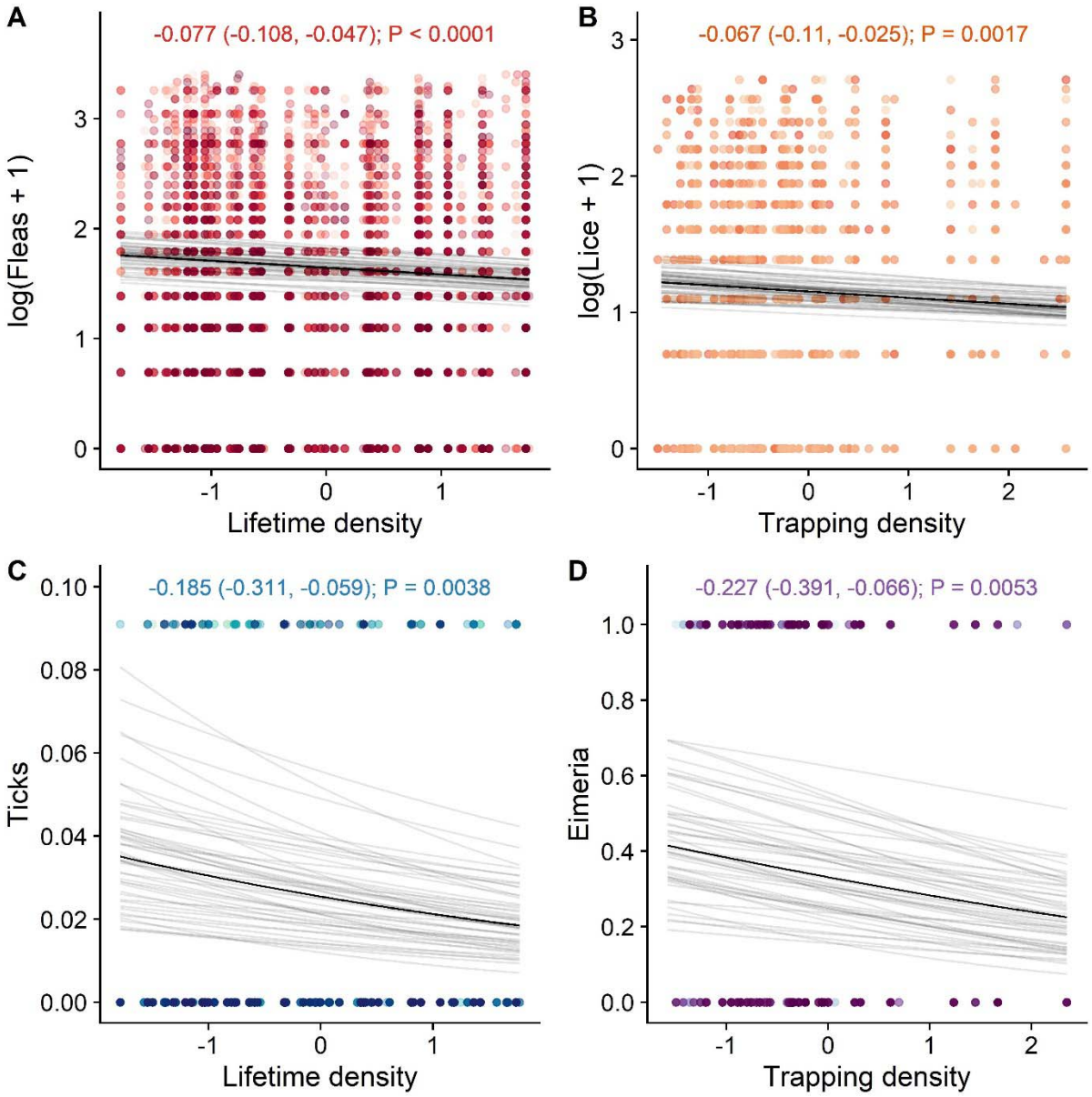

Figure 2: Negative associations between population density and parasite infection. Badgers living at higher densities had fewer fleas (A), fewer lice (B), lower tick prevalence (C), and lower *Eimeria melis* prevalence (D). B represents juveniles only. Points represent individual samples (N=8270), with colours randomised along a colour palette for plotting clarity. Opaque black lines are derived from linear model fits, taking the mean of the posterior distribution. Transparent grey lines represent 100 fits drawn randomly from the posterior estimate distributions of each model, to demonstrate error in the slope and intercepts. Text at the top of the figures communicates slope estimates, with lower and upper 95% credibility intervals in brackets, and P values. NB: in panel C, the y axis scale and the location of the positive points have been altered for plotting clarity and to better visualise the slope, due to low tick prevalence.

If density-parasite covariance is detectable at the within-individual level, it could indicate social ostracism or altruistic self-removal of highly parasitized individuals, both of which have been reported in social animals (*33*, *34*). We therefore used multi-response mixed-effects models to estimate the covariance between density and parasitism when accounting for fixed effects, and to decompose within- and between-individual covariance. All four parasites exhibited substantial between-individual covariance with density, and little within-individual covariance (Figure 3B). This finding reinforces the understanding that badgers occupy ranges with inherently different local densities and concordant parasite loads, rather than moving to areas of different densities over the course of their lives according to their parasite burden. As such, we uncovered no evidence for ostracism or self-removal in the badger population. After eliminating the competing hypotheses, we concluded that previously reported individual-level parasite avoidance behaviours (*23*) magnify at the population level to produce negative parasite-density correlations, where most badgers prefer to inhabit setts in areas that are poorly suited to parasite survival and transmission, and those that do not/cannot do so suffer increased burdens.

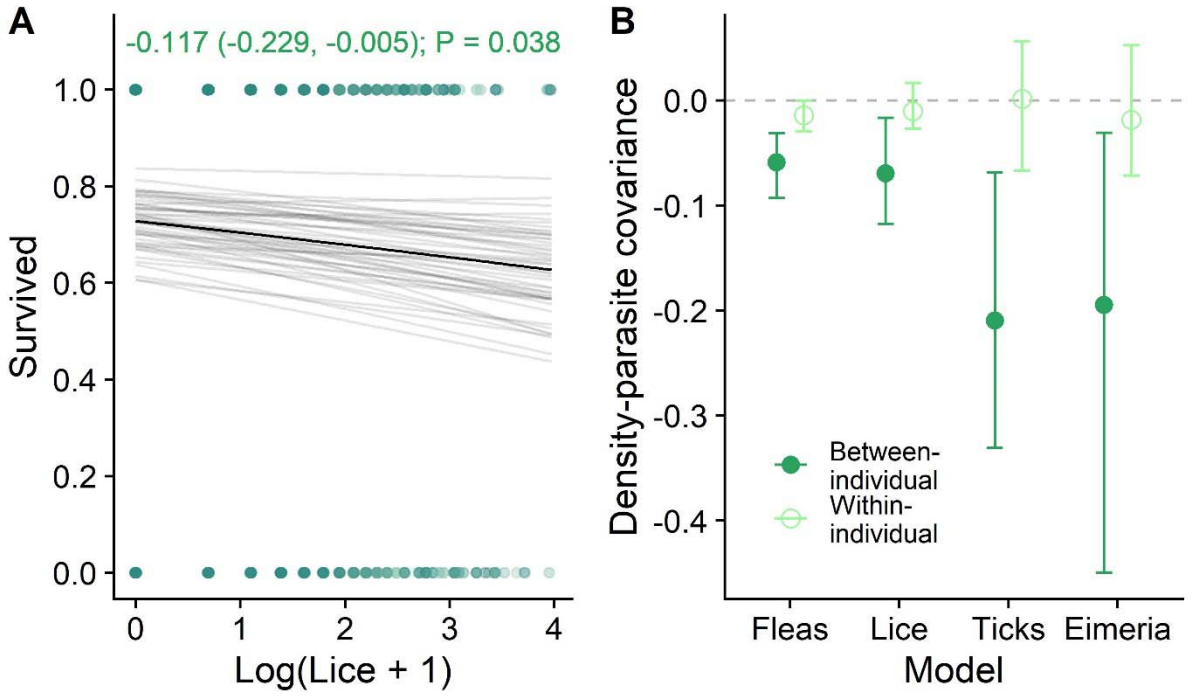

Figure 3: Associations of parasitism with survival and density-parasitism covariance partitioning. A) Louse burden was negatively associated with individual survival probability in juveniles. Opaque black line=linear model fit. Transparent grey lines=100 fits drawn randomly from the posterior estimate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

Potential mechanism	Conclusion	Reason for conclusion
Co-habitation/ cooperation benefits	No	No direct social effects or body condition effects
Allo-grooming	No	No direct social effects; grooming not possible for endoparasites
Nutrition-associated immune benefits	No	No body condition effects
Local host die-offs	No	Survival associations only discovered for lice
Social ostracism/self-isolation	No	Low within-individual covariance
Avoidance	Yes	All other possibilities eliminated; consistent with individual-level behavioural responses

Table 1: Reasoning surrounding our hypothesis testing. We rejected all hypotheses for our observed negative density effects other than parasite avoidance.

Although disease-induced "landscapes of disgust" are well-theorized (*10*, *12*, *13*), evidence for parasite avoidance in wild mammals has thus far been restricted to short-term avoidance of faeces (*9*, *35*), corpses (*36*), or conspecifics themselves (*11*). We show that badgers enduringly structure their society according to parasitism, congregating in areas of lower infection. This effect contrasts with the more common expectation that sociality will exacerbate parasitism by increasing exposure (*2*, *7*, *8*), and implies that socio-spatial structuring may allow group-living organisms to evade or reduce the harmful disease-related implications of increased social contacts. The same is likely true of human populations. The examined parasites all exhibit a combination of direct (contact-driven) and indirect (environmentally latent) transmission modes; future studies of additional pathogens such as sexually transmitted infections may reveal whether the badgers are similarly able to avoid more direct or frequency-dependent parasites. Our study identified simultaneous avoidance of multiple parasites with contrasting spatial distributions; this might facilitate their coexistence across the population, while maintaining between-individual immune heterogeneity (*13*). These findings emphasise the importance of considering individual behavioural immunity and emergent socio-spatial structuring when investigating the costs and benefits of sociality empirically, and when incorporating density into epidemiological models.

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Methods

Data collection

Population sampling

Code and data for our analyses are available a https://github.com/gfalbery/Badgeworks. Badgers were sampled as part of a long-term study in Wytham Woods, Oxfordshire, UK (51.778°N, 1.313°W), established in 1987 and recording one of the highest local badger densities ever reported (*1*). A full description of the project is given by Macdonald, Newman, & Buesching (*2*). Badgers were trapped overnight at their dens ("setts") in steel-mesh cages baited with peanuts, and collected the next morning. They were transported to a handling facility in holding cages and sedated in turn via intramuscular injection of ketamine hydrochloride at 0.2ml per kg bodyweight. Once sedated, badgers were individually identified by a tattoo applied on first trapping (typically as cubs), then measures were taken of head-body length (mm) and weight (to the nearest 0.1kg), *inter alia*. We calculated a standardised index of body condition by dividing log(weight) by log(body length). The site was trapped seasonally (winter: Jan/ Feb/ March; spring: April/ May/ June; summer: July/ Aug/ Sept; autumn: Oct/ Nov/ Dec) in 4 quadrants, for 3 days per quadrant. Our dataset included 9016 captures of 1369 badgers, trapped over 29 years (1990-2018).

The population currently comprises 23 social groups (mean group size=11; range 2-29 individuals). Social groups generally comprise more than one sett, with the affiliation of setts to groups established via baitmarking to identify social group range borders (*3*, *4*). Badgers were assigned to groups using a set of established residency rules (*5*). 16.4% of individuals are commonly trapped at a different social group to their previous capture history and 19.8% away from their natal group, although 35.8% are never caught away from their natal group (*6*). Furthermore, 48% of cubs have extra-group paternity, according to a genetic pedigree (*5*). We computed social networks based on co-trapping using a "gambit of the group" approach based on co-trapping events, where individuals that were trapped in the same sett in the same year were assumed to have interacted (*7*).

Ectoparasite counts included fleas (*Paraceras melis*), lice (*Trichodectes melis*), and ticks (*Ixodes* sp.). They were counted throughout the study period (N=8270). Fleas were counted during a stereotyped 20-second inspection of the badger's full body, and ticks and lice were counted by inspecting a 4x4cm square of heavily parasitised skin near the groin (per Cox *et al.* 1999). Faecal sampling for endoparasites was carried out during two main periods: 1993-1997 and 2009-2017 (N=1287 counts). Faecal samples were induced using a soapy enema, collected in plastic pots and mixed with 2.5% aqueous potassium dichromate as preservative, leaving parasitic eggs and oocysts intact, and stored at 4°C. We examined these samples for two protozoan parasites: *Eimeria melis* and *Isospora melis* (henceforth referred to as *Eimeria* and *Isospora*, respectively). Endoparasite prevalence was measured using a salt flotation technique (*9*, *10*). Faecal samples were homogenised and mixed with a 1:9 saturated salt solution. Parasites adherent to a cover-slip after five minutes were then examined and counted under a McMaster microscope slide to quantify parasite burden. Each count was duplicated, and the data were reduced to a binary infected/uninfected status (rather than counts) because of their highly overdispersed distribution.

Statistical Analysis

Covariates

Statistical analysis and data manipulation were carried out in R version 3.6.0 (*11*). Models were constructed using the `inla` package (*12*, *13*). Our five response variables included counts of fleas and lice (negative binomial distribution) and prevalence of ticks, *Eimeria*, and *Isospora*. Explanatory covariates included: Year (continuous); Month (categorical); Age Category (categorical: cub, yearling, and adult); Sex (male and female); and Body Condition (continuous). In these and all other models, all continuous covariates were scaled to have a mean of zero and a standard deviation of one before fitting. Individual Identity and Year were also fitted throughout as categorical random effects.

1. Spatiotemporal models

We first fitted models that accounted for continuous spatial autocorrelation in parasitism across the population, to identify generalised spatial patterns and to quantify their temporal consistency (*12–14*). We fitted a base model with only the base covariates (Year, Month, Age Category, Sex) and individual and annual random effects. We then added an SPDE random effect, which

controls for spatial autocorrelation in the response variable in space. This SPDE model was then compared with the base model to investigate whether accounting for spatial autocorrelation improves model fit. We used Deviance Information Criterion (DIC) as a measure of model fit, where models within 2 ΔDIC were deemed competitive.

2. Density models

We then fitted models that replaced the SPDE effects with individual measures of local population density (see below). We incorporated these effects without the SPDE effect because, being spatially heterogeneous, they might compete with the spatial autocorrelation terms, providing an inaccurate picture of population density effects (*15*). Our models included a range of social/spatial density measures, calculated using a combination of different methods. Spatial density metrics are representations of the numbers of individuals in a given space, and therefore tread the line between social and spatial behavioural traits. We computed these by creating space use distribution kernels with the `adehabitathr` package in R (*16*). We rasterised the usage distribution, and then assigned each individual a local density based on the raster value for their location on the map (Figure 1). These measures included: 1) **Lifetime density**: the density of individuals' annual centroids across the study period, preventing repeat inclusion of individuals in a given year. 2) **Trapping density**: the density of trapping events, incorporating multiple captures of the same individual in a given year. 3) **Annual density**: the density of individuals' centroids in the year of sampling, calculated from annual density kernels. Only one spatial density measure was allowed in a given model, as the measures were all well-correlated (R>0.5) and fitting several measures in the same model produced spurious, unexpected correlations in the opposite direction to that expected from data exploration. We also used two social metrics based on co-trapping patterns. **Degree centrality** was the number of unique badgers that a given individual was trapped in the same sett as in a given year. **Group size** was the total number of individuals trapped in a given social group in a given year. Following the methods used for the spatial autocorrelation models, we conducted a model selection procedure for the behavioural metrics, using 2 ΔDIC as the cut off.

P values were calculated for the social/spatial fixed effects by drawing values 100,000 times from the posterior estimate distribution and investigating what proportion of estimates overlapped with zero and multiplying it by two, per a two-tailed test (i.e., if 2.5% of values were

above zero and the rest were not, the P value would be 0.05 (*17*). We conducted these models for four datasets: the overall dataset (N=9016); adults only, fitting age in years as a fixed covariate (age 2+; N=6159); and cubs only (N=1639).

3. Multi-response models

To investigate whether parasites were associated with variation in badger density across the population at the within- or between-individual level, we constructed multi-response models in MCMCglmm with an unstructured covariance matrix (*18*, *19*). This model formulation fitted both parasites and local density as response variables, so that their covariance could be estimated when accounting for other fixed effects and decomposed at the within- and between-individual level. A negative within-individual (residual) correlation between density and parasites could imply that individuals with higher burden or prevalence (compared to their baseline) moved to lower density areas during their lives, supporting gradual social ostracism, or sickness behaviours. In contrast, negative between-individual covariance would imply that individuals inhabiting lower densities generally had inherently greater parasitism. We only constructed these models for the parasite-host age category combinations that demonstrated density effects in our main INLA models.

4. Survival models

To investigate whether parasites were associated with host mortality, we fitted models with survival as a binary response variable. Survival was scored as a 1 if the animal was seen in any subsequent year, or as a 0 if it was not (i.e., if the focal year was the last capture year of that individual). The models included the same covariates as the parasite models, plus parasite prevalence/burden and badger density measures. Parasite measures were either continuous and log-transformed (fleas, lice) or binary (ticks, *Eimeria*, and *Isospora*). We conducted another model selection procedure, adding parasite or density metrics successively if they improved model fit, and only allowing one best-fitting spatial density measure. This exercise was carried out for adults and cubs separately.

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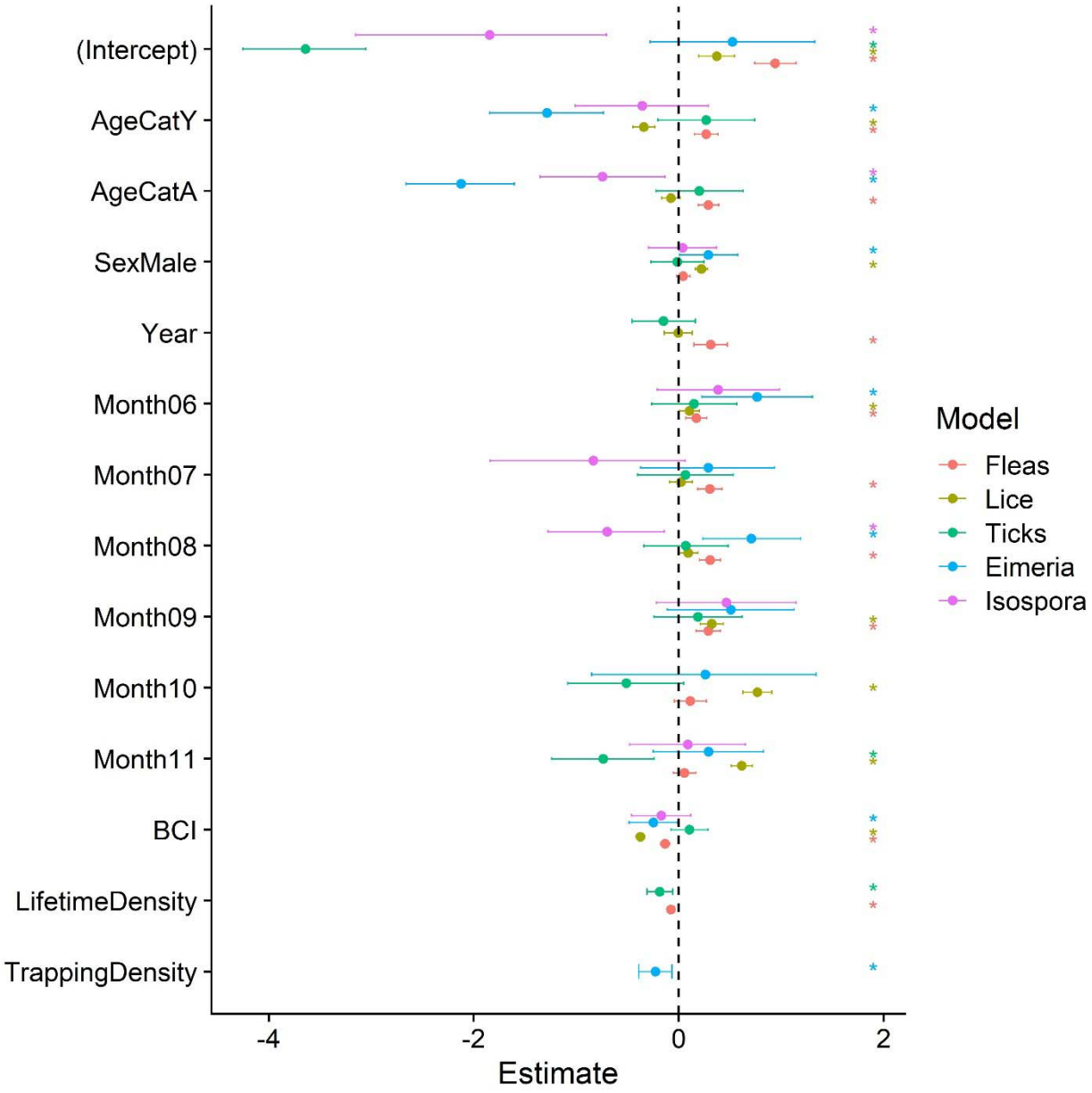
Supplement: Negative density-dependent parasitism in a group-living carnivore

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

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



Supplementary Figure 1: Model effect outputs for the full dataset INLA density models. Points represent modes of the posterior distribution of the effect estimates; error bars represent the 95% credibility intervals. Asterisks denote significant results, whose 95% credibility intervals did not overlap with zero. Only the behavioural traits that improved the model fit (DeltaDIC<-2) and were kept in the final model are shown.

	Round	Variable	Delta	Kept
Fleas	1	Degree	2.027351	0
	1	GroupSize	1.640061	0
	1	*LifetimeDensity*	-16.3195	1
	1	TrappingDensity	1.080452	0
	1	AnnualDensity	-8.01928	0
	1	PopN	0.039209	0
	2	Degree	0.962656	0
	2	GroupSize	1.818357	0
	2	PopN	0.042724	0
Lice	1	Degree	1.733585	0
	1	GroupSize	1.730202	0
	1	LifetimeDensity	1.694362	0
	1	TrappingDensity	0.144866	0
	1	AnnualDensity	1.590572	0
	1	PopN	-0.45812	0
Ticks	1	Degree	0.595885	0
	1	GroupSize	3.39051	0
	1	*LifetimeDensity*	-2.47157	1
	1	TrappingDensity	0.751509	0
	1	AnnualDensity	-0.69739	0

	1	PopN	-1.3643	0
	2	Degree	-0.30384	0
	2	GroupSize	3.616796	0
	2	PopN	-1.14286	0
Eimeria	1	Degree	1.084996	0
	1	GroupSize	1.805727	0
	1	LifetimeDensity	1.163577	0
	1	*TrappingDensity*	-5.8299	1
	1	AnnualDensity	1.845523	0
	1	PopN	0.218567	0
	2	Degree	1.919633	0
	2	GroupSize	1.233882	0
	2	PopN	0.138332	0
Isospora	1	Degree	1.883396	0
	1	GroupSize	1.857583	0
	1	LifetimeDensity	1.867343	0
	1	TrappingDensity	1.492772	0
	1	AnnualDensity	1.701301	0
	1	PopN	-0.83121	0

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

	Round	Variable	Delta	Kept
Fleas	1	Degree	1.002167	0
	1	GroupSize	-2.32199	0
	1	*LifetimeDensity*	-15.1643	1
	1	TrappingDensity	1.331664	0
	1	AnnualDensity	-9.92206	0
	1	PopN	-0.77113	0
	2	Degree	1.613645	0
	2	GroupSize	1.661839	0
	2	PopN	-0.59538	0
Lice	1	Degree	-3.42159	0
	1	GroupSize	1.116333	0
	1	LifetimeDensity	-4.28759	0
	1	*TrappingDensity*	-8.77296	1
	1	AnnualDensity	-2.73243	0
	1	PopN	-0.57475	0
	2	Degree	1.171586	0

	2	GroupSize	1.853335	0
	2	PopN	-0.31734	0
Ticks	1	Degree	1.558359	0
	1	GroupSize	0.552836	0
	1	LifetimeDensity	-0.23012	0
	1	TrappingDensity	0.966616	0
	1	AnnualDensity	-0.41961	0
	1	*PopN*	-3.74127	1
	2	Degree	1.192264	0
	2	GroupSize	1.322215	0
	2	LifetimeDensity	-1.50327	0
	2	TrappingDensity	0.090169	0
	2	AnnualDensity	-0.2454	0
Eimeria	1	Degree	1.258817	0
	1	GroupSize	0.755473	0
	1	LifetimeDensity	0.024514	0
	1	*TrappingDensity*	-7.72854	1
	1	AnnualDensity	-0.98835	0
	1	PopN	0.201886	0
	2	Degree	1.301408	0
	2	GroupSize	1.541995	0

	2	PopN	0.21748	0
Isospora	1	Degree	1.714806	0
	1	GroupSize	1.210279	0
	1	LifetimeDensity	1.772975	0
	1	TrappingDensity	1.533789	0
	1	AnnualDensity	1.70609	0
	1	PopN	-0.50035	0

Table 3: DIC Changes associated with density measure model addition for the juvenile models. Negative Delta-DIC values correspond to increased model fit. In each round, the variable that increased model the most was retained, and then the process was repeated, until no variables improved the model by decreasing Delta-DIC by more than -2. Variables that were retained are highlighted by asterisks.