

1 Opposite-sex associations are linked with annual fitness, but sociality is stable over
2 lifetime.

3

4 *Jamie Dunning¹, Terry Burke², Alex Hoi Hang Chan^{1,3,4}, Heung Ying Janet Chik^{5,6}, Tim
5 Evans⁷, Julia Schroeder¹.

6 ¹Department of Life Sciences, Imperial College London, United Kingdom

7 ²Ecology and Evolutionary Biology, School of Biosciences, The University of Sheffield,
8 United Kingdom

9 ³Centre for the Advanced Study of Collective Behaviour, University of Konstanz, Germany

10 ⁴Max Plank Institute of Animal Behaviour, Germany

11 ⁵Groningen Institute for Evolutionary Life Sciences, University of Groningen, Netherlands

12 ⁶School of Natural Sciences, Macquarie University, Australia

13 ⁷Center for Complexity Science, Imperial College London, United Kingdom

14 *Corresponding author – jamiedunning8@gmail.com

15

16

17 Abstract

18 Animal sociality, an individual's propensity to associate with others, has fitness
19 consequences through mate choice, for example, directly, by increasing the pool of
20 prospective partners, and indirectly through increased survival, and individuals benefit
21 from both. Annually, fitness consequences are realised through increased mating success
22 and subsequent fecundity. However, it remains unknown whether these consequences
23 translate to life-time fitness. Here, we quantified social associations and their link to fitness
24 annually and over lifetime, using a multi-generational, genetic pedigree. We used social
25 network analysis to calculate variables representing different aspects of an individual's
26 sociality. Sociality showed high within-individual repeatability. We found that birds with
27 more opposite-sex associates had higher annual fitness than those with fewer, but this did
28 not translate to lifetime fitness. Instead, for lifetime fitness, we found evidence for
29 stabilizing selection on opposite-sex sociality, and sociality in general, suggesting that
30 reported benefits are only short-lived in a wild population, and that selection favours an
31 average sociality.

32 Keywords: sociality, social network analysis, selection, social behaviour, genetic pedigree,
33 long-term fitness, de-lifing, lifetime reproductive success

34

35

36 Background

37

38 Some individuals are consistently more sociable than others, demonstrated by within-
39 individual repeatability of social traits across vertebrate groups (Aplin et al. 2015; Thys et
40 al. 2017; Dimitriadou, Croft and Darden 2019; Plaza et al. 2019; Beck, Valcu, and
41 Kempnaers 2020; Proops et al. 2021; Strickland et al. 2021). This variation in individual
42 sociality is positively linked with fitness in some taxa (Silk 2007; Silk et al. 2009) and is
43 therefore expected to be subject to selection (Krause and Ruxton 2002). Fitness is a relative
44 measure of an individual's genetic contribution to the population in the next generation,
45 and thus, can only be represented comprehensively and precisely by measures of traits
46 spanning an organism's lifetime (Endler 1986; Blankenhorn 2010; Reid et al. 2019; Moiron,
47 Charmantier and Bouwhuis 2022). A comprehensive definition of fitness is fundamental to
48 understand the evolutionary pressures that shape variation in sociality. In practice,
49 however, many studies must rely on fitness correlates instead (e.g., number of broods, or
50 survival, instead of genetic contribution). For example, in mammal societies, both variation
51 in within- and between-sex affiliations (Archie et al. 2014) have been linked to lifetime
52 fitness correlates, survival and longevity (Cameron, Setsaas and Linklater 2009; Silk,
53 Alberts and Altman 2003; Silk et al. 2010; Stanton and Mann 2012, but also see Thompson
54 and Cords 2018). Whereas, in birds, the subject of this study, the use of fitness correlates
55 (eggs laid, chicks fledged, within-year survival etc.) are frequent over more precise fitness
56 measures (Moiron, Charmantier and Bouwhuis 2022), that require intensive field work
57 over a long period of time.

58 Although some benefits are linked with sociality during the breeding period most of these
59 tend to be short-term and contextual (Bebbington et al. 2017; Riehl and Strong 2018).
60 Instead, benefits associated with reproduction are often linked with non-breeding sociality
61 (Firth and Sheldon 2016; Kohn 2017; Maldonado-Chaparro et al. 2018; Beck, Farine, and
62 Kempnaers 2020), when group cohesion is stronger (Silk et al. 2014; Kurvers 2020).
63 Sociality may influence fitness in different ways, through benefits to reproductive success
64 or increased survival, and so, the mechanism of selection acting on social traits may also

65 differ. For example, communal foraging between socially associated individuals during the
66 non-breeding period facilitates resource information transfer (Aplin et al. 2012; Firth,
67 Sheldon and Farine 2016; Hillemann et al. 2020) and reduces predation risk (Cresswell
68 1994; Cresswell and Quinn 2011; Sorato et al. 2012), increasing survival. However, these
69 benefits may also incur costs associated with competition for resources and mate choice
70 (Birkhead and Biggins 1987; Le Galliard et al. 2005; Forstmeier et al. 2011; Mayer and
71 Pasinelli 2013; Grant and Grant 2019; but also see Lea et al. 2010). Sociality may also
72 benefit individuals who hold more central social network positions or have access to
73 opposite-sex associates, through enhanced mate choice (McDonald 2007; Oh and Badyaev
74 2010; Firth et al. 2018; Beck, Farine, and Kempenaers 2021). Although the association
75 between annual fitness correlates and non-breeding sociality has been well described,
76 testing how selection acts on social traits requires lifetime fitness measures, and remains
77 unresolved.

78 With the recent development of tools to construct and analyse social networks (Wey et al.
79 2008; Farine and Whitehead 2015) the study of sociality has become popular among
80 behavioural ecologists. Yet, to describe the association between sociality and fitness any
81 potential study must first overcome two problems: (1) A social association must be clearly
82 defined relative to the behavior of the study system (Figure 1; Psorakis et al. 2012, 2015),
83 and (2) to study the evolution of social behaviour, precise measures of individual fitness
84 must be quantified to test for correlation with a social trait – selection. Although annual
85 fitness correlates are widely used, lifetime fitness is more precise and without the
86 stochasticity of annual measures (Dobson, Murie and Viblanc 2020; Alif et al. 2022) and
87 thus, can better describe selection pressure acting on a trait (Endler 1986; Blankenhorn
88 2010; Reid et al. 2019). However, lifetime fitness requires wild animals to be monitored
89 throughout their whole lives, and all breeding attempts, and the fates of their offspring,
90 must be recorded to determine recruitment. All of these require a multi-generational,
91 genetic pedigree (Kruuk 2004; Korsten et al. 2013).

92 Our study system, an island population of house sparrows *Passer domesticus* (hereafter,
93 sparrow/s) where we monitor all individuals from birth to death, without capture bias

94 (Simons et al. 2015), overcomes both problems. (1) We have sociality data from birds that
95 are electronically registered visiting a feeder. Social centrality measures are repeatable
96 across different timescales and contexts in this and other populations (Plaza et al. 2019).
97 (2) We have lifetime recruitment data available, from a multi-generational genetic pedigree
98 that, because our population is closed, meaningly there is no movement of sparrows to or
99 from the island, and that our study covers all sparrows on the island, we can use to
100 compute precise annual and lifetime fitness estimates (Schroeder et al. 2015; Alif et al.
101 2022).

102 We tested predictions based on arguments presented above to understand the potential for
103 selection on sociality: (1) We confirmed that the social traits we measured were
104 meaningful by testing for individual repeatability of sociality; (2) We tested the prediction
105 that non-breeding sociality has fitness benefits, either driven by reproductive success
106 through opposite-sex association or through increased survival through network centrality
107 measures and is subject to selection.

108
109
110
111

Methods

Study system

113 We used data from the Lundy sparrow system, a long-term study based on the island of
114 Lundy (51.11N, 4.40W), \approx 19 km off North Devon, UK, in the Bristol Channel. The sparrows
115 on Lundy breed in nest boxes, sited in groups around the only village on the island. The
116 island is rodent-free and therefore the sparrows have no predators but for the occasional
117 vagrant raptor. House sparrows are a model organism in behavioral ecology and evolution,
118 and much is known about their biology, physiology and life-history (Andersson 1994;
119 Sánchez-Tójar et al. 2018). House sparrow are socially monogamous, but 25% of broods
120 show they can be genetically promiscuous (Schroeder et al. 2016). On Lundy, they have on
121 average 2-3 broods of 4-5 eggs per breeding season (Westneat et al. 2014). The sex ratio is
122 stable, and the mean lifespan of recruits is three years (Alif et al. 2022). Although sparrows
123 are territorial during the breeding season, during the non-breeding period they form

124 gregarious groups that forage communally for seed and at supplementary bird feeders
125 (Summer-Smith 1963), both of which are available year-round on Lundy.

126 Most sparrows were first captured, and tissue sampled in nest boxes at their natal site
127 during the breeding season (April to August) or using mist nets during the post-fledging
128 period (Schroeder et al. 2011; Girndt et al. 2019). Tissue samples were either blood or
129 mouth swabs and were stored in ethanol and refrigerated at 3°C prior to analysis. We
130 genotyped sparrow DNA at <22 microsatellite loci suitable for parentage assignment in
131 sparrows (Dawson et al. 2012). Using the genetic data, we assembled a near-complete
132 genetic pedigree (Schroeder et al. 2015, 2016), which at the time of writing spans twenty
133 years, 2000–2019, and 8,379 individuals. We fitted all sparrows with a unique
134 combination of a coded metal ring and three coloured leg rings. We also provided each
135 sparrow with a subcutaneous Passive Identification Transponder (PIT tag; TROVANID100:
136 11.5 × 2.1 mm and 0.1 g), under the skin of the breast, which we have previously shown
137 have no detrimental effect on subsequent fitness (for details see Schroeder et al. 2011).
138 These tagged individuals were then recorded when they visited a custom made 19.8cm x
139 19.8cm Radio Frequency Identification antenna (RFID; DorsetID) mounted on a seed
140 reservoir (for photo see Sánchez-Tójar et al. 2017; Brandl et al. 2019), positioned centrally
141 within our study site. The feeder was open access, and explicitly not limited to a single bird
142 feeding at one time, as is the case at hanging bird feeders (Youngblood 2019; Beck, Farine
143 and Kempnaers 2020). Our feeder recorded visiting birds every day that the island
144 generators were running (6am – midnight, seven days a week).

145
146 Social centrality measures

147 To quantify the sociality of individual sparrows we calculated measures of social centrality
148 (hereafter centrality measures) using presence data from the RFID antenna, collected
149 during the non-breeding periods, November–January, of 2015/16 (15 weeks) and 2016/17
150 (13 weeks, hereafter referred to events). An association between birds observed from
151 these data can reflect either, individuals that choose to maintain some social cohesion,
152 which we consider to be a non-random association, or individuals without pre-established
153 social cohesion who coincide in time and space, which we consider random mixing. These

154 data record the presence of birds without distinguishing between these two types of
155 association. Further, dyadic interactions can also be aggressive interactions, and our data
156 cannot exclude these cases. Although in sparrows', dominance hierarchies are typically
157 linear, there is no evidence for a correlation with reproductive fitness (Sánchez-Tójar
158 2018).

159

160 The 'gambit of the group' is a common approach used to identify discrete groups among all
161 associating individuals (Whitehead and Dufault 1999; Figure 1A). However, given the
162 gregarious nature of sparrows and the high activity at our feeder, at which non-discrete
163 groups of sparrows accumulated, the gambit of the group approach overestimated
164 associations between individuals (Figure 1A; also see Ferreira et al. 2020). One solution to
165 this would be to define a non-random association where two individuals overlapped by a
166 defined period (Δ_t) at our bird feeder. However, in our system, again due to the near
167 constant visitations, this resulted in linear network structures, e.g., linking the first bird to
168 the second, then the second to the third, and so on (Figure 1B). To account for the social
169 behaviour of sparrows, we derived a method to infer non-random associations that
170 assumed that non-random social associations are established before they attend the feeder
171 (suggested by Summer-Smith 1963). We therefore defined an association as two
172 individuals that arrived to feed within 150 seconds (Δ_t) of each other. Here an arrival is
173 defined as the (re)appearance of the individual at the feeder after being absent for a period
174 of minimally >300 seconds (Δ_l). We defined that $\Delta_t = 150$ seconds was sufficient to detect
175 and link individuals who arrive together in a group (see Figure 1C), and the resulting data
176 better sampled non-random associations between individuals in our system, from
177 watching sparrows in the field and on pre-recorded footage, arriving at our feeder (Plaza et
178 al., 2019).

179 From the resulting association matrices of the two events, 2015/16 and 2016/17, we built
180 a series of weighted, non-directional, social networks (hereafter, network/s), where the
181 vertices represent individual sparrows and interconnecting edges their associations. First,
182 we built individual networks for each of the 15 weeks in 2015/16, and 13 weeks in

183 2016/17, to estimate within-individual repeatability in centrality network metrics. This
184 was to validate these centrality measures against the individual repeatability already
185 demonstrated in this system using both RFID and video data (Plaza et al. 2019). Then, we
186 built a network for each event to extract non-breeding sociality. Finally, we also built two
187 bipartite networks from each event (sub-graphs), which only considered association
188 strength between opposite-sex individuals.

189 From the first non-breeding networks we extracted three centrality measures representing
190 different aspects of sociality for each individual using the ‘iGraph’ R package (Csardi and
191 Nepusz 2006): We selected centrality measures to reflect aspects of an individual’s social
192 preference, following similar studies on sociality (McDonald 2007; Farine and Whitehead
193 2015; Beck, Farine and Kempenaers 2021). Degree represents the number of associates,
194 and may impact fitness through enhanced mate choice, where individuals position
195 themselves alongside others of lesser quality (Oh and Badyaev 2010;), or where same-sex
196 associates benefit reproduction in cooperative breeding species (Bebbington et al. 2017;
197 Riehl and Strong 2018). Strength represents the quality of those relationships and may
198 influence the structure and behaviour of reproductive communities (Firth and Sheldon
199 2016; Culina, Firth and Hinde 2020). We calculated strength following (Farine 2013), using
200 the sum of dyadic Simple Ratio Indices (the association probability between a dyad, from 0,
201 never associated, to 1, always associated), which we transformed to give a measure of net
202 association quality (Eq. 1, where S denotes strength, $d_{(i)}$ and $\sum SRI_{(i)}$ the degree and SRI
203 of a given individual respectively and $N(V)$ = the number of vertices in a network)

$$(Eq. 1) \quad S = d_{(i)} \frac{SRI_{(i)}}{N(V)}$$

204 We used eigenvector centrality (following McDonald 2007, hereafter centrality) to quantify
205 the influence of an individual to all others within the network (Newman 2004; Oh and
206 Badyaev 2010); Finally, we extracted opposite-sex degree from the two bipartite sub-
207 graphs, the number of opposite-sex associations, which we used to represent an
208 individual’s pool of potential reproductive partners, as a fourth measure of sociality
209 (following Beck, Farine and Kempenaers 2021). Given the high density of sparrows visiting

210 the feeder, and the frequency at which those birds were detected we did not threshold our
211 networks (using only a sample of the birds attending an antenna, following Farine and
212 Whitehead 2015) to maintain network structure, although only birds who arrived in a dyad
213 (where degree > 0) were included in our networks.

214
215 Fitness measures

216 For each of the sparrows that survived to the following breeding period we used the
217 genetic pedigree to calculate two fitness measures, and for each of these, we calculated one
218 annual measure, and one across the lifetime of the sparrow. Both fitness measures are
219 based on the number of recruits, and we have shown that they correlate well with
220 reproductive value, thus represent fitness in an evolutionarily meaningful way (Alif et al.
221 2022). We defined recruits as offspring that survived and produced genetic offspring
222 themselves.

223 (1) *Recruits*. For the number of annual recruits, we summed individual recruits within the
224 breeding year following the social events. We then again summed individual recruits across
225 a lifetime, or up to 2020 as a measure of lifetime recruits. Note that the latter category only
226 contained five sparrows that were still alive at the point of census, and as such, our
227 recruitment data can be considered near complete. We excluded birds which did not
228 survive to breed, and yearlings which had zero recruits.

229 (2) *De-lifed fitness*. As a second fitness measure, we used de-lifed fitness (p_{ti} ; Eq. 2), which
230 estimates an individual's genetic contribution to the population (Coulson et al. 2006). De-
231 lifed fitness is a retrospective measure of realized fitness, relative to the population each
232 year, calculated by removing (de-lifing) an individual and its offspring from the pedigree
233 and recalculating the resulting change in population growth.

$$(Eq. 2) \quad p_{ti} = \frac{\xi_{t(i)} - w_{t(i)}}{N_t - 1}$$

234 Here, p_{ti} is the contribution of individual (i) to population growth during a specific period t .
235 Further, $\xi_{t(i)}$ is a measure of individual performance, here the number of surviving
236 offspring of individual i at the end of the breeding period t . We added a value of one if the

237 individual i itself survived to the next breeding period $t + 1$. The population size at time t is
238 N_t at the beginning of each breeding cycle (here April). To estimate the individual's
239 contribution to population growth, we use w_t , which represents the ratio of the population
240 size at $t + 1$ to the population size at t . This de-lifed fitness p_{ti} is an annual value per
241 individual, and we calculated it for all birds which produced at least one recruit. We then
242 also summed p_{ti} , within individuals as a lifetime de-lifed fitness measure, p_i .

243

244

245 Individual repeatability in sociality

246 First, we validated our centrality measures by confirming that they were repeatable within-
247 individuals between weeks. We modelled degree, strength, centrality and opposite-sex
248 degree respectively, as response variables each in four Gaussian linear mixed models
249 against the intercept, and with bird identity modelled as a random effect to compensate for
250 repeat identities between years. We then divided the variance explained by bird identity by
251 the total phenotypic variance of the trait to quantify repeatability (see Nakagawa and
252 Schielzeth 2010). We ran repeatability models using package MCMCglmm default
253 parameters and priors – the models converged robustly and reliably.

254

255 Selection on sociality – annual and lifetime fitness

256 We quantified the association between centrality measures and fitness. As all four
257 centrality measures are inherently correlated, we modeled each separately to avoid
258 collinearity (Webster, Schneider and Vander Wal 2020). For each centrality measure, we
259 ran two models, with annual recruits and annual de-lifed fitness as the response variables.
260 In the models with annual numbers of recruits as response, we assumed a Poisson error
261 distribution with a log link function, and in the models explaining de-lifed fitness we
262 assumed a Gaussian error distribution. We mean-centered all centrality measures within
263 each year, eliminating between-year differences, and modelled them as fixed covariates.
264 We also added each sociality variable as a quadratic effect to test for stabilizing or
265 disruptive selection where averages are favored over the extremes (Wolf et al. 2007). Bird
266 identity was modelled as a random effect on the intercept to account for pseudo-

267 replication, and cohort to account for environmental stochasticity. We modelled fixed
268 effects for sex (male, 1 or female, 0) and age (in calendar years) and age as a quadratic
269 effect, to account for variation in fitness as explained by demography (Schroeder et al.
270 2012). We added sex as an interaction term with age to account for the extra-pair
271 behaviour of older males (Girndt et al. 2018).

272 We modelled lifetime recruits and lifetime de-lifed fitness in the same way as the annual
273 ones, but instead of age we used lifespan, or maximum age at year 2020. Because each bird
274 was only represented once in this dataset, we only modelled cohort as a random effect.

275 We used Bayesian Markov Monte-Carlo simulations, using MCMCglmm (Hadfield 2010), to
276 run all models. For all models we used inverse Wishart priors for random effects, and ran
277 each over 343,000 iterations, with a burn-in of 3,000 and a thinning interval of 200. We
278 visually checked the posterior trace plots for all model outputs and ensured that
279 autocorrelation was below 0.1 and effective sample sizes between 1,000 and 2,000. The
280 fixed effects were considered statistically significant when the 95% credible interval (CI) of
281 its posterior distribution did not span zero.

282

283 Null models and dominance interactions

284 We ran a node-permutation null-model by shuffling the identities of birds visiting the
285 feeder between existing arrival times in our association matrices, thereby breaking any link
286 between sociality and fitness, over 1000 randomized permutations (following Farine,
287 2017). We used these randomized association matrices to construct 1000 new networks
288 and extracted the mode for our four centrality measures. We used these randomized
289 centrality measures to re-run all fitness models. Finally, to exclude the possibility that
290 dominance was interacting with our observed centrality measures, we tested for
291 correlations between the centrality measures and dominance from videos recorded during
292 the same period of our social network events. We represented individual dominance by
293 calculating ELO ratings, based on antagonistic interactions at the bird feeder (for further
294 details see Sánchez-Tójar 2018). We did not include the randomised centrality measures
295 from our null models in these correlations.

296

297 Results

298 The data consisted of 150 individual birds making 410,114 visits to the RFID feeder within
299 our study period (mean = 2,734 visits per bird, SD = 8,116), across both events. Excluding
300 birds that died prior to the start of our study or those that were ringed after, 160 tagged
301 birds survived in our system in November 2015, an additional 90 birds were tagged prior
302 to the 2017 breeding period, although not all survived to sampling. After constructing the
303 arrival networks, we identified 3,783 associations between 118 PIT tagged individuals
304 during 2015/2016, and 874 associations between 69 individuals in 2016/2017. These
305 networks contained 66.3% of 122 and 26.3% of 205 breeding birds in 2016 and 2017
306 respectively. Combined, we had 130 records for annual and lifetime fitness from 102
307 individuals, 33 were recorded in both years (for summary statistics see Table 1). Degree
308 and opposite-sex degree are closely correlated, implying that those with more opposite-sex
309 associates also tend to have more associates of either sex (supplementary material table 1)

310

311 Individual repeatability in sociality

312 We confirmed individual repeatability by week in all four centrality measures between 15
313 weeks in 2015/16: Degree, $R=0.29$ (0.15 – 0.39), Strength, $R=0.22$ (0.10 – 0.32), Centrality,
314 0.15 (0.03 – 0.27) and, Opposite sex degree, 0.27 (0.13 – 0.4); and, 13 weeks in 2016/17:
315 Degree, $R=0.29$ (0.15 – 0.39), Strength, $R=0.22$ (0.10 – 0.32), Centrality, 0.15 (0.03 – 0.27)
316 and, Opposite sex degree, 0.27 (0.13 – 0.4) (Table 1).

317

318 Selection on sociality – annual and lifetime fitness

319 Opposite-sex degree had a statistically significant linear relationship with the number of
320 annual recruits and annual de-lifed fitness. Strength and centrality had a negative quadratic
321 association with annual recruitment (Figure 2; Table 2; Table 3). Age and sex both also
322 predicted annual recruits, with younger individuals and females recruiting more offspring.
323 Age also positively predicted annual de-lifed fitness (Table2; Table3).

324

325 None of our centrality measures statistically significantly predicted lifetime recruitment
326 (Supplementary material table 4), however, all four had a statistically significant negative
327 quadratic relationship with lifetime de-lifed fitness (Figure 2).

328

329

330 Null models and dominance interactions

331 We found no link between fitness and sociality, nor any evidence of selection from our null
332 models (supplementary material figure 3). Likewise, dominance was not strongly
333 correlated with any centrality measure, implying that our method of assigning associations
334 based on arrival time, rather than shared space at a bird feeder, is unlikely to be influenced
335 by dominance (supplementary material table 1).

336

337 Table 1. Summary statistics for recruitment and centrality measures for individual house sparrows on Lundy Island during
 338 two non-breeding events (November–January 2015/2016 and 2016/2017). Each measure is given as mean, standard
 339 deviation and sample size, and including repeatability (R) and 95% CI for centrality measures.

| Summary statistics of recruitment | | | | | |
|---|----------|-------------------------------|------------------------------|--------------|-----------------|
| Fitness Variable | Scale | 2015/16 Mean, SD (n = 118) | 2016/17 Mean, SD (n = 69) | | |
| Recruits | Annual | 2.65, 1.98 | 0.78, 1.07 | | |
| | Lifetime | 5.34, 3.76 | 4.15, 3.86 | | |
| Summary statistics and repeatability of centrality measures | | | | | |
| Centrality measure | | Mean, SD | R, 95CI | Mean, SD | R, 95CI |
| Degree | | 64.11, 32.03 | 0.29, 0.15–0.39 | 25.33, 17.37 | 0.35, 0.16–0.49 |
| Strength | | 0.06, 0.05 | 0.22, 0.10–0.32 | 0.09, 0.13 | 0.33, 0.16–0.48 |
| Centrality | | 0.35, 0.30 | 0.15, 0.03–0.27 | 0.25, 0.31 | 0.23, 0.10–0.36 |
| Opposite-sex degree | | 32.00, 15.86 | 0.27, 0.13–0.4 | 12.18, 9.19 | 0.45, 0.24–0.61 |

340

341

342 Table 2. Annual recruitment model outputs from GLMMs for each of our four centrality measures (Degree, Strength, Centrality
 343 and Opposite-sex degree), derived of 410,114 visits to an RFID baited feeder by 150 individuals. Centrality measure of house
 344 sparrows on Lundy Island, modeled against annual recruits. We inferred significance where the 95% CI did not span zero,
 345 positive effects on the response variable are highlighted in red, and negative in blue.

| Annual recruits Variable | Posterior mode 95% credible intervals | | | |
|---------------------------------|--|----------------------|----------------------|----------------------|
| | Degree | Strength | Centrality | Opposite-sex degree |
| <i>Fixed terms</i> | | | | |
| (Intercept) | 3.49 1.46—6.11 | 3.69 1.58—6.46 | 4.19 1.60—6.31 | 3.78 1.58—6.50 |
| Centrality measure | 0.17 -0.01—0.34 | 0.22 -0.03—0.44 | 0.26 -0.01—0.45 | 0.25 0.05—0.41 |
| Centrality measure ² | -0.1 -0.26—0.06 | -0.12 -0.32—0.07 | -0.16 -0.34—0.08 | -0.04 -0.16—0.10 |
| Sex (male) | -0.67 -1.41—0.05 | -0.7 -1.46—0 | -0.74 -1.48—0 | -0.57 -1.47—0 |
| Age | -1.14 -2.03—-0.30 | -1.15 -2.04—-0.28 | -1.27 -1.99—-0.26 | -1.07 -2.00—-0.26 |
| Age ² | 0.05 -0.07—0.17 | 0.04 -0.08—0.17 | 0.06 -0.08—0.16 | 0.03 -0.07—0.17 |
| Age*Sex (male) | 0.21 -0.01—0.48 | 0.22 -0.02—0.46 | 0.28 -0.02—0.49 | 0.21 0—0.49 |
| <i>Random terms</i> | | | | |
| *Bird ID | 0 0—0.13 | 0 0—0.12 | 0 0—0.12 | 0 0—0.13 |
| *Cohort | 1.88 0.25—15.69 | 1.5 0.19—15.57 | 2.09 0—15.89 | 2.29 0.11—16.90 |
| Residuals | 0 0—0.27 | 0 0—0.28 | 0 0—0.29 | 0 0—0.24 |

346

347 Table 3. Lifetime recruitment model outputs from GLMMs for each of our four centrality measures (Degree, Strength,
 348 Centrality and Opposite-sex degree), derived of 410,114 visits to an RFID baited feeder by 150 individuals. Centrality measure
 349 of house sparrows on Lundy Island, modelled against lifetime recruits. We inferred significance where the 95% CI do not span
 350 zero, positive effects on the response variable are highlighted in red, and negative in blue. († Age in lifetime models denotes
 351 either lifespan, or age in 2020, whichever is greatest)

| Variable | Lifetime recruits | | | |
|---------------------------------|---------------------|---------------------|---------------------|---------------------|
| | Degree | Strength | Centrality | Opposite-sex degree |
| <i>Fixed term</i> | | | | |
| (Intercept) | 0.85 0—1.93 | 0.85 0.02—1.95 | 0.99 -0.06—1.87 | 0.8 -0.03—1.83 |
| Centrality measure | 0.1 -0—0.25 | 0.1 -0.09—0.3 | 0.12 -0.07—0.31 | 0.14 -0.05—0.25 |
| Centrality measure ² | -0.05 -0.19—0.11 | -0.01 -0.24—0.11 | -0.07 -0.24—0.11 | -0.03 -0.16—0.12 |
| Sex (male) | 0.33 -0.35—0.99 | 0.28 -0.36—0.91 | 0.28 -0.33—0.98 | 0.48 -0.24—1.03 |
| †Age | 0.1 0—0.23 | 0.11 0—0.24 | 0.09 0.01—0.25 | 0.12 0—0.24 |
| †Age*Sex (male) | -0.06 -0.20—0.07 | -0.07 -0.19—0.07 | -0.07 -0.2—0.06 | -0.06 -0.21—0.04 |
| <i>Random effects</i> | | | | |
| *Cohort | NA 0.07—2.78 | 0.47 0.07—2.76 | 0.45 0.06—3 | 0.39 0.10—2.77 |
| Residuals | NA 0—0.27 | 0.12 0.01—0.29 | 0.11 0.02—0.28 | 0.14 0—0.26 |

352

353 Discussion

354 We found evidence for annual fitness benefits of sociality, where individuals with more
355 opposite-sex associates had higher fitness in the breeding period, than those with fewer,
356 but that this did not translate to lifetime fitness. For lifetime fitness, we found evidence for
357 stabilising selection on sociality, including opposite-sex degree, suggesting that such
358 benefits are only short-lived, or contextual, in a wild population.

359 We constructed our networks by linking dyads of birds that arrived together to a bird
360 feeder, but ignored the time that they spent there, to eliminate most random associations.
361 Other studies have adapted similar approaches in high-density and open feeder systems, or
362 have considered the same implicit problems (Gomes, Boogert and Cardoso, 2021). Ferreira
363 et al. (2020), for example, identified flocks arriving, but then defined associations by spatial
364 proximity at a series of feeder boxes. Further research could optimize our approach for
365 other systems, either by refining the time after which an individual is determined to have
366 left the feeder (Δ_i), or similarly, the time it takes for all members of a group to interact with
367 the feeder upon arrival (Δ_t). Further work may also consider defining associations only
368 where a dyad visit together more often than would be expected by chance but doing so
369 must also consider some method of retaining peripheral associations. Although RFID
370 systems sample sociality well at a feeder, we cannot be sure that sociality traits are
371 maintained in other contexts – future works might consider tracking social behaviour
372 across time and space (For example see Ripperger and Carter 2021).

373 Where previous studies on wild birds have suggested links between aspects of sociality and
374 annual reproductive success (for examples see Firth and Sheldon 2016; Kohn 2017; Beck,
375 Farine, and Kempenaers 2020), we were also able to use lifetime measures, which better
376 reflect the genetic contribution of the individual to population growth, and thus, fitness.
377 This also allowed us to also describe how selection acts upon sociality across the
378 population. We found that sociality had little influence on fitness at the annual scale, apart
379 from for opposite-sex association, which was linked to increased recruitment and de-liferd
380 fitness. Our study corroborates that annual fitness benefits described elsewhere,

381 particularly regarding mate choice (Oh and Badyaev 2010; Beck, Farine, and Kempenaers
382 2021, Beck, Farine, and Kempenaers 2020) directly translate into increased annual fitness.
383 At the lifetime scale, our study also provides some insight into the evolution of social
384 behaviors, which we found to be maintained at the population average through stabilizing
385 selection. We are therefore, to the best of our knowledge, the first study to link sociality
386 with lifetime fitness benefits in a wild bird (but see Formica et al. 2021; Philson and
387 Blumstein 2022). Our results may also suggest a mechanism for selection on sociality
388 through enhanced mate choice, but the impact on survival was difficult to determine in this
389 study. Sociality is predicted to increase survival through reduced predation risk or
390 information transfer (Sorato et al. 2012; Hillemann et al 2020), but we found no evidence
391 to suggest that either was selected for, through higher centrality, in our analyses.

392 Stabilizing selection in this case may be driven by factors such as high mate fidelity or
393 changing sociality with age (Oh and Badyaev 2010; Albery et al. 2022), removing the need
394 to constantly maintain opposite-sex associations over lifetime while maintaining individual
395 fitness. However, those opposite-sex associations may also be beneficial in an extra-pair
396 context from the male perspective (Beck, Farine, and Kempenaers 2020) and requires
397 further research.

398 Our centrality measures were associated with lifetime, but not with annual de-lifed fitness,
399 and only opposite-sex degree was associated with recruitment at the annual scale. We
400 found no relationship between social centrality and dominance in our study using arrival
401 time to define sociality, but aggressive interactions are probably also reduced over the
402 non-breeding period (Summer-Smith 1963). None of our centrality metrics were linked
403 with recruitment at the lifetime scales. Overall, de-lifed fitness better represents fitness as
404 it is a relative measure of the contribution to population growth (Alif et al. 2022). The
405 number of recruits, while intuitively appealing, is not relative, and in good years, more
406 birds may have a higher number of recruits, while in poor years, having one recruit may be
407 an achievement. As such, this measure is not always comparable between years and may
408 explain our results. Further, recruitment is also dependent on parental effects and
409 relationships within the breeding season, which were not quantified here, although they

410 have been suggested elsewhere (Bebbington et al. 2017; Riehl and Strong 2018), whereas
411 de-lifed fitness also captures long-term survival. We found that older males recruited more
412 offspring, likely by virtue of older males siring more extra-pair offspring (Girndt et al.
413 2018). Likewise, younger birds had lower annual de-lifed fitness, because younger birds
414 had not recruited any offspring in previous years that would contribute to their current de-
415 lifed fitness.

416 In conclusion, we suggest a link between opposite-sex association and reproductive success
417 at the annual scale, suggesting a mechanism for selection to shape social behaviour. At the
418 lifetime scale we suggest that selection on sociality is stable, suggesting greater fitness for
419 those at the population mean, in a wild population of passerine birds.

420
421
422

423 Acknowledgments

424 We would like to thank the Lundy Landmark trust and the Lundy Field Society for their
425 ongoing support, particularly Dean Jones, Rosie Ellis and Tom Carr. This research was
426 supported by the QMEE CDT, funded by NERC grant number NE/P012345/1 (JD), a
427 fellowship from the Volkswagen Foundation (JS), a grant from the German Research
428 Foundation: Deutsche Forschungsgemeinschaft (JS), a European Research Council grant,
429 CIG PCIG12-GA-2012-333096 (JS), and by NERC grant NE/J024597/1 (TB). We also thank
430 two anonymous reviewers for their helpful feedback.

431

432 Data availability

433 Analyses reported in this article can be reproduced using the data provided by Dunning,
434 Jamie et al. (2022), Opposite-sex associations are linked with annual fitness, but sociality is
435 stable over lifetime, Dryad, Dataset, <https://doi.org/10.5061/dryad.z08kprrh>

436

437 Bibliography

438 Alif, Ž., J. Dunning, H.Y.J. Chik., T. Burke., and J Schroeder. 2022. What is the best fitness
439 measure in wild populations? A case study on the power of short-term fitness proxies to
440 predict reproductive value. *PLoS One*. 17(4):
441 e0260905. doi.org/10.1371/journal.pone.0260905

442
443 Andersson, M. 1994. *Sexual Selection*. Princeton University Press, New Jersey.

444
445 Aplin, L. M., D. R. Farine, J. Morland-Ferron, and B. C. Sheldon. 2012. Social networks predict
446 patch discovery in a wild population of songbirds. *Proc. R. Soc. B*. 279(1745): 4199–4205.
447 doi.org/10.1098/rspb.2012.1591

448

449 Aplin, L. M., D. R. Farine, J. Morand-Ferron, E. F. Cole, A. Cockburn, and B. C. Sheldon. 2013.
450 Individual personalities predict social behaviour in wild networks of great tits (*Parus*
451 *major*). *Ecol. Lett.* 16 (11): 1365–72. doi.org/10.1111/ele.12181.

452 Aplin, L. M., J. A. Firth, D. R. Farine, B. Voelkl, R. A. Crates, A. Culina, C. J. Garroway. 2015.
453 Consistent individual differences in the social phenotypes of wild great tits, *Parus major*.
454 *Anim. Behav.* 108: 117-127. doi.org/10.1016/j.anbehav.2015.07.016.

455 Aplin, L. M., D. R. Farine, R. P. Mann, and B. C. Sheldon. 2014. Individual-level personality
456 influences social foraging and collective behaviour in wild birds. *Proc. R. Soc. B. Sci.* 281
457 (1789): 20141016. doi.org/10.1098/rspb.2014.1016.

458
459 Archie, E. A., J. Tung., M. Clark., J. Altmann., and S.C. Alberts. 2014. Social affiliation matters:
460 Both same-sex and opposite-sex relationships predict survival in wild female baboons.
461 *Proc. R. Soc. B*. 281(1793): 20141261. doi.org/10.1098/rspb.2014.1261
462

463 Bebbington, K., S. A. Kingma, E. A. Fairfield, H. L. Dugdale, J. Komdeur, L. G. Spurgin, and D. S.
464 Richardson. 2017. Kinship and familiarity mitigate costs of social conflict between
465 Seychelles warbler neighbors. *PNAS*. 114(43): E9036 - E9045.
466 doi.org/10.1073/pnas.1704350114.

467 Beck, K. B., M. Valcu, and B. Kempenaers. 2020. Analysis of within-individual variation in
468 extrapair paternity in blue tits (*Cyanistes caeruleus*) shows low repeatability and little
469 effect of changes in neighborhood. *Behav. Ecol.* 31(6):1303—1315.
470 doi.org/10.1093/beheco/araa069.

471 Beck, K. B., D. R. Farine, and B. Kempenaers. 2020. Winter associations predict social and
472 extra-pair mating patterns in a wild songbird. *Proc. R. Soc. B*. 287(1921): 20192606.
473 doi.org/10.1098/rspb.2019.2606.

- 474 Beck, K. B., D. R. Farine, and B. Kempenaers. 2021. Social network position predicts male
475 mating success in a small passerine. *Behav. Ecol.* 32(5):856 – 864.
476 doi.org/10.1093/beheco/arab034.
- 477 Birkhead, T. R., and J. D. Biggins. 1987. Reproductive synchrony and Extra-pair copulation
478 in birds. *Ethology.* 74(4): 320 - 334. doi.org/10.1111/j.1439-0310.1987.tb00942.x.
- 479 Blankenhorn, W. 2010. *The quantitative study of sexual and natural selection*, in, *Animal*
480 *Behaviour: Evolution and Mechanisms*. P. Kappeler (Ed.). Springer. Germany.
- 481 Brandl, H. B., D. R. Farine, C. Funghi, W. Schuett, and S. C. Griffith. 2019. Early-life social
482 environment predicts social network position in wild zebra finches. *Proc. R. Soc. B.* 286:
483 20182579—20182579. doi.org/10.1098/rspb.2018.2579.
- 484 Cameron, E. Z., T.H. Setsaas, and W.L. Linklater. 2019. Social bonds between unrelated
485 females increase reproductive success in feral horses. *PNAS.* 106(33):13850 - 13853.
486 doi10.1073pnas.0900639106
- 487 Carter, K. D., R. Brand, J.K. Carter, B. Shorrocks, and A.W. Goldizen. 2013. Social networks,
488 long-term associations and age-related sociability of wild giraffes. *Anim. Behav.* 86(5):901 -
489 910. doi.org/10.1016/j.anbehav.2013.08.002.
- 490 Coulson, T., T. G. Benton, P. Lundberg, S. R. X. Dall, B. E. Kendall, and J. M. Gaillard. 2006.
491 Estimating individual contributions to population growth: Evolutionary fitness in
492 ecological time. *Proc. R. Soc. B.* 273 (1586): 547–55. doi.org/10.1098/rspb.2005.3357.
- 493 Croft, D. P., R. James, and J. Krause. 2008. *Exploring Animal Social Networks*. Princeton
494 University Press, NJ.
- 495 Cresswell, W. 1994. Flocking is an effective anti-predation strategy in redshanks, *Tringa*
496 *totanus*. *Anim. Behav.* 47(2): 433 - 442. doi.org/10.1006/anbe.1994.1057.
- 497 Cresswell, W., and J. L. Quinn. 2011. Predicting the optimal prey group size from predator
498 hunting behaviour. *J. Anim. Ecol.* 80(2):310-319. doi.org/10.1111/j.1365-
499 2656.2010.01775.x.
- 500 Csardi, G., and T. Nepusz. 2006. The igraph software package for complex network
501 research. *Inter J. Complex Syst.* 1695(5): 1 - 9.
- 502 Culina, A., J.A. Firth, and C.A. Hinde. 2020. Familiarity Breeds Success: Pairs That Meet
503 Earlier Experience Increased Breeding Performance in a Wild Bird Population. *Proc. R. Soc.*
504 *B. Proc. R. Soc. B.* 287 (1941): 20201554.
- 505 Dawson, D. A., G.J. Horsburgh, A.P. Krupa, Stewart, S. Skjelseth, H. Jensen, A.D. Ball, L.G.
506 Spurgin, M.E. Mannarelli, S. Nakagawa, J. Schroeder, C. Vangestel, G.N. Hinten and T. Burke.
507 2012. Microsatellite resources for Passeridae species: A predicted microsatellite map of the
508 house sparrow *Passer domesticus*. *Mol. Ecol. Res.* 12(3): 501 – 523. doi:10.1111/j.1755-
509 0998.2012.03115.x.

- 510
511 Dimitriadou, S., D.P. Croft, D.P. and S.K. Darden. 2019. Divergence in social traits in
512 Trinidadian guppies selectively bred for high and low leadership in a cooperative
513 context. *Sci Rep* 9(17194):. doi.org/10.1038/s41598-019-53748-4
514
- 515 Dobson, F., J. Murie and V. Viblanc. 2020. Fitness Estimations for Ecological Studies: An
516 Evaluation in Columbian Ground Squirrels. *Front. Ecol, Evol.* 8.
517 doi.org/10.3389/fevo.2020.00216
518
- 519 Endler, J.A., 1986. Natural Selection in the Wild. Princeton University Press, New Jersey.
520
- 521 Falconer, D.S. and T.F.C. Mackay. 1996. Introduction to Quantitative Genetics, Edinburgh.
522
- 522 Farine, D. R., and H. Whitehead. 2015. Constructing, conducting and interpreting animal
523 social network analysis. *J. Anim. Ecol.* 84(5):1144 - 1163. doi.org/10.1111/1365-
524 2656.12418.
- 525 Farine, D. R. 2017. A guide to null models for animal social network analysis. *Methods Ecol.*
526 *Evol.* 8(10): 1309 – 20. doi.org/10.1111/2041-210X.12772.
- 527 Farine, D. R., and B. C. Sheldon. 2015. Selection for territory acquisition is modulated by
528 social network structure in a wild songbird. *J. Evol. Biol.* 28(3): 547 - 556.
529 doi.org/10.1111/jeb.12587.
- 530 Farine, D. R. 2013. Animal Social Network Inference and Permutations for Ecologists in R
531 using asnipe. *Meth. Ecol. Evol.* 4(12): 1187 – 1194. doi/full/10.1111/2041-210X.12121.
532
- 533 Ferreira, A. C., R. Covas, L. R. Silva, S. C. Esteves, I. F. Duarte, R. Fortuna, F. Theron, C.
534 Doutrelant, and D. R. Farine. 2020. How to make methodological decisions when inferring
535 social networks. *Ecol. Evol.* 10 (17): 9132 – 9143. doi.org/10.1002/ece3.6568.
- 536 Firth, J. A., E. F. Cole, C. C. Ioannou, J. L. Quinn, L. M. Aplin, A. Culina, K. McMahon, and B. C.
537 Sheldon. 2018. Personality shapes pair bonding in a wild bird social system. *Nat. Ecol. Evol.*
538 2(11):1696 - 1699. doi.org/10.1038/s41559-018-0670-8.
- 539 Firth, J. A., and B. C. Sheldon. 2016. Social carry-over effects underpin trans-seasonally
540 linked structure in a wild bird population. *Ecol. Lett.* 19(11):1324 - 1332.
541 doi.org/10.1111/ele.12669.
- 542 Firth, J. A., B. C. Sheldon, and D. R. Farine. 2016. Pathways of information transmission
543 among wild songbirds follow experimentally imposed changes in social foraging structure.
544 *Biol. Lett.* 12(6). doi.org/10.1098/rsbl.2016.0144.
- 545 Formica, V., H. Donald, H. Marti, Z. Iregebay, and E. Brodie III. 2021. Social network position
546 experiences more variable selection than weaponry in wild subpopulations of forked
547 fungus beetles. *J Anim Ecol.* 90(1): 168-182. doi.org/10.1111/1365-2656.13322

- 548 Forstmeier, W., K. Martin, E. Bolund, H. Schielzeth, and B. Kempenaers. 2011. Female
549 extrapair mating behavior can evolve via indirect selection on males. *PNAS*. 108(26): 10608
550 - 10613. doi.org/10.1073/pnas.1103195108.
- 551 Franks, D. W., G. D. Ruxton, and R. James. 2010. Sampling animal association networks with
552 the gambit of the group. *Behav. Ecol. Sociobiol.* 64(3): 493 - 503. doi.org/10.1007/s00265-
553 009-0865-8.
- 554 Girndt, A., C. W. T. Chng, T. Burke, and J. Schroeder. 2018. Male age is associated with extra
555 pair paternity, but not with extra-pair mating behaviour. *Sci. Rep.* 8:8378.
556 doi.org/10.1038/s41598-018-26649-1
- 557 Girndt, A., G. Cockburn, A. Sánchez-Tójar, M. Hertel, T. Burke, and J. Schroeder. 2019. Male
558 age and its association with reproductive traits in captive and wild house sparrows. *J. Evol.*
559 *Biol.* 32(12):1431 - 1443. doi.org/10.1111/jeb.13542.
- 560 Grant, P.R., and B.R. Grant. 2019. Adult sex ratio influences mate choice in Darwin's finches.
561 *PNAS*. 116(25): 12372 - 12382. doi.org/10.1073/pnas.1903838116.
562
- 563 Gomes, A.C.R., N.J. Boogert, G.C. Cardoso. 2021. Network structure and the optimization of
564 proximity-based association criteria. *Meth. Ecol. Evo.* 12(1):88 -
565 100. doi.org/10.1111/2041-210X.13387.
566
- 567 Hadfield, J.D. 2010. MCMC methods for multi-response generalized linear mixed models:
568 The MCMCglmm R package. *J. Stat. Softw.* 33 (2):1 - 22. doi.org/10.18637/jss.v033.i02.
- 569 Hillemann, F., E. F. Cole, B. C. Sheldon, and D. R. Farine. 2020. Information use in foraging
570 flocks of songbirds: no evidence for social transmission of patch quality. *Anim. Behav.* 165:
571 35-41. doi.org/10.1016/j.anbehav.2020.04.024.
- 572 Kohn, G. M. 2017. Friends give benefits: autumn social familiarity preferences predict
573 reproductive output. *Anim. Behav.* 132: 201 - 208. doi.org/10.1016/j.anbehav.2017.08.013.
- 574 Korsten, P., T. Van Overveld, F. Adriaensen, and E. Matthysen. 2013. Genetic integration of
575 local dispersal and exploratory behaviour in a wild bird. *Nat. Comm.* 4: 2362.
576 doi.org/10.1038/ncomms3362.
- 577 Krause, J. U., and G. D. Ruxton. 2002. Living in groups. Oxford Series in Ecology and
578 Evolution. Oxford: Oxford University Press.
- 579 Kruuk, L. E. B. 2004. Estimating genetic parameters in natural populations using the
580 "animal model." *Proc. R. Soc. B.* 359(1446):873 - 890. doi.org/10.1098/rstb.2003.1437.
- 581 Kurvers, R. H. J. M., L. Prox, D. R. Farine, C. Jongeling, and L. Snijders. 2020. Season-specific
582 carryover of early life associations in a monogamous bird species. *Anim. Behav.* 164:25-37.
583 doi.org/10.1016/j.anbehav.2020.03.016.

- 584 Lea, A.J., D.T. Blumstein, T.W. Wey, and J.G.A. Martin. 2010. Heritable victimization and the
585 benefits of agonistic relationships. *PNAS*. 107(50): 21587–21592.
586 doi.org/10.1073/pnas.1009882107.
- 587 Le Galliard, J. F., P. S. Fitze, R. Ferrière, and J. Clobert. 2005. Sex ratio bias, male aggression,
588 and population collapse in lizards. *PNAS*.102(50): 18231–18236.
- 589 Maldonado-Chaparro, A. A., P. O. Montiglio, W. Forstmeier, B. Kempenaers, and D. R. Farine.
590 2018. Linking the fine-scale social environment to mating decisions: a future direction for
591 the study of extra-pair paternity. *Biol. Rev.* 93(3): 1558—1577.
592 doi.org/10.1111/brv.12408.
- 593 Mayer, C., and G. Pasinelli. 2013. New support for an old hypothesis: Density affects extra-
594 pair paternity. *Ecol. Evol.* 3(3):694 - 705. doi.org/10.1002/ece3.489.
- 595 McDonald, D. B. 2007. Predicting fate from early connectivity in a social network. *PNAS*.
596 104(26):10910–10914. doi.org/10.1073/pnas.0701159104.
- 597 McDonald, G.C., N. Engel, S. S. Ratão, T. Székely, and A. Kosztolányi. 2020. The impact of
598 social structure on breeding strategies in an island bird. *Sci. Rep.* 10(1): 13872.
599 doi.org/10.1038/s41598-020-70595-w.
- 600 Moiron, M., Charmantier, A. and Bouwhuis, S. 2022. The quantitative genetics of fitness sin
601 a wild seabird. *Evolution*. Doi:10.1111/evo.14516 [online ahead of print]
- 602 Nakagawa, S., and H. Schielzeth. 2010. Repeatability for Gaussian and non-Gaussian data: a
603 practical guide for biologists. *Biol. Rev.* 85(4): 935 - 956. [10.1111/J.1469-](https://doi.org/10.1111/J.1469-185x.2010.00141.X)
604 [185x.2010.00141.X](https://doi.org/10.1111/J.1469-185x.2010.00141.X)
605
- 606 Oh, K. P., and A. V. Badyaev. 2010. Structure of social networks in a passerine bird:
607 Consequences for sexual selection and the evolution of mating strategies. *Am. Nat.* 176(3):
608 E80—E89. doi.org/10.1086/655216.
- 609 Philson, C.S., Blumstein, D.T. 2022. Group social structure has limited impact on
610 reproductive success in a wild mammal. *Behav. Ecol.*
611 *arac102*, <https://doi.org/10.1093/beheco/arac102>
- 612 Plaza, M., T. Burke, T. Cox, A. F. Carroll, A. Girndt, G. Halford, D. A. Martin, et al. 2019. Social
613 network node-based metrics can function as proxies for animal personality traits. *J. Evol.*
614 *Biol.* 33(11): 1634 - 1642. doi.org/10.32942/OSF.IO/YVQ9D.
- 615 Proops, L., C. A. Troisi, T. K. Kleinhappel, and T. Romero. 2021. Non- \square random associations
616 in group housed rats (*Rattus norvegicus*). *Sci. Rep.* 11(1):15349. [doi.org/10.1038/s41598-](https://doi.org/10.1038/s41598-021-94608-4)
617 [021-94608-4](https://doi.org/10.1038/s41598-021-94608-4).
- 618 Psorakis, I., S. J. Roberts, I. Rezek, and B. C. Sheldon. 2012. Inferring social network
619 structure in ecological systems from spatiotemporal data streams. *J. R. Soc. Interface.* 9(76):
620 3055 – 3066. doi.org/10.1098/rsif.2012.0223.

- 621 Psorakis, I., B. Voelkl, C. J. Garroway, R. Radersma, L. M. Aplin, R. A. Crates, A. Culina, D. R.
622 Farine, J. A. Firth, C. A. Hinde, L. R. Kidd, N. D. Milligan, S. J. Roberts, B. Verhelst and B. C.
623 Sheldon . 2015. Inferring social structure from temporal data. *Behav. Ecol. Sociobiol.* 69: 857
624 - 866. doi.org/10.1007/s00265-015-1906-0.
- 625 R Core Team. 2022. R: A Language and Environment for Statistical Computing. Vienna,
626 Austria: R Foundation for Statistical Computing. <http://www.R-project.org/>.
- 627 Reid, J.M., Nietlisbach, P., Wolak, M.E., Keller, L.F. and Arcese, P. 2019. Individuals expected
628 genetic contributions to future generations, reproductive value, and short-term metrics of
629 fitness in free-living song sparrows (*Melospiza meolodia*). *Evolution Letters*. 3(3):271 – 285.
630 doi/pdf/10.1002/evl3.118
- 631 Riehl, C., and M. J. Strong. 2018. Stable social relationships between unrelated females
632 increase individual fitness in a cooperative bird. *Proc. R. Soc. B.* 285(20180130).
633 doi.org/10.1098/rspb.2018.0130.
- 634 Ripperger, S.P and Carter, G.C. 2021. Social Foraging in Vampire Bats Is Predicted by Long-
635 Term Cooperative Relationships. *PLoS Biology* 19 (9):e3001366.
- 636 Sánchez-Tójar, A., I. Winney, A. Girndt, M. J. P. Simons, S. Nakagawa, T. Burke, and J.
637 Schroeder. 2017. Winter territory prospecting is associated with life-history stage but not
638 activity in a passerine. *J. Avian Biol.* 48(3):407 - 416. doi.org/10.1111/jav.01055.
- 639 Sánchez-Tójar, A., Nakagawa, S., Sánchez-Fortún, M., Martin, D. A., Ramani, S., Girndt, A.,
640 Bókony, V., Kempenaers, B., Liker, A., Westneat, D. F., Burke, T., and Schroeder, J. 2018.
641 Meta-analysis challenges a textbook example of status signalling and demonstrates
642 publication bias. *ELife*. 7: e37385. doi.org/10.7554/eLife.37385
643
- 644 Sánchez-Tójar, A. 2018. *The evolution of social dominance in house sparrows*. [http://nbn-
645 resolving.de/urn:nbn:de:bsz:352-2-985014uzuvk43](http://nbn-resolving.de/urn:nbn:de:bsz:352-2-985014uzuvk43)
646
- 647 Schroeder, J., I. R. Cleasby, S. Nakagawa, N. Ockendon, and T. Burke. 2011. No evidence for
648 adverse effects on fitness of fitting passive integrated transponders (PITs) in wild house
649 sparrows *Passer domesticus*. *J. Avian Biol.* 42(3):271 - 275. doi.org/10.1111/j.1600-
650 048X.2010.05271.x.
- 651 Schroeder, J., S. Nakagawa, I. R. Cleasby, and T. Burke. 2012. Passerine birds breeding under
652 chronic noise experience reduced fitness. *PLoS One*. 7(7): E39200.
653 doi.org/10.1371/journal.pone.0039200.
- 654 Schroeder, J., T. Burke, M.E. Mannarelli, D.A. Dawson, and S. Nakagawa. 2012A. Maternal
655 effects and heritability of annual productivity. *J. Evol. Biol.* 24(1):149 - 156. doi:
656 10.1111/j.1420-9101.2011.02412.x.
657

- 658 Schroeder, J., S. Nakagawa, M. Rees, M. E. Mannarelli, and T. Burke. 2015. Reduced fitness in
659 progeny from old parents in a natural population. *PNAS*. 112(13): 4021 - 4025.
660 doi.org/10.1073/pnas.1422715112.
- 661 Schroeder, J., Y.H. Hsu, I. Winney, M. Simons, S. Nakagawa, and T. Burke. 2016. Predictably
662 philandering females prompt poor paternal provisioning. *Am. Nat.* 180(2): 219 - 230.
663 doi.org/10.1086/687243.
664
- 665 Silk, J. B., S.C. Alberts, and J. Altmann. 2003. Social Bonds of Female Baboons Enhance Infant
666 Survival. *Science*, 302(5648): 1227–1231. doi.org/10.1126/science.1088474
667
- 668 Silk, J. B. 2007. The adaptive value of sociality in mammalian groups. *Philos. Trans. R. Soc.*
669 *Biol. Sci.* 362(1480): 539 - 59. doi.org/10.1098/rstb.2006.1994.
- 670 Silk, J. B., J. C. Beehner, T. J. Bergman, C. Crockford, A. L. Engh, L. R. Moscovice, R. M. Wittig,
671 R. M. Seyfarth, and D. L. Cheney. 2009. The benefits of social capital: Close social bonds
672 among female baboons enhance offspring survival. *Proc. R. Soc. B.* 276 (1670): 3099–3104.
673 doi.org/10.1098/rspb.2009.0681.
- 674 Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R.
675 M., Seyfarth, R. M., and Cheney, D. L. 2010. Strong and consistent social bonds enhance the
676 longevity of female baboons. *Curr. Biol.* 20(15): 1359–1361.
677 doi.org/10.1016/j.cub.2010.05.067.
678
- 679 Silk, M. J., D. P. Croft, T. Tregenza, and S. Bearhop. 2014. The importance of fission-fusion
680 social group dynamics in birds. *Ibis*. 156(4):701 - 715. doi.org/10.1111/ibi.12191.
- 681 Simons, M. J. P., I. Winney, S. Nakagawa, T. Burke, and J. Schroeder. 2015. Limited catching
682 bias in a wild population of birds with near-complete census information. *Ecol. Evol.*
683 5(16):3500 - 3506. doi.org/10.1002/ece3.1623.
- 684 Sorato, E., P.R. Gullet, S.C. Griffith, and A.F. Russell. 2012. Effects of Predation Risk on
685 Foraging Behaviour and Group Size: Adaptations in a Social Cooperative Species. *Animal*
686 *Behaviour* 84 (4): 823–34.
- 687 Summer-Smith, D. 1963. *The House Sparrow*. Collins. UK.
- 688 Stanton, M. A., and J. Mann. 2012. Early Social Networks Predict Survival in Wild Bottlenose
689 Dolphins. *PLoS One*. 7(10):E47508. doi.org/10.1371/journal.pone.0047508.
- 690 Strickland, K., D. J. Mitchell, C. Delmé, and C. H. Frère. 2021. Repeatability and heritability of
691 social reaction norms in a wild agamid lizard. *Evolution*. 75(8): 1953–65.
692 doi.org/10.1111/evo.14298.
- 693 Thompson, N. A., and Cords, M. 2018. Stronger social bonds do not always predict greater
694 longevity in a gregarious primate. *Ecol. Evol.* 8(3): 1604–1614. doi.org/10.1002/ece3.3781
695

- 696 Thys, B., M. Eens, S. Aerts, A. Delory, A. Iserbyt, and R. Pinxten. 2017. Exploration and
697 sociability in a highly gregarious bird are repeatable across seasons and in the long-term
698 but are unrelated. *Anim. Behav.* 123: 339–48. doi.org/10.1016/j.anbehav.2016.11.014.
- 699 Voelkl, B., J. A. Firth, and B. C. Sheldon. 2016. Nonlethal predator effects on the turn-over of
700 wild bird flocks. *Sci. Rep.* 6: 33476. doi.org/10.1038/srep33476.
- 701 Webber, Q. M. R., D. C. Schneider and E. Vander Wal. 2020. Is less more? A commentary on
702 the practice of ‘metric hacking’ in animal social network analysis. *Anim. Behav.*, 168: 109–
703 120. doi.org/10.1016/j.anbehav.2020.08.011.
- 704 Westneat, D. F., Bókony, V., Burke, T., Chastel, O., Jensen, H., Kvalnes, T., Lendvai, Á. Z., Liker,
705 A., Mock, D., Schroeder, J., Schwagmeyer, P. L., Sorci, G., & Stewart, I. R. K. 2014. Multiple
706 aspects of plasticity in clutch size vary among populations of a globally distributed
707 songbird. *J. Anim. Ecol.* 83(4): 876–887. doi.org/10.1111/1365-2656.12191
708
- 709 Wey, T., D. T. Blumstein, W. Shen, and F. Jordán. 2008. Social network analysis of animal
710 behaviour: a promising tool for the study of sociality. *Anim. Behav.* 75(2): 333 – 44.
711 doi.org/10.1016/j.anbehav.2007.06.020.
- 712 Whitehead, H., and S. Dufault. 1999. Techniques for Analyzing Vertebrate Social Structure
713 Using Identified Individuals: Review and Recommendations. *Adv. Study Behav.* 28: 33 - 74.
714 doi.org/10.1016/S0065-3454(08)60215-6.
- 715 Wolf, M., G.S. van Doorn, O. Leimar, F.J. Weissing. 2007. Life-history trade-offs favour the
716 evolution of animal personalities. *Nature*, 447(7144): 581 - 584.
717
- 718 Youngblood, M. 2019. A Raspberry Pi-based, RFID-equipped birdfeeder for the remote
719 monitoring of wild bird populations. *Ring. Migr.* 34(1): 25 – 32.
720 doi.org/10.1080/03078698.2019.1759908

722 Figure 1. Three versions of a simulated event (A, B and C) show the interval over which five individuals (1–5, black/grey bars)
723 spent at a resource over time (t), and the derived social networks from each approach: A = gambit of the group, which links all
724 individuals in a discrete group equally; B = time-window overlap (by Δ_t), which links individuals who overlap at a resource;
725 and C = arrival time (developed for this study), which links individuals who arrive together to a resource. Red boxes denote
726 the time period during which individuals are considered to be associated, and overlaps represent an association: A, all
727 individuals within a group; B, where they are physically present at the same time (red box), or shortly after they depart to
728 account for birds which were present, but not currently being recorded by the antenna, in that case, over-lapping by Δ_t (red
729 over-hanging box, typically a few seconds); or, C, where they arrive within Δ_t of each other, but the subsequent time spent at a
730 feeder is irrelevant. However, note that the function of Δ_t differs between B and C; Where in B, Δ_t functions to detect when
731 birds are in the same place but where one (or more) are not currently being detected by the antenna, in C the function is to
732 link all individuals which arrive together, while ignoring those already present at the resource, which has the potential to link
733 two separate groups in A and B. In the case of C, an additional interval (Δ_i) is required to define when birds have left the
734 resource, after which they can be recorded as arriving again.

735

736

737 Figure 2. De-lifed fitness as response variables against Centrality measures from 8 linear mixed models, at two scales, from the
738 Lundy Island house sparrows, derived of 410,114 visits to an RFID baited feeder by 150 individuals: Explanatory variables for
739 Annual de-lifed fitness (A); and Lifetime de-lifed fitness (B), where 2 denotes a quadratic function, also shown in the four
740 adjacent panels for A and B, and their 95% credible intervals. Credible intervals are given as solid bars for each explanatory
741 variable, where a solid point denotes the posterior mode. Black bars denote no effect on the response variable; red denote a
742 positive and blue, a negative, relationship with the response. In adjacent panels, quadratic functions of each response variable
743 presented in A and B (on the Y axis: A Centrality, Degree, Opp. Degree, Strength, and B Centrality, Degree, Opp. Degree,
744 Strength). Blue curves represent a negative interaction with fitness measures (on the X axis). Measures with no effect are not
745 shown in figure. We found no link to sex, and age was also subject to stabilising selection, (given in supplementary material
746 table 4).

747

