

# Disease-Dependent Social Responses to Local Disease Composition in a Wild Reptile

Authors: Felix Requena-Garcia<sup>1\*</sup>, Nicola Jackson<sup>1</sup>, Angela C. Mitchell<sup>1</sup>, and Celine H. Frere<sup>1</sup>

<sup>1</sup> School of the Environment, The University of Queensland, St Lucia, QLD 4067, Australia

\*Corresponding author: [felix.requena.garcia@gmail.com](mailto:felix.requena.garcia@gmail.com)

## Abstract

Emerging infectious diseases can generate persistent and locally heterogeneous patterns of risk across animal populations, yet how animal social behaviour varies under these conditions remains poorly understood. When pathogens persist in the environment, individuals may need to respond to disease conditions at fine spatial and temporal scales rather than rely on fixed social strategies. Here, we examine how individual disease status and local conditions relate to social behaviour in a free-ranging population of eastern water dragons (*Intellagama lesueurii*) affected by the fungal pathogen *Nannizziopsis barbatae* (Nb). Using 16,855 sightings of 201 individually identified lizards collected between 2018 and 2023, we quantified gregariousness at each observation and tested how it varied with local conspecific abundance, local disease composition, and individual disease status. Gregariousness increased strongly with local conspecific abundance and varied with local disease composition according to individual disease status. Among diseased individuals, gregariousness decreased with increasing local disease composition, whereas healthy individuals showed no clear relationship across the same gradient. Together, these findings suggest that social behaviour under persistent fungal disease pressure varies with fine-scale local conditions and individual disease status, highlighting the context-dependent nature of social behaviour in wildlife disease systems.

## Introduction

Infectious diseases are widespread in the environments in which animals live and evolve [1, 2]. This is particularly evident for emerging infectious fungal diseases, as many fungal pathogens can persist in the environment independently of their hosts [3]. As a result, infection risk can be persistent rather

25 than limited to discrete transmission events, posing increasing threats to biodiversity, particularly  
26 among amphibians, bats, and reptiles [4-10]. The environmental persistence and dispersal of fungal  
27 propagules, including spores, can contribute to spatially heterogeneous pathogen distributions shaped  
28 by environmental conditions and pathogen-specific traits [4, 9]. Consequently, animals may  
29 experience sustained and locally variable infection risk [11]. While disease exposure can elicit  
30 behavioural responses, local variation in disease risk may shape how such responses are expressed  
31 across an individual's immediate environment [8, 12].

32 Social behaviour is highly plastic, with individuals adjusting their interactions in response to internal  
33 conditions and environmental cues [13-15]. Although sociality provides benefits such as information  
34 sharing and reduced predation risk [16, 17], it can also increase exposure to pathogens [18].  
35 Behavioural plasticity may therefore play an important role in mediating disease transmission, but the  
36 nature of these responses likely depends on the mode of transmission [19]. For directly transmitted  
37 pathogens, individuals may reduce infection risk by avoiding close contact with infected conspecifics,  
38 whereas for indirectly transmitted pathogens, behavioural responses may also involve avoidance of  
39 contaminated environments [20, 21]. This trade-off between social benefits and infection risk is  
40 inherently context-dependent [22]. Despite its ecological importance, context-dependent behavioural  
41 responses under persistent disease pressure remain poorly understood, particularly in wild populations  
42 affected by fungal infections [23].

43 Behavioural responses to disease are often considered in the context of sickness behaviour, including  
44 reduced activity, lethargy, or social withdrawal in diseased individuals [24, 25]. However, behavioural  
45 adjustment is not restricted to diseased animals; healthy individuals may also modify their social  
46 behaviour in environments with elevated disease risk to reduce the likelihood of infection [1, 20, 26].  
47 Such responses may be particularly important when disease conditions vary through time and space  
48 [11]. Studies based on broad comparisons between infected and uninfected individuals may therefore  
49 provide limited insight into how behavioural responses are shaped by local variation in disease risk.

50 Large-scale studies of sociality and disease have revealed general patterns across wildlife systems,  
51 including density- and disease-context-dependent behavioural variation in eastern water dragons and  
52 other species [27, 28]. However, these approaches often characterise broader patterns of social  
53 organisation and may overlook short-term behavioural responses to immediate environmental  
54 conditions. In systems with spatially heterogeneous disease risk, social behaviour may vary with local  
55 density and features of the social environment that influence exposure risk [29, 30]. For example, in  
56 domestic lambs, infected individuals reduced their contact frequency following infection, while non-  
57 infected lambs maintained their interactions with infected conspecifics, showing that behavioural  
58 responses depended on the infection status of conspecifics within the group [31]. Examining behaviour  
59 at this fine scale is therefore important for understanding how animals balance the costs and benefits  
60 of sociality under persistent disease pressure.

61 Here, we address this gap using long-term behavioural data from a free-ranging population of eastern  
62 water dragons inhabiting Roma Street Parklands in Brisbane, Australia. This population has been  
63 monitored since 2010, providing a rare opportunity to examine individual behaviour in a spatially  
64 structured wild population [13, 14, 32-34]. Since 2013, the population has experienced a sustained  
65 outbreak of *Nannizziopsis barbatae* (*Nb*), a fungal pathogen that causes both sublethal and lethal  
66 effects [6-8, 12]. Transmission is primarily indirect, with the pathogen persisting in the environment  
67 [8], although individuals may avoid severely diseased conspecifics [12] and show density-dependent  
68 behavioural patterns associated with variation in their broad-scale social environment [27]. However,  
69 because the pathogen persists in the environment, it remains difficult to determine how individuals  
70 adjust their social behaviour in relation to fine-scale variation in local disease composition.

71 We hypothesise that eastern water dragon gregariousness does not vary solely with the presence of  
72 visibly diseased individuals, but also with variation in the number of diseased conspecifics in the social  
73 environment, which we refer to as local disease composition. Specifically, we predict that variation in  
74 gregariousness associated with disease status is strongest in areas with more diseased conspecifics,

75 where individuals must balance the benefits of social aggregation against the risk of infection.  
76 Accordingly, we ask (i) whether gregariousness varies with local crowding and local disease  
77 composition, and (ii) whether responses to local disease composition differ according to focal  
78 individual disease status. By analysing behaviour at the level of individual sightings, we quantify  
79 repeated behavioural variation across varying local conditions.

## 80 **Methods**

### 81 *Study population*

82 The study focused on a population of eastern water dragons inhabiting Roma Street Parklands in  
83 Brisbane, Australia (27°27'46'S, 153°1'11'E), with an estimated population size of 336 individuals [34-  
84 36]. The 16-hectare park features a mosaic of vegetation patches and water sources, bordered by roads  
85 and urban infrastructure [37]. Data were collected between September 2018 and April 2023,  
86 encompassing the period during which the population was actively monitored for disease status.  
87 Surveys were conducted during peak activity seasons, when individuals were most likely to be detected  
88 [32, 35, 36, 38, 39]. Dragons, especially males, commonly engage in agonistic encounters and show  
89 both overlapping space use and strong fidelity to specific sites [36, 40, 41]. Individuals in this  
90 population are highly habituated to human presence [34], allowing behavioural observations to be  
91 conducted at relatively close range. Observers approached individuals slowly before recording  
92 behavioural observations and measurements.

### 93 *Data collection*

94 During the study period, behavioural surveys were conducted three days per week from September to  
95 April each year [13, 34]. The survey transects covered approximately 85% of the known population  
96 [35]. Surveys were conducted between 07:30 and 10:30 in the morning and 1:00 and 4:00 p.m. A  
97 GARMIN eTrex10 handheld GPS device was used to record individual locations for subsequent  
98 behavioural analysis [37, 38]. Following established protocols, left and/or right facial profile

99 photographs were taken using a Canon EOS 600 digital camera. Individuals were identified using I3S  
100 Manta software based on their unique head scale patterns and colouration, with manual validation to  
101 ensure identification accuracy [35, 42].

102 Because social behaviour differs between juveniles and adults of eastern water dragons, only adult  
103 individuals were included in this study [33]. Individuals were classified as adults based on a  
104 combination of morphological characteristics, including the length and shape of head-crest spikes,  
105 colouration patterns between the eye and ear, eye size, and presence of scars or missing spikes on the  
106 head crest [12]. We additionally classified individuals with a snout–vent length (SVL)  $\geq 150$  mm as  
107 adults, following the operational classification used by Becker, Albery [8]. Sex was determined from  
108 sexual dichromatism and secondary sexual characteristics, including body size, head morphology and  
109 ventral colouration [35, 36].

#### 110 *Disease status determination*

111 Most individuals were captured up to twice per year for disease monitoring between 2018 and 2023,  
112 during March–April and September–October, using a handheld lasso in Roma Street Parklands [38,  
113 43]. Individuals were visually inspected for signs of *Nb* infection, with suspected cases identified by  
114 the presence of yellowish-brown crusted skin lesions [6-8, 12].

115 All captured individuals were skin swabbed using sterile saline-moistened swabs, which were applied  
116 for up to 30 seconds to both lesioned and non-lesioned skin. Samples were analysed using quantitative  
117 PCR (qPCR) targeting *Nb* DNA [44]. DNA was extracted from skin swabs using DNeasy Plant Pro  
118 kits (Qiagen, Hilden, Germany). The presence of *Nb* was assessed using a species-specific qPCR assay  
119 following Powell, Schwessinger [44]. Reactions were performed using primers 5'-  
120 TGATCATGTTTAGTCTCTGAAGGT-3' (forward) and 5'-AGGCTAAGCTGATTTGGTCTC-3'  
121 (reverse), along with a fluorescent probe. Each reaction contained 10  $\mu$ l of 2  $\times$  GoTaq Enviro Mix  
122 (Promega), 0.4  $\mu$ M of each primer, 0.1  $\mu$ M probe, and 2  $\mu$ l of template DNA, brought to a total volume

123 of 20 µl with molecular-grade water. All qPCR reactions were run in duplicate, and positive and non-  
124 template controls were included in all runs under the following thermocycling conditions: an initial  
125 denaturation at 95 °C for 5 min, followed by 40 cycles of 95 °C for 20 s and 63 °C for 30 s. Samples  
126 were considered positive when amplification crossed the cycle threshold (Ct) in at least one of the two  
127 replicates, as determined using CFX96 Manager software (Bio-Rad Laboratories, Hercules, CA,  
128 USA).

129 Disease status was evaluated using a combination of visual inspection during captures and molecular  
130 diagnostics. Diseased individuals were defined as those with both a positive qPCR result and visible  
131 signs of *Nb* infection, such as skin lesions or discolouration. Healthy individuals showed no visible  
132 lesions and tested negative for *Nb* by qPCR [7, 12]. Individuals that tested positive for *Nb* but showed  
133 no visible clinical signs were classified as asymptomatic. The biological significance of this state  
134 remains uncertain, and may, among other possibilities, reflect infections that have not yet progressed  
135 to clinically apparent disease [45]. Consequently, these individuals could not be reliably categorised  
136 as either healthy or diseased for behavioural comparisons. Previous work in this population considered  
137 capture-based disease status to reflect behavioural observations collected around capture events  
138 because clinical *Nb* disease progresses slowly and there is limited evidence that associated lesions heal  
139 [12]. Nevertheless, because disease monitoring was conducted twice per year, the precise timing of  
140 changes in disease status between capture events could not be determined [8].

141 Asymptomatic individuals were relatively rare ( $n = 75$ ; ~12%) and were excluded from subsequent  
142 analyses. Their limited representation and uncertain biological status constrained reliable estimation  
143 of their behavioural patterns and increased the risk of misclassification if grouped with either healthy  
144 or diseased individuals. However, as a sensitivity analysis to assess the robustness of our main finding,  
145 we ran an additional model that included focal asymptomatic individuals (see Statistical Analyses and  
146 Results).

147

## 148 *Data preparation*

149 The full dataset consisted of approximately 86,131 observations. Restricting the dataset to adult  
150 individuals, following the SVL and morphological criteria described in the Data Collection section,  
151 and to the focal study period (2018–2023) reduced it to 26,631 observations. At this stage, observations  
152 from 75 unique individuals (~12% of individuals) were excluded from further data preparation and the  
153 primary analysis but were retained in the sensitivity analysis (Table S4). Social associations were  
154 subsequently calculated, resulting in 24,060 records. To ensure reliable estimation of individual social  
155 behaviour and social environment, only observations from field seasons in which an individual had at  
156 least 30 sightings were retained, yielding a final analytical dataset of 16,855 sightings.

## 157 *Gregariousness estimation*

158 Gregariousness was estimated following established approach in this system, in which social  
159 associations are defined based on non-aggressive spatial proximity between individuals [13, 33, 34,  
160 36, 46]. Specifically, two individuals were considered socially associated if they were within 1.85 m  
161 of each other, approximately equivalent to two adult dragon body lengths [39, 43]. For each focal  
162 sighting, gregariousness was coded as 1 if the individual formed at least one social association (i.e.  
163 had at least one non-aggressive conspecific within 1.85 m during the same survey), and 0 if no such  
164 associations were detected. This definition links pairwise proximity-based associations to a sighting-  
165 level measure of sociality. The 1.85 m distance threshold was quantitatively derived and identified as  
166 a reliable and biologically meaningful measure [36]. Despite its inherent limitations, spatial proximity  
167 is commonly used as a proxy for social interaction in animal social systems [47].

## 168 *Social environment metrics*

169 To address our key research questions, we first quantified each individual's local social environment  
170 using the individual-centred social environment (ICSE) framework. We then used the individual-  
171 specific ICSE distance to derive two measures of the local social environment: (i) local conspecific

172 abundance, and (ii) local disease composition. Together, these metrics allowed us to assess how social  
173 behaviour varied with fine-scale variation in social crowding and disease composition. Because local  
174 conspecific abundance and local disease composition were quantified within the ICSE distance, this  
175 measurement was also included as a covariate in subsequent models to account for differences in the  
176 spatial extent of the local social environment among individuals.

177 To quantify each individual's local social environment, we followed the individual-centred social  
178 environment (ICSE) framework described by Strickland and Frère [14]. This approach uses an  
179 individual-specific spatial scale derived from the focal individual's core home range to quantify the  
180 social environment experienced at each sighting. For each individual and field season, ICSE was  
181 calculated from the geometry of its season-specific core home range (50% utilisation distribution),  
182 estimated using kernel density estimation with a fixed bandwidth ( $h = 7$ ) implemented in the  
183 *adehabitatHR* package [35, 48]. ICSE was defined as the minimum distance between the centroid of  
184 the core home range and its boundary. Only individual–season combinations with at least 30 sightings  
185 were retained to ensure reliable kernel estimates [49].

186 Following Strickland and Frère [14], this individual-specific ICSE distance was then used to quantify  
187 each individual's local social environment at each sighting. For each observation, all conspecifics  
188 present during the same survey occasion were identified, and distances from the focal individual to  
189 each conspecific were calculated. Conspecifics located within a distance  $\leq$  ICSE were considered part  
190 of the focal individual's local social environment. From this, two variables were derived: local  
191 conspecific abundance (*Local\_Num\_Total*), defined as the number of conspecifics within the ICSE,  
192 and local disease composition (*Local\_Num\_Diseased*), defined as the number of diseased conspecifics  
193 among them. Because this metric quantifies the number of diseased conspecifics within the focal  
194 individual's local environment, it represents local disease composition rather than a direct measure of  
195 environmental pathogen load or infection risk.

196 We quantified local disease composition as the absolute number of diseased individuals rather than

197 disease prevalence because our objective was to characterise the local abundance of diseased  
198 conspecifics while simultaneously controlling for the total number of conspecifics present within the  
199 focal individual's local environment. Consequently, when *Local\_Num\_Total* is included in the model,  
200 the effect of *Local\_Num\_Diseased* represents variation in the number of diseased neighbours while  
201 holding total local conspecific abundance constant; it describes variation in disease composition  
202 conditional on overall local abundance.

203 Because our primary aim was to test whether the relationship between local disease composition and  
204 gregariousness differed according to an individual's disease status, we modelled the interaction  
205 between disease status and *Local\_Num\_Diseased*. In contrast, *Local\_Num\_Total* was included as a  
206 covariate to account for variation in overall local conspecific abundance rather than to test for  
207 differences in density-dependent relationships. *Local\_Num\_Total* and *Local\_Num\_Diseased* were  
208 strongly positively correlated (Pearson's  $r = 0.85$ ), as expected because diseased individuals form a  
209 subset of the total local conspecific count. Both predictors were retained in the primary model because  
210 they address distinct biological components of the local environment, with *Local\_Num\_Total*  
211 accounting for overall conspecific abundance, whereas *Local\_Num\_Diseased* quantified variation in  
212 local disease composition conditional on that abundance.

### 213 *Statistical analysis*

214 We used a Bayesian multilevel Bernoulli regression model implemented in the *brms* package [50] in  
215 R [51]. We tested whether gregariousness varied with individual disease status, local conspecific  
216 abundance (*Local\_Num\_Total*), and local disease composition (*Local\_Num\_Diseased*), and whether  
217 the relationship between local disease composition and gregariousness differed between diseased and  
218 healthy individuals. Gregariousness was modelled as a binary response (0/1), with analyses conducted  
219 at the level of individual sightings to quantify fine-scale variation in gregariousness across local  
220 conditions.

Fixed effects included focal disease status (diseased vs. healthy), local disease composition (*Local\_Num\_Diseased*), their interaction, local conspecific abundance (*Local\_Num\_Total*), ICSE distance, SEASON (breeding vs. non-breeding), and sex (male vs. female). Random effects included individual identity (ID), sighting date and time (datetime), field season (FIELD\_SEAS), and Location, a categorical variable representing five distinct spatial areas within the park: Spectacle Gardens (Spec), Lake, Baobabs (BBabs), Arid, and Playground (Pground), to account for repeated observations and spatiotemporal non-independence. All continuous predictors were z-standardised (mean = 0, SD = 1) prior to analysis. Models were fitted using four Markov chains with 5,000 iterations each, including 2,000 warm-up iterations. Sampling was performed with *adapt\_delta* = 0.99 and *max\_treedepth* = 15 to improve sampler stability. No custom priors were specified, and models were fitted using the default priors implemented in *brms*.

To assess whether the estimated relationships between local disease composition and gregariousness were sensitive to the strong correlation between *Local\_Num\_Total* and *Local\_Num\_Diseased* (Pearson's  $r = 0.85$ ), we refitted the primary model excluding *Local\_Num\_Total*. This sensitivity model allowed us to determine whether the relationship between *Local\_Num\_Diseased* and gregariousness, including its interaction with focal disease status, was robust to the inclusion of overall local conspecific abundance. All other fixed and random effects were retained unchanged (Table S3). In a separate sensitivity analysis, we included asymptomatic individuals as an additional focal disease status category to assess whether the interaction between local disease composition and focal disease status was robust to their inclusion (Table S4).

#### *Model performance*

Collinearity diagnostics indicated no evidence of severe multicollinearity (maximum VIF = 3.09; Table S1), consistent with values reported in similar multivariable ecological studies [52-54]. Model convergence was assessed using trace plots (Figure S1), R-hat values, and effective sample sizes (ESS), with R-hat values < 1.01 and both bulk and tail ESS values exceeding 1000 for all parameters.

246 Posterior predictive checks were used to evaluate model fit (Figure S2), and PSIS-LOO cross-  
247 validation diagnostics were used to evaluate predictive performance and potentially influential  
248 observations (Figure S3).

#### 249 *Ethical notes*

250 Data collection adhered to animal ethics guidelines and received approval from the Animal Ethics  
251 Committee of the University of the Sunshine Coast (ANS1858 and ANA20161) at The University of  
252 Queensland (2022/AE000453). Research was conducted under Queensland Parks and Wildlife Service  
253 (QPWS) permit P-PTUKI-100129158.

## 254 **Results**

### 255 *Summary statistics*

256 The final analytical dataset comprised 16,855 focal sightings from 201 individually identified dragons  
257 observed between 2018 and 2023. Descriptive statistics for behavioural surveys, field seasons, disease  
258 status, sex, gregariousness, local conspecific abundance, local disease composition, and ICSE are  
259 provided in Table 1.

260 **Table 1. Summary statistics for the gregariousness analysis.** Descriptive statistics for focal  
261 sightings, behavioural records, field seasons, disease status, sex, gregariousness, local conspecific  
262 abundance, local disease composition, and individual-centred social environment (ICSE). All values  
263 are presented as mean  $\pm$  SD, unless otherwise indicated

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| Variable                                                         | Value                            |
|------------------------------------------------------------------|----------------------------------|
| <b>Focal sightings</b>                                           | 16,855                           |
| <b>Behavioural surveys</b>                                       | 523                              |
| <b>Field seasons</b>                                             | 5                                |
| <b>Unique individuals</b>                                        | 201                              |
| <b>Males</b>                                                     | 86                               |
| <b>Females</b>                                                   | 115                              |
| <b>Healthy individuals</b>                                       | 101 (50.2%)                      |
| <b>Diseased individuals</b>                                      | 100 (49.8%)                      |
| <b>Gregarious focal sightings</b>                                | 3,716 (22%)                      |
| <b>Local conspecific count, mean <math>\pm</math> SD (range)</b> | 1.85 $\pm$ 3.1 (range: 0-23)     |
| <b>Local diseased count, mean <math>\pm</math> SD (range)</b>    | 0.74 $\pm$ 1.44 (range: 0-10)    |
| <b>ICSE (m), mean <math>\pm</math> SD (range)</b>                | 9.33 $\pm$ 2.97 (range: 0-50.56) |

268

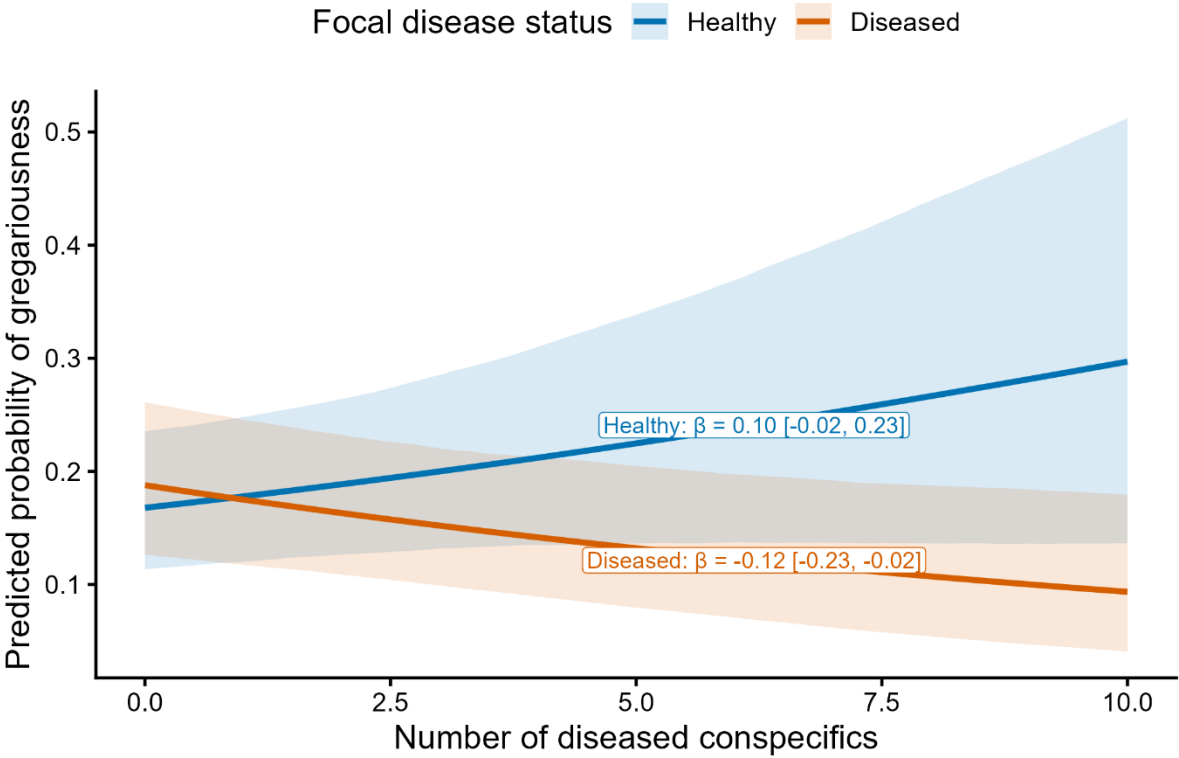
#### 269 *Disease effects on gregariousness*

270 The Bernoulli model indicated that gregariousness varied with local conspecific abundance and local  
271 disease composition according to focal disease status (Table 2; Figure 1). Local conspecific abundance  
272 was strongly positively associated with gregariousness overall (posterior mean = 2.30, 95% CrI =  
273 [2.17, 2.44]). In contrast, focal disease status as a main predictor showed no clear association with  
274 gregariousness, and among healthy individuals there was no clear relationship between local disease  
275 composition and gregariousness (posterior mean = 0.10, 95% CrI = [-0.02, 0.23]).

276 **Table 2. Posterior estimates from a Bayesian multilevel Bernoulli regression model testing**  
277 **whether the relationship between local disease composition and gregariousness differed**  
278 **according to focal disease status, while accounting for local conspecific abundance, individual-**  
279 **centred social environment (ICSE), season, and sex.** Estimates are presented as posterior means,  
280 posterior standard deviations (SD), and 95% credible intervals (CrI). Random-effect standard  
281 deviations are reported for datetime, field season, individual identity (ID), and location

| Parameter                                               | Posterior mean | Posterior SD | 95% CrI                 |
|---------------------------------------------------------|----------------|--------------|-------------------------|
| <b>Fixed effects</b>                                    |                |              |                         |
| <b>Intercept</b>                                        | <b>-1.566</b>  | 0.227        | <b>[-2.003, -1.129]</b> |
| Disease status (Diseased)                               | 0.021          | 0.076        | [-0.128, 0.172]         |
| <b>Local diseased count</b>                             | <b>0.102</b>   | 0.065        | <b>[-0.024, 0.231]</b>  |
| <b>ICSE</b>                                             | <b>-0.47</b>   | 0.039        | <b>[-0.546, -0.395]</b> |
| <b>Local conspecific count</b>                          | <b>2.303</b>   | 0.067        | <b>[2.172, 2.436]</b>   |
| Season (non-breeding)                                   | -0.021         | 0.076        | [-0.174, 0.126]         |
| Sex (Male)                                              | -0.146         | 0.088        | [-0.325, 0.027]         |
| <b>Disease status (Diseased) × Local diseased count</b> | <b>-0.226</b>  | 0.073        | <b>[-0.371, -0.085]</b> |
| <b>Random effects (SD)</b>                              |                |              |                         |
| <b>Datetime</b>                                         | <b>0.537</b>   | 0.039        | <b>[0.462, 0.615]</b>   |
| <b>Field season</b>                                     | <b>0.334</b>   | 0.246        | <b>[0.082, 0.965]</b>   |
| <b>Individual identity (ID)</b>                         | <b>0.453</b>   | 0.041        | <b>[0.377, 0.538]</b>   |
| <b>Location</b>                                         | <b>0.18</b>    | 0.153        | <b>[0.009, 0.537]</b>   |

283 A clear interaction between disease status and local disease composition indicated that the relationship  
 284 between local disease composition and gregariousness differed according to disease status (posterior  
 285 mean = -0.23, 95% CrI = [-0.37, -0.09]). Among diseased individuals, gregariousness decreased with  
 286 increasing local disease composition (posterior mean slope = -0.12, 95% CrI = [-0.23, -0.02]). The  
 287 negative interaction indicated that the relationship between local disease composition and  
 288 gregariousness was more negative for diseased individuals than for healthy individuals (Figure 1).



289  
 290 **Figure 1. Predicted relationship between local disease composition and gregariousness according**  
 291 **to individual disease status in eastern water dragons.** Lines show posterior mean predictions from  
 292 a Bayesian multilevel Bernoulli regression model across the observed range of local disease  
 293 composition (number of diseased conspecifics) for healthy (blue) and diseased (orange) individuals.  
 294 Shaded areas represent 95% credible intervals. Predicted gregariousness decreased with increasing  
 295 local disease composition among diseased individuals, whereas healthy individuals showed no clear  
 296 relationship. Annotations show the disease-status-specific simple slopes ( $\beta$ ) and their 95% credible

intervals, indicating the direction and magnitude of the relationship between local disease composition and gregariousness for each disease-status group. Slope estimates are on the log-odds scale and represent the change associated with a one-standard-deviation increase in local disease composition. The disease status  $\times$  local disease composition interaction was also supported in the sensitivity model excluding local conspecific abundance (posterior mean = -0.32, 95% CrI = [-0.45, -0.18]; Table S3), retaining the same direction and inferential outcome as the primary analysis. The sensitivity model including asymptomatic individuals produced an interaction similar in direction and magnitude to that of the primary model (posterior mean = -0.27, 95% CrI = [-0.42, -0.13]; Table S4). There was no clear evidence that the relationship between local disease composition and gregariousness differed for asymptomatic individuals. Thus, the disease status  $\times$  local disease composition interaction remained supported when asymptomatic individuals were included.

## Discussion

Our findings indicate that social behaviour in eastern water dragons varies with local social conditions and with the interaction between individual disease status and local disease composition. Gregariousness varied with the immediate social and disease conditions experienced by individuals, highlighting fine-scale behavioural variation across the population. These patterns suggest that social behaviour is associated with locally experienced disease composition rather than uniform population-level conditions, consistent with a spatially heterogeneous landscape of infection risk [2]. Such context-dependent behavioural variation may be particularly important in systems with persistent, environmentally transmitted pathogens, where infection risk cannot be mitigated solely by avoiding infected individuals [8, 9].

Among diseased individuals, gregariousness decreased as local disease composition increased, indicating that the relationship between local disease composition and gregariousness differed according to disease status. This pattern is consistent with sickness-associated behavioural changes,

321 such as reduced activity or social motivation, which may reduce social connectivity or the propensity  
322 to associate with nearby conspecifics [24, 25]. Similar infection-related reductions in sociality have  
323 been documented across taxa, where physiological constraints or sickness responses can alter  
324 behaviour and may indirectly reduce transmission [1, 55, 56]. In this system, more severely diseased  
325 individuals were avoided by conspecifics regardless of their own disease status, supporting the broader  
326 interpretation that clinical disease expression may modulate social behaviour in dragons [12].

327 In contrast, healthy individuals showed no clear relationship between local disease composition and  
328 gregariousness. More broadly, this is consistent with previous findings that social behaviour in this  
329 species varies strongly with local social density [14], as well as evidence that density is an important  
330 driver of social and spatial connectivity across animal populations [28]. One possibility is that the  
331 absence of a clear relationship among healthy individuals reflects continued reliance on social  
332 information, benefits associated with aggregation, or variation in the availability and detectability of  
333 infection cues in conspecifics [20, 22, 57]. Similar patterns have been observed in other systems, where  
334 social organisation persists despite infection risk and can itself modulate pathogen transmission,  
335 sometimes limiting disease spread among social groups [58, 59].

336 One alternative explanation is that disease-associated variation in gregariousness among diseased  
337 individuals contributes to passive restructuring of the local social environment. Withdrawal by  
338 diseased individuals may reduce local connectivity and alter patterns of social interaction, thereby  
339 changing the social environment experienced by other individuals [24]. More broadly, such changes  
340 may form part of reciprocal feedback between host behaviour, social organisation, and parasite  
341 dynamics [58, 60]. As a result, the extent to which observed social behaviour reflects passive social  
342 restructuring, active behavioural responses, or a combination of both cannot be determined from the  
343 current data. Disentangling active behavioural responses from passive social reorganisation will  
344 require explicit data on group composition, movement dynamics, and interaction networks [28, 30,  
345 61].

346 An alternative, but not mutually exclusive, mechanism involves socially mediated avoidance. In other  
347 vertebrates, cues associated with infection or sickness can elicit avoidance by healthy individuals,  
348 reducing contact with infected conspecifics even in the absence of active withdrawal by diseased  
349 individuals [1, 62]. Such forms of behavioural immunity have been documented across taxa and may  
350 plausibly occur in social reptiles such as eastern water dragons. Supporting this possibility, previous  
351 work in this population found severity-dependent avoidance of diseased conspecifics [12], consistent  
352 with severity-dependent avoidance in response to visible disease cues [20]. These socially mediated  
353 processes could therefore contribute to the observed relationship between disease status, local disease  
354 composition and gregariousness. Such patterns may arise through avoidance or reduced interaction  
355 rather than through withdrawal alone.

356 Together, these findings support the view that animal social behaviour varies with disease status and  
357 local disease composition. More broadly, such context-dependent behavioural variation is consistent  
358 with evidence for behavioural plasticity in wild animals [15]. Our study provides empirical evidence  
359 of disease-status-dependent variation in social behaviour associated with local disease composition in  
360 a free-ranging population experiencing sustained pathogen exposure. Although the costs and benefits  
361 of sociality are widely recognised as context-dependent [18, 63, 64], our findings extend this  
362 framework to a wild population experiencing sustained fungal disease pressure, a context in which  
363 behavioural responses remain comparatively poorly understood [23].

364 Asymptomatic individuals included in the sensitivity analysis did not show a clearly distinct pattern in  
365 relation to local disease composition, consistent with previous findings in this study system [27]. That  
366 work similarly showed no clear behavioural effect of asymptomatic status at the broader spatial scale,  
367 suggesting that healthy and asymptomatic individuals may show similar behavioural patterns under  
368 some conditions. However, subclinical infection can produce measurable behavioural changes in other  
369 systems [45]. Without implying clear directionality or causality, this pattern suggests that variation in  
370 social behaviour may be associated with disease status and, particularly, with the expression of clinical

371 disease.

372 There are two limitations to consider in this study. First, measures of gregariousness quantify patterns  
373 of proximity rather than moment-to-moment dynamics of social interaction, making it difficult to  
374 disentangle disease-related constraints, such as reduced activity or mobility, from active behavioural  
375 responses, such as social avoidance. Second, collinearity between predictors can affect the  
376 interpretation and precision of individual fixed-effects estimates [65, 66]. However, variance inflation  
377 factors remained moderate (maximum VIF = 3.09), and the sensitivity model excluding  
378 *Local\_Num\_Total* retained the disease status  $\times$  local disease composition interaction, with the same  
379 direction and inferential outcome as the primary analysis (Table S3). These predictors should therefore  
380 be interpreted as biologically linked rather than as fully independent ecological effects.

381 Such context-dependent variation in social behaviour has the potential to influence both individual  
382 fitness and pathogen transmission dynamics [18, 60], particularly in systems dominated by indirect  
383 environmental transmission, where infection risk may not be fully reduced through social avoidance  
384 alone [8, 21]. Future work integrating movement data, spatial overlap, pathogen load, and detailed  
385 behavioural observations will be important for understanding how fine-scale social behaviour varies  
386 under changing infection conditions. Such integrative approaches are particularly important in reptiles  
387 and other ectothermic vertebrates, where behavioural responses to infection remain comparatively  
388 poorly characterised in field settings [67]. Overall, our findings highlight that social behaviour under  
389 persistent disease pressure is context-dependent, with individual disease status and fine-scale local  
390 disease composition jointly contributing to variation in gregariousness.

#### 391 **Data accessibility**

392 The data and code supporting this study are currently held in a private repository during journal peer  
393 review.

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## 402 **References**

- 403 [1] Lopes, P.C., French, S.S., Woodhams, D.C. & Binning, S.A. 2022 Infection avoidance behaviors across  
404 vertebrate taxa: Patterns, processes, and future directions. In *Animal Behavior and Parasitism* (eds. V.  
405 Ezenwa, S.M. Altizer & R. Hall), pp. 237–256, Oxford University Press.
- 406 [2] Weinstein, S.B., Buck, J.C. & Young, H.S. 2018 A landscape of disgust. *Science* **359**, 1213–1214.  
407 (doi:10.1126/science.aas8694).
- 408 [3] Nnadi, N.E. & Carter, D.A. 2021 Climate change and the emergence of fungal pathogens. *PLoS Pathogens*  
409 **17**, e1009503. (doi:10.1371/journal.ppat.1009503).
- 410 [4] Fisher, M.C., Henk, D.A., Briggs, C.J., Brownstein, J.S., Madoff, L.C., McCraw, S.L. & Gurr, S.J. 2012  
411 Emerging fungal threats to animal, plant and ecosystem health. *Nature* **484**, 186–194.  
412 (doi:10.1038/nature10947).
- 413 [5] Scheele, B.C., Pasmans, F., Skerratt, L.F., Berger, L., Martel, A., Beukema, W., Acevedo, A.A.,  
414 Burrowes, P.A., Carvalho, T., Catenazzi, A., et al. 2019 Amphibian fungal panzootic causes catastrophic and  
415 ongoing loss of biodiversity. *Science* **363**, 1459–1463. (doi:10.1126/science.aav0379).
- 416 [6] Peterson, N.R., Rose, K., Shaw, S., Hyndman, T.H., Sigler, L., Kurtboke, D.I., Llinas, J., Littleford-  
417 Colquhoun, B.L., Cristescu, R. & Frere, C. 2021 Publisher Correction: Cross-continental emergence of  
418 *Nannizziopsis barbatae* disease may threaten wild Australian lizards. *Scientific Reports* **11**, 6871.  
419 (doi:10.1038/s41598-021-86463-0).
- 420 [7] Class, B., Powell, D., Terraube, J., Albery, G., Delmé, C., Bansal, S. & Frère, C.H. 2021 The  
421 epidemiology and genomics of a virulent emerging fungal pathogen in an Australian reptile. *bioRxiv*.  
422 (doi:10.1101/2021.10.22.465237).
- 423 [8] Becker, S.C., Albery, G.F., Jackson, N., Prewett, E., Mitchell, A.C., McGuigan, K. & Frere, C.H. 2025  
424 Indirect pathogen transmission underlies an emerging infectious fungal disease outbreak in a wild reptile  
425 population. *Proc Biol Sci* **292**. (doi:10.1098/rspb.2025.2188).
- 426 [9] Bahram, M. & Netherway, T. 2022 Fungi as mediators linking organisms and ecosystems. *FEMS*  
427 *Microbiology Reviews* **46**. (doi:10.1093/femsre/fuab058).
- 428 [10] Casadevall, A. 2017 Don't Forget the Fungi When Considering Global Catastrophic Biorisks. *Health*  
429 *Secur* **15**, 341–342. (doi:10.1089/hs.2017.0048).

430 [11] Parratt, S.R., Numminen, E. & Laine, A.-L. 2016 Infectious Disease Dynamics in Heterogeneous  
431 Landscapes. *Annual Review of Ecology, Evolution, and Systematics* **47**, 283–306. (doi:10.1146/annurev-  
432 ecolsys-121415-032321).

433 [12] Tacey, J., Class, B., Delmé, C., Powell, D. & Frère, C.H. 2023 Impacts of fungal disease on dyadic social  
434 interactions in a wild agamid lizard. *Animal Behaviour* **200**, 125–136. (doi:10.1016/j.anbehav.2023.04.002).

435 [13] Piza-Roca, C., Strickland, K., Schoeman, D. & Frere, C.H. 2018 Eastern water dragons modify their  
436 social tactics with respect to the location within their home range. *Animal Behaviour* **144**, 27–36.  
437 (doi:10.1016/j.anbehav.2018.08.001).

438 [14] Strickland, K. & Frère, C.H. 2019 Individual Variation in the Social Plasticity of Water Dragons. *The*  
439 *American Naturalist* **194**, 194–206. (doi:10.1086/704089).

440 [15] Dingemanse, N.J., Bouwman, K.M., van de Pol, M., van Overveld, T., Patrick, S.C., Matthysen, E. &  
441 Quinn, J.L. 2012 Variation in personality and behavioural plasticity across four populations of the great tit  
442 *Parus major*. *Journal of Animal Ecology* **81**, 116–126. (doi:10.1111/j.1365-2656.2011.01877.x).

443 [16] Silk, J.B. 2007 Social components of fitness in primate groups. *Science* **317**, 1347–1351.  
444 (doi:10.1126/science.1140734).

445 [17] Alexander, R.D. 1974 The Evolution of Social Behavior. *Annual Review of Ecology and Systematics* **5**,  
446 325–383. (doi:10.1146/annurev.es.05.110174.001545).

447 [18] Kappeler, P.M., Cremer, S. & Nunn, C.L. 2015 Sociality and health: impacts of sociality on disease  
448 susceptibility and transmission in animal and human societies. *Philos Trans R Soc Lond B Biol Sci.* **370**.  
449 (doi:10.1098/rstb.2014.0116).

450 [19] VanderWaal, K.L., Ezenwa, V.O. & Hawley, D. 2016 Heterogeneity in pathogen transmission:  
451 mechanisms and methodology. *Functional Ecology* **30**, 1606–1622. (doi:10.1111/1365-2435.12645).

452 [20] Curtis, V.A. 2014 Infection-avoidance behaviour in humans and other animals. *Trends in Immunology*  
453 **35**, 457–464. (doi:10.1016/j.it.2014.08.006).

454 [21] Gibson, A.K. & Amoroso, C.R. 2022 Evolution and Ecology of Parasite Avoidance. *Annu Rev Ecol Evol*  
455 *Syst* **53**, 47–67. (doi:10.1146/annurev-ecolsys-102220-020636).

456 [22] Stockmaier, S., Stroeymeyt, N., Shattuck, E.C., Hawley, D.M., Meyers, L.A. & Bolnick, D.I. 2021  
457 Infectious diseases and social distancing in nature. *Science* **371**. (doi:10.1126/science.abc8881).

458 [23] McKenzie, J.M., Price, S.J., Connette, G.M., Bonner, S.J. & Lorch, J.M. 2021 Effects of snake fungal  
459 disease on short-term survival, behavior, and movement in free-ranging snakes. *Ecol Appl* **31**, e02251.  
460 (doi:10.1002/eap.2251).

461 [24] Lopes, P.C., Block, P. & König, B. 2016 Infection-induced behavioural changes reduce connectivity and  
462 the potential for disease spread in wild mice contact networks. *Scientific Reports* **6**. (doi:10.1038/srep31790).

463 [25] Hart, B.L. 1988 Biological basis of the behavior of sick animals. *Neurosci Biobehav Rev* **12**, 123–137.  
464 (doi:10.1016/s0149-7634(88)80004-6).

465 [26] Hawley, D.M., Gibson, A.K., Townsend, A.K., Craft, M.E. & Stephenson, J.F. 2021 Bidirectional  
466 interactions between host social behaviour and parasites arise through ecological and evolutionary processes.  
467 *Parasitology* **148**, 274–288. (doi:10.1017/S0031182020002048).

468 [27] Requena-García, F., Jackson, N., Class, B., Mitchell, A.C., Cramp, R.L. & Frere, C.H. 2026 Social  
469 Distancing Responses to Fungal Disease in an Australian Wild Lizard Population. *bioRxiv*  
470 (doi:10.64898/2026.04.06.716608).

471 [28] Albery, G.F. & Becker, D.J. & Firth, J.A. & De Moor, D. & Ravindran, S. & Silk, M. & Sweeny, A.R. &  
472 Vander Wal, E. & Webber, Q. & Allen, B., et al. 2025 Density-dependent network structuring within and  
473 across wild animal systems. *Nature Ecology & Evolution* **9**, 2002–2013. (doi:10.1038/s41559-025-02843-z).

474 [29] Elliot, S.L. & Hart, A.G. 2010 Density-dependent prophylactic immunity reconsidered in the light of host  
475 group living and social behavior. *Ecology* **91**, 65–72. (doi:10.1890/09-0424.1).

476 [30] Albery, G.F., Kirkpatrick, L., Firth, J.A. & Bansal, S. 2021 Unifying spatial and social network analysis  
477 in disease ecology. *Journal of Animal Ecology* **90**, 45–61. (doi:10.1111/1365-2656.13356).

478 [31] Morris, A.M.M., Innocent, G.T., Cunningham, E.J.A., Croft, D.P., Athanasiadou, S., Hutchings, M.R. &  
479 Smith, L.A. 2025 Parasite induced changes in contact behaviour is affected by parasitic status of group  
480 members. *Behavioral Ecology and Sociobiology* **79**, 65. (doi:10.1007/s00265-025-03595-3).

481 [32] Class, B., Strickland, K., Potvin, D., Jackson, N., Nakagawa, S. & Frere, C. 2024 Sex-Specific  
482 Associations between Social Behavior, Its Predictability, and Fitness in a Wild Lizard. *The American*  
483 *Naturalist* **204**, 501–516. (doi:10.1086/732178).

484 [33] Delmé, C., Class, B., Strickland, K. & Frère, C.H. 2024 Adult males are less social than juveniles and  
485 adult females in a wild agamid species. *Animal Behaviour* **218**, 37–53. (doi:10.1016/j.anbehav.2024.09.006).

486 [34] Delmé, C., Jackson, N., Class, B., Strickland, K., Potvin, D.A. & Frere, C.H. 2023 Adaptive significance  
487 of affiliative behaviour differs between sexes in a wild reptile population. *Proc Biol Sci.* **290**. 20230805.  
488 (doi:10.1098/rspb.2023.0805).

489 [35] Gardiner, R.Z., Doran, E., Strickland, K., Carpenter-Bundhoo, L. & Frere, C. 2014 A face in the crowd: a  
490 non-invasive and cost effective photo-identification methodology to understand the fine scale movement of  
491 eastern water dragons. *PLoS One* **9**, e96992. (doi:10.1371/journal.pone.0096992).

492 [36] Strickland, K., Gardiner, R., Schultz, A.J. & Frere, C.H. 2014 The social life of eastern water dragons:  
493 sex differences, spatial overlap and genetic relatedness. *Animal Behaviour* **97**, 53–61.  
494 (doi:10.1016/j.anbehav.2014.08.009).

495 [37] Littleford-Colquhoun, B.L., Clemente, C., Thompson, G., Cristescu, R.H., Peterson, N., Strickland, K.,  
496 Stuart-Fox, D. & Frere, C.H. 2019 How sexual and natural selection shape sexual size dimorphism: Evidence  
497 from multiple evolutionary scales. *Functional Ecology* **33**, 1446–1458. (doi:10.1111/1365-2435.13337).

498 [38] Piza-Roca, C., Strickland, K., Kent, N., Frere, C.H. & Pruitt, J. 2019 Presence of kin-biased social  
499 associations in a lizard with no parental care: the eastern water dragon (*Intellagama lesueurii*). *Behavioral*  
500 *Ecology* **30**, 1406–1415. (doi:10.1093/beheco/arz093).

501 [39] Strickland, K., Frère, C.H. & Taborsky, M. 2018 Predictable males and unpredictable females:  
502 repeatability of sociability in eastern water dragons. *Behavioral Ecology* **29**, 236–243.  
503 (doi:10.1093/beheco/arx148).

504 [40] Baird, T.A., Baird, T.D. & Shine, R. 2012 Aggressive transition between alternative male social tactics in  
505 a long-lived Australian dragon (*Physignathus lesueurii*) living at high density. *PLoS One* **7**, e41819.  
506 (doi:10.1371/journal.pone.0041819).

507 [41] Ball, S., Potvin, D.A., Class, B. & Frère, C.H. 2023 Agonism does not covary with territoriality in a  
508 gregarious reptile. *Behavioral Ecology and Sociobiology* **77**, 73. (doi:10.1007/s00265-023-03348-0).

509 [42] Van Tienhoven, A.M., Den Hartog, J.E., Reijns, R.A. & Peddemors, V.M. 2007 A computer-aided  
510 program for pattern-matching of natural marks on the spotted raggedtooth shark *Carcharias taurus*. *Journal of*  
511 *Applied Ecology* **44**, 273–280. (doi:10.1111/j.1365-2664.2006.01273.x).

512 [43] Littleford-Colquhoun, B.L., Clemente, C., Whiting, M.J., Ortiz-Barrientos, D. & Frere, C.H. 2017  
513 Archipelagos of the Anthropocene: rapid and extensive differentiation of native terrestrial vertebrates in a  
514 single metropolis. *Molecular Ecology* **26**, 2466–2481. (doi:10.1111/mec.14042).

515 [44] Powell, D., Schwessinger, B. & Frere, C.H. 2023 Whole-mitochondrial genomes of *Nannizziopsis*  
516 provide insights in evolution and detection. *Ecology and Evolution* **13**, e9955. (doi:10.1002/ece3.9955).

517 [45] Grabow, M., Ullmann, W., Landgraf, C., Sollmann, R., Scholz, C., Nathan, R., Toledo, S., Luhken, R.,  
518 Fickel, J., Jeltsch, F., et al. 2024 Sick without signs. Subclinical infections reduce local movements, alter  
519 habitat selection, and cause demographic shifts. *Commun Biol* **7**, 1426. (doi:10.1038/s42003-024-07114-4).

520 [46] Strickland, K., Mitchell, D.J., Delme, C. & Frere, C.H. 2021 Repeatability and heritability of social  
521 reaction norms in a wild agamid lizard. *Evolution* **75**, 1953–1965. (doi:10.1111/evo.14298).

522 [47] Farine, D.R. 2015 Proximity as a proxy for interactions: issues of scale in social network analysis. *Animal*  
523 *Behaviour* **104**, e1–e5. (doi:10.1016/j.anbehav.2014.11.019).

524 [48] Calenge, C. 2006 The package "adehabitat" for the R software: A tool for the analysis of space and  
525 habitat use by animals. *Ecological Modelling* **197**, 516–519. (doi:10.1016/j.ecolmodel.2006.03.017).

526 [49] Strickland, K., Levensgood, A., Foroughirad, V., Mann, J., Krzyszczyk, E. & Frere, C.H. 2017 A  
527 framework for the identification of long-term social avoidance in longitudinal datasets. *Royal Society Open*  
528 *Science* **4**. (doi:10.1098/rsos.170641).

529 [50] Bürkner, P.-C. 2021 Bayesian Item Response Modeling in R with brms and Stan. *Journal of Statistical*  
530 *Software* **100**, 1–54. (doi:10.18637/jss.v100.i05).

531 [51] R Core Team. 2026 R: A language and environment for statistical computing. Vienna, Austria: R  
532 Foundation for Statistical Computing. *CRAN*.

533 [52] Sabbi, K.H., Kurilla, S.E., Monroe, I.G., Zhang, Y., Menante, A., Cole, M.F., Otali, E., Kobusingye, M.,  
534 Emery Thompson, M., Muller, M.N., et al. 2024 Ecological variation in adult social play reveals a hidden cost  
535 of motherhood for wild chimpanzees. *Current Biology* **34**, 1364–1369. (doi:10.1016/j.cub.2024.02.025).

536 [53] Tagg, N., McCarthy, M., Dieguez, P., Bocksberger, G., Willie, J., Mundry, R., Stewart, F., Arandjelovic,  
537 M., Widness, J., Landsmann, A., et al. 2018 Nocturnal activity in wild chimpanzees (*Pan troglodytes*):  
538 Evidence for flexible sleeping patterns and insights into human evolution. *American Journal of Biological*  
539 *Anthropology* **166**, 510–529. (doi:10.1002/ajpa.23478).

540 [54] Bro-Jørgensen, J. & Beeston, J. 2015 Multimodal signalling in an antelope: fluctuating facemasks  
541 and knee-clicks reveal the social status of eland bulls. *Animal Behaviour* **102**, 231–239.  
542 (doi:10.1016/j.anbehav.2015.01.027).

543 [55] Butler, M.J., IV & Behringer, D.C. 2021 Behavioral Immunity and Social Distancing in the Wild: The  
544 Same as in Humans? *BioScience* **71**, 571–580. (doi:10.1093/biosci/biaa176).

545 [56] Hart, B.L. & Hart, L.A. 2019 Sickness Behavior in Animals: Implications for Health and Wellness. In  
546 *Encyclopedia of Animal Behavior* (pp. 171–175). (doi:10.1016/B978-0-12-809633-8.20750-4).

547 [57] Poirotte, C., Massol, F., Herbert, A., Willaume, E., Bomo, P.M., Kappeler, P.M. & Charpentier, M.J.E.  
548 2017 Mandrills use olfaction to socially avoid parasitized conspecifics. *Science Advances* **3**, e1601721.  
549 (doi:10.1126/sciadv.1601721).

550 [58] Altizer, S., Nunn, C.L., Thrall, P.H., Gittleman, J.L., Antonovics, J., Cunningham, A.A., Dobson, A.P.,  
551 Ezenwa, V., Jones, K.E., Pedersen, A.B., et al. 2003 Social Organization and Parasite Risk in Mammals:  
552 Integrating Theory and Empirical Studies. *Annual Review of Ecology, Evolution, and Systematics* **34**, 517–  
553 547. (doi:10.1146/annurev.ecolsys.34.030102.151725).

- 554 [59] Manlove, K.R., Cassirer, E.F., Cross, P.C., Plowright, R.K. & Hudson, P.J. 2014 Costs and benefits of  
555 group living with disease: a case study of pneumonia in bighorn lambs (*Ovis canadensis*). *Proc Biol Sci.* **281**.  
556 20153078. (doi:10.1098/rspb.2014.2331).
- 557 [60] Ezenwa, V.O., Archie, E.A., Craft, M.E., Hawley, D.M., Martin, L.B., Moore, J. & White, L. 2016 Host  
558 behaviour-parasite feedback: an essential link between animal behaviour and disease ecology. *Proc Biol Sci.*  
559 **283**. (doi:10.1098/rspb.2015.3078).
- 560 [61] Silk, M.J., Croft, D.P., Delahay, R.J., Hodgson, D.J., Boots, M., Weber, N. & McDonald, R.A. 2017  
561 Using Social Network Measures in Wildlife Disease Ecology, Epidemiology, and Management. *Bioscience*  
562 **67**, 245–257. (doi:10.1093/biosci/biw175).
- 563 [62] Hart, L.A. & Hart, B.L. 2021 How Does the Social Grouping of Animals in Nature Protect Against  
564 Sickness? A Perspective. *Frontiers in Behavioral Neuroscience* **15**. (doi:10.3389/fnbeh.2021.672097).
- 565 [63] Silk, M.J. & Fefferman, N.H. 2021 The role of social structure and dynamics in the maintenance of  
566 endemic disease. *Behav Ecol Sociobiol* **75**, 122. (doi:10.1007/s00265-021-03055-8).
- 567 [64] Lopes, P.C. 2014 When is it socially acceptable to feel sick? *Proc Biol Sci* **281**, 20140218.  
568 (doi:10.1098/rspb.2014.0218).
- 569 [65] Graham, M.H. 2003 Confronting Multicollinearity in Ecological Multiple Regression. *Ecology* **84**, 2809–  
570 2815. (doi:10.1890/02-3114).
- 571 [66] Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B.,  
572 Lafourcade, B., Leitão, P.J., et al. 2013 Collinearity: a review of methods to deal with it and a simulation  
573 study evaluating their performance. *Ecography* **36**, 27–46. (doi: 10.1111/j.1600-0587.2012.07348.x).
- 574 [67] Cabanzo-Olarte, L.C., Cardoso Bicego, K. & Navas Iannini, C.A. 2024 Behavioral responses during  
575 sickness in amphibians and reptiles: Concepts, experimental design, and implications for field studies. *J*  
576 *Therm Biol* **123**, 103889. (doi:10.1016/j.jtherbio.2024.103889).

577

578 **Supplementary material for: *Disease-Dependent Social Responses to Local Disease Composition in a Wild***  
579 ***Reptile***

580 **Table S1:** Collinearity diagnostic (variance inflation factors) for the primary model fitted to the 30-sightings  
581 analytical dataset

582 **Figure S1:** Stan trace plots

583 **Figure S2:** Posterior predictive checks for the primary gregariousness model

584 **Figure S3:** PSIS-LOO cross-validation diagnostics for the primary gregariousness model

585 **Table S2:** Full Bayesian model output for the primary Bernoulli mixed-effects model examining gregariousness  
586 in eastern water dragons.

587 **Table S3.** Sensitivity analysis excluding *Local\_Num\_Total* from the primary Bernoulli mixed-effects model of  
588 gregariousness.

589 **Table S4.** Full Bayesian model output for the asymptomatic sensitivity analysis including healthy,  
590 asymptomatic, and symptomatic/diseased disease-status categories

591

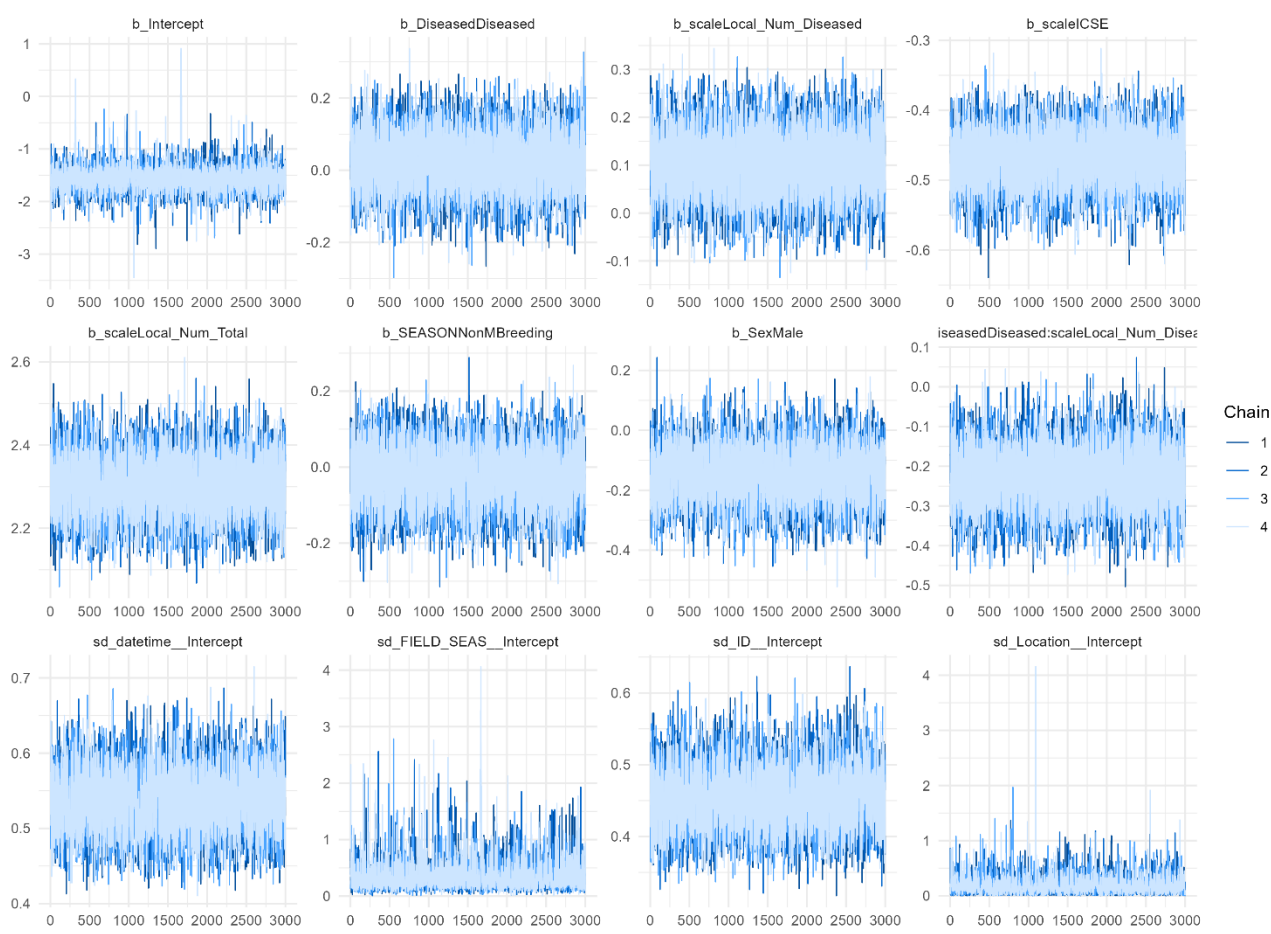
592 Table S1: Collinearity diagnostic (variance inflation factors) for the primary model fitted to the 30-  
593 sightings analytical dataset. Multicollinearity among fixed effects was evaluated using the VIF, with  
594 associated 95% confidence intervals. All predictors showed low VIF values, indicating that collinearity  
595 was unlikely to influence model inference.

596

| Parameter               | VIF   | Increased SE | Tolerance |
|-------------------------|-------|--------------|-----------|
| Disease status          | 3.087 | 1.757        | 0.324     |
| Local diseased count    | 1.114 | 1.055        | 0.898     |
| ICSE                    | 1.731 | 1.316        | 0.578     |
| Local conspecific count | 1.01  | 1.005        | 0.99      |
| Season                  | 1.018 | 1.009        | 0.982     |
| Sex                     | 2.495 | 1.58         | 0.401     |

597

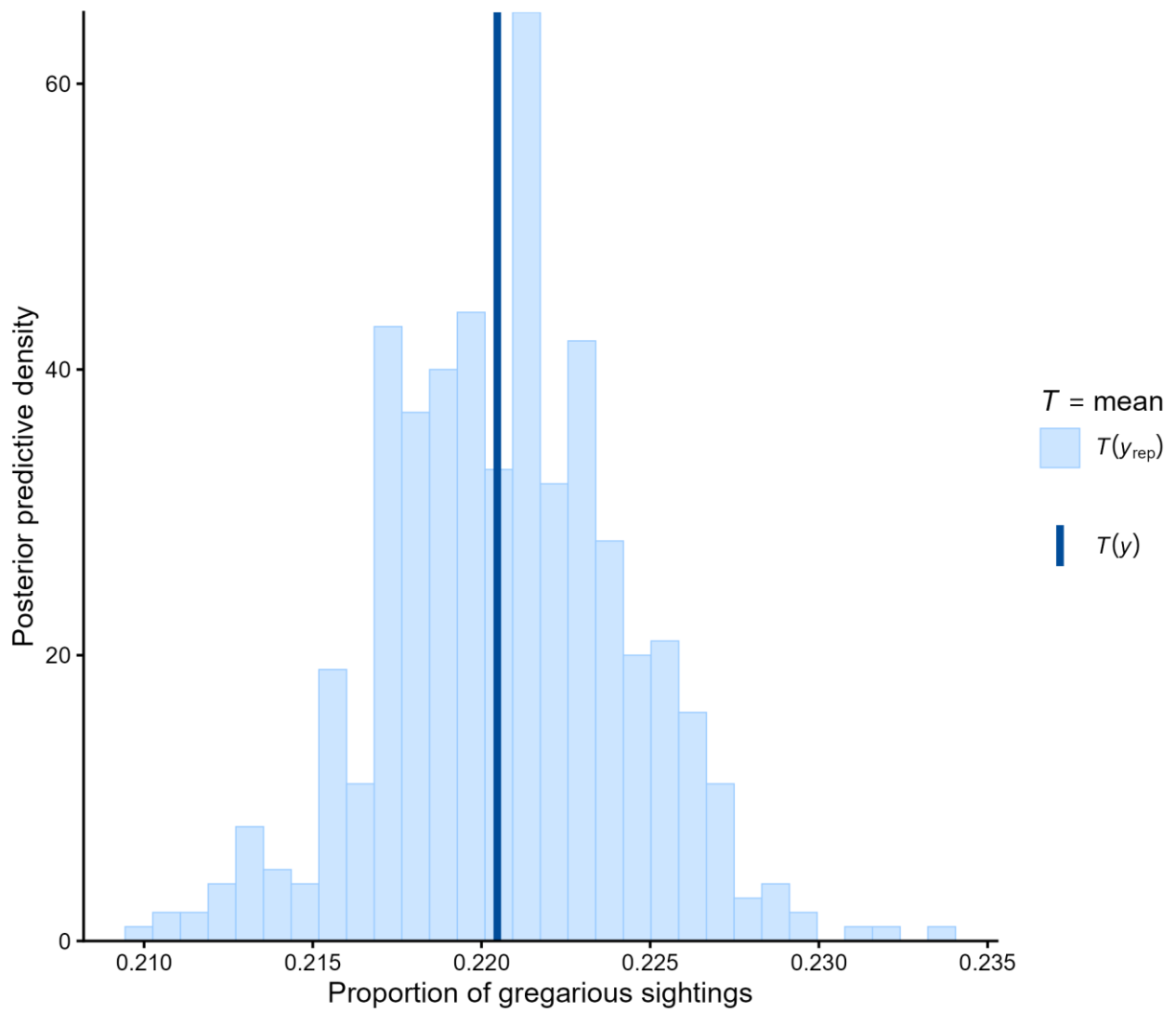
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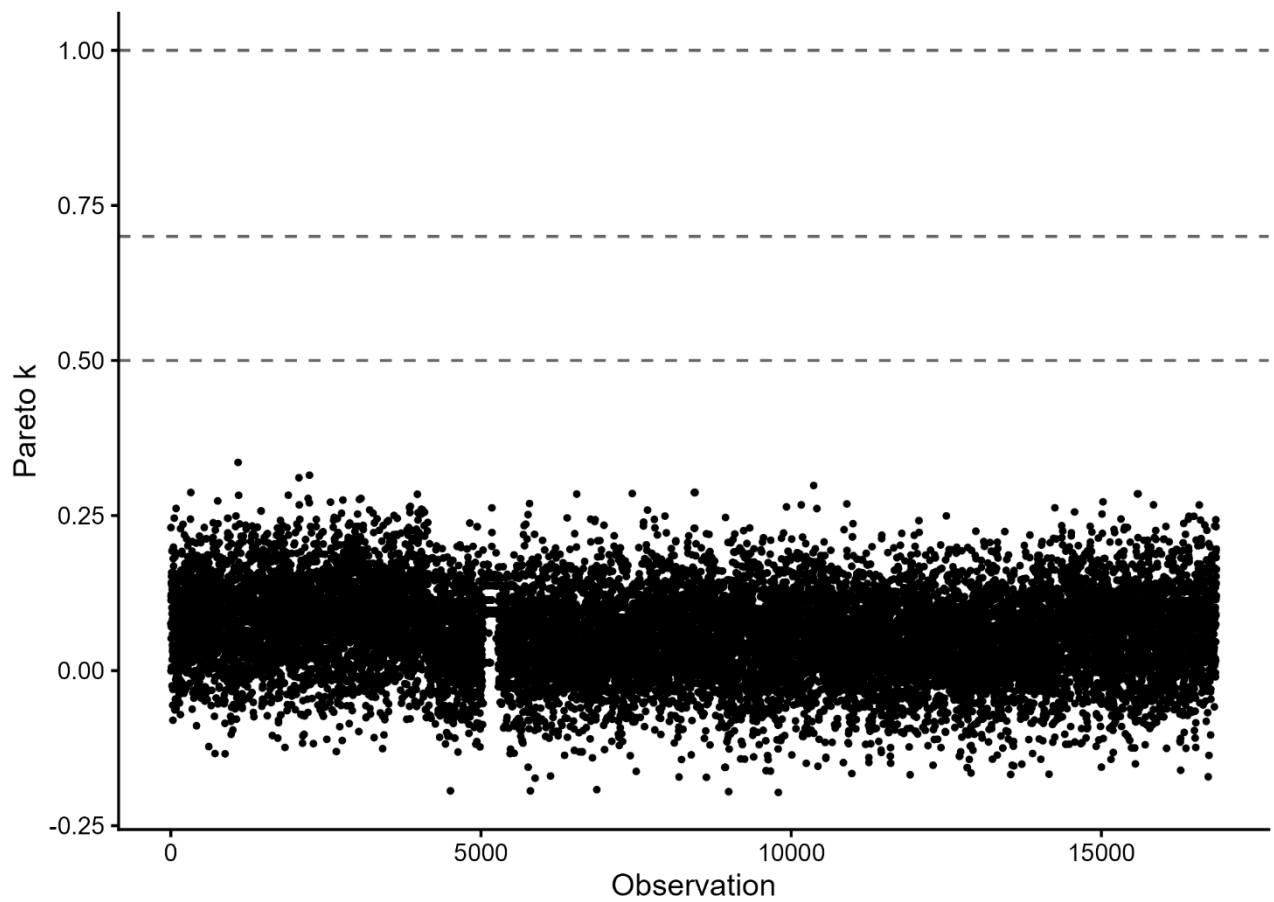
601 Figure S1: Stan trace plots. Convergence of Markov chain Monte Carlo sampling was assessed using trace plots  
602 and the Gelman-Rubin statistic ( $\hat{R}$ ). Visual inspection of trace plots indicated good mixing and stationarity  
603 across chains, indicating satisfactory convergence.

604



605

606 Figure S2: Posterior predictive check for the primary gregariousness model. The distribution represents  
 607 the mean proportion of gregarious sightings across posterior predictive datasets, while the vertical line  
 608 indicates the observed proportion.  
 609



610

611 Figure S3: PSIS-LOO cross-validation diagnostics for the primary gregariousness model. Pareto- $k$   
612 values were below 0.5 for all observations, indicating reliable importance-sampling estimates and no  
613 problematic influential observations.  
614

615 Table S2: Full Bayesian model output for the primary Bernoulli mixed-effects model examining  
616 gregariousness in eastern water dragons. The model was fitted to the 30-sighting analytical dataset.  
617 Estimates are presented as posterior means, posterior standard deviations (SD), and 95% credible  
618 intervals (CrI). Random-effect standard deviations are reported for datetime, field season, individual  
619 identity (ID), and location

| Parameter                                        | Posterior mean | Posterior SD | Lower 95% CrI | Upper 95% CrI |
|--------------------------------------------------|----------------|--------------|---------------|---------------|
| Fixed effects                                    |                |              |               |               |
| Intercept                                        | -1.566         | 0.227        | -2.003        | -1.129        |
| Disease status (Diseased)                        | 0.021          | 0.076        | -0.128        | 0.172         |
| Local diseased count                             | 0.102          | 0.065        | -0.024        | 0.231         |
| ICSE                                             | -0.47          | 0.039        | -0.546        | -0.395        |
| Local conspecific count                          | 2.303          | 0.067        | 2.172         | 2.436         |
| Season (non-breeding)                            | -0.021         | 0.076        | -0.174        | 0.126         |
| Sex (Male)                                       | -0.146         | 0.088        | -0.325        | 0.027         |
| Disease status (Diseased) × Local diseased count | -0.226         | 0.073        | -0.371        | -0.085        |
| Random effects (SD)                              |                |              |               |               |
| Datetime                                         | 0.537          | 0.039        | 0.462         | 0.615         |
| Field season                                     | 0.334          | 0.246        | 0.082         | 0.965         |
| Individual identity (ID)                         | 0.453          | 0.041        | 0.377         | 0.538         |
| Location                                         | 0.18           | 0.153        | 0.009         | 0.537         |

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622 Table S3. Sensitivity analysis excluding *Local\_Num\_Total* from the primary Bernoulli mixed-effects  
623 model of gregariousness. The model was fitted to the same 30-sighting analytical dataset as the primary  
624 model, with all other fixed and random effects retained unchanged. Estimates are presented as posterior  
625 means, posterior standard deviations (SD), and 95% credible intervals (CrI). Random-effect standard  
626 deviations are reported for datetime, field season, individual identity (ID), and location

| Parameter                                        | Posterior mean | Posterior SD | Lower 95% CrI | Upper 95% CrI |
|--------------------------------------------------|----------------|--------------|---------------|---------------|
| Fixed effects                                    |                |              |               |               |
| Intercept                                        | -1.691         | 0.475        | -2.626        | -0.699        |
| Disease status (Diseased)                        | -0.035         | 0.085        | -0.201        | 0.132         |
| Local diseased count                             | 1.283          | 0.056        | 1.175         | 1.394         |
| ICSE                                             | -0.199         | 0.044        | -0.287        | -0.114        |
| Season (non-breeding)                            | -0.225         | 0.082        | -0.384        | -0.063        |
| Sex (Male)                                       | -0.167         | 0.121        | -0.407        | 0.073         |
| Disease status (Diseased) × Local diseased count | -0.32          | 0.07         | -0.455        | -0.183        |
| Random effects (SD)                              |                |              |               |               |
| Datetime                                         | 0.617          | 0.04         | 0.541         | 0.698         |
| Field season                                     | 0.711          | 0.403        | 0.277         | 1.761         |
| Individual identity (ID)                         | 0.697          | 0.053        | 0.599         | 0.808         |
| Location                                         | 0.612          | 0.299        | 0.275         | 1.376         |

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629 Table S4. Full Bayesian model output for the asymptomatic sensitivity analysis including healthy,  
630 asymptomatic, and symptomatic/diseased disease-status categories. The model was fitted using the  
631 same 30-sighting individual-season threshold as the primary analysis. Estimates are presented as  
632 posterior means, posterior standard deviations (SD), and 95% credible intervals (CrI). Random-effect  
633 standard deviations are reported for datetime, field season, individual identity (ID), and location

| Parameter                                                          | Posterior mean | Posterior SD | Lower 95% CrI | Upper 95% CrI |
|--------------------------------------------------------------------|----------------|--------------|---------------|---------------|
| Fixed effects                                                      |                |              |               |               |
| Intercept                                                          | -1.147         | 0.287        | -1.707        | -0.561        |
| Disease status (Asymptomatic)                                      | -0.171         | 0.099        | -0.366        | 0.022         |
| Disease status<br>(Symptomatic/Diseased)                           | 0.011          | 0.071        | -0.127        | 0.152         |
| Local diseased count                                               | 0.287          | 0.064        | 0.163         | 0.411         |
| ICSE                                                               | -0.359         | 0.033        | -0.424        | -0.295        |
| Local conspecific count                                            | 2.294          | 0.06         | 2.176         | 2.41          |
| Season (non-breeding)                                              | -0.137         | 0.066        | -0.266        | -0.006        |
| Sex (Male)                                                         | -0.068         | 0.08         | -0.227        | 0.089         |
| Disease status (Asymptomatic) ×<br>Local diseased count            | -0.058         | 0.109        | -0.269        | 0.158         |
| Disease status<br>(Symptomatic/Diseased) × Local<br>diseased count | -0.271         | 0.074        | -0.418        | -0.128        |
| Random effects (SD)                                                |                |              |               |               |
| Datetime                                                           | 0.48           | 0.035        | 0.414         | 0.55          |
| Field season                                                       | 0.482          | 0.286        | 0.171         | 1.22          |
| Individual identity (ID)                                           | 0.424          | 0.035        | 0.358         | 0.497         |
| Location                                                           | 0.267          | 0.171        | 0.06          | 0.69          |

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