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

*Jamie Dunning[1], Terry Burke[2], Alex Hoi Hang Chan[1], Heung Ying Janet Chik[3,4], Tim Evans[5], Julia Schroeder[1].

[1]Department of Life Sciences, Imperial College London, United Kingdom

[2]Ecology and Evolutionary Biology, School of Biosciences, The University of Sheffield, United Kingdom

[3]Groningen Institute for Evolutionary Life Sciences, University of Groningen, Netherlands

[4]School of Natural Sciences, Macquarie University, Australia

[5]Center for Complexity Science, Imperial College London, United Kingdom

*Corresponding author – jamiedunning8@googlemail.com

Lay Summary

How many social connections birds have is linked to their success in the following breeding season. However, we do not know whether this holds true across a birds' lifetime. Our research confirms that birds with more connections to the other sex have higher annual breeding success. However, over a lifetime we find that birds with an average amount of social connections have better fitness than those at the extremes. This suggests that evolution may favour an average sociality.

Abstract

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

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

Background

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

Although some benefits of maintaining close social associations are linked with social behaviors during the breeding period (Bebbington et al. 2017; Riehl and Strong 2018), most of these benefits tend to be short-term and contextual. Instead, benefits associated with reproduction are often linked with social behaviour during the non-breeding period (Firth and Sheldon 2016; Kohn 2017; Maldonado-Chaparro et al. 2018; Beck, Farine, and Kempenaers 2020), when group cohesion is stronger (Silk et al. 2014; Kurvers 2020). For example, communal foraging between socially associated individuals during the non-breeding period facilitates resource information transfer (Aplin et al. 2012; Firth, Sheldon

and Farine 2016; Hillemann et al. 2020) and reduces predation risk (Cresswell 1994; Cresswell and Quinn 2011). However, these benefits may also incur costs associated with competition for resources, and during the breeding period, competition for mates (Birkhead and Biggins 1987; Le Galliard et al. 2005; Forstmeier et al. 2011; Mayer and Pasinelli 2013; Grant and Grant 2019; but also see Lea et al. 2010). Likewise, individuals that hold more central social network positions in the non-breeding period may increase their breeding success, by maximizing their opportunity for mate choice (McDonald 2007; Oh and Badyaev 2010; Firth et al. 2018; Beck, Farine and Kempenaers 2021). Although the association between annual fitness correlates and non-breeding sociality has been well described, data on the link with lifetime fitness, and selection of sociality, remains scarce.

With the recent development of tools to construct and analyse social networks (Wey et al. 2008; Farine and Whitehead 2015) the study of sociality has become popular in ecology and evolution. Yet, to describe the association between sociality and fitness any potential study must first overcome two problems: (1) A social association must be clearly defined relative to the behavior of the study system (Figure 1; Psorakis et al. 2012, 2015), and (2) to study the evolution of social behaviour, precise measures of individual fitness must be quantified to test for correlation with a social trait – selection. Although annual fitness correlates are widely used, lifetime fitness is more precise than correlates, not subject to the stochasticity of annual measures (Dobson, Murie and Viblanc 2020; Alif et al. 2022) and thus, can better describe selection pressure acting on a trait (Endler 1986; Blankenhorn 2010; Reid et al. 2019). However, lifetime fitness requires wild animals to be monitored throughout their whole lives, and all breeding attempts, and the fates of their offspring, must be recorded to determine recruitment. All of these require a multi-generational, genetic pedigree (Kruuk 2004; Korsten et al. 2013).

Our study system, an island population of house sparrows *Passer domesticus* (hereafter, sparrow/s) where we monitor all individuals from birth to death, without capture bias (Simons et al. 2015), overcomes both problems. (1) We have sociality data from birds that are electronically registered visiting a feeder. Sociality measures are repeatable across different timescales and contexts in this and other populations (Plaza et al. 2019). (2) We have lifetime recruitment data available, from a multi-generational genetic pedigree that,

because our population is closed, we can use to compute precise annual and lifetime fitness estimates (Schroeder et al. 2015; Alif et al. 2022).

Here, we aim to better understand the potential for selection on sociality, and therefore, our two aims are: (1) We confirmed that the sociality traits we measured were meaningful by testing for individual repeatability of sociality. (2) We tested for selection on non-breeding sociality using annual, and lifetime fitness measures.

Methods

Study system

We used data from the Lundy sparrow system, a long-term study based on the island of Lundy (51.11N, 4.40W), ≈19 km off North Devon, UK, in the Bristol Channel. The sparrows on Lundy breed in nest boxes, sited in groups around the only village on the island. The island is rodent-free and therefore the sparrows have no predators but for the occasional vagrant raptor. House sparrows are a model organism in behavioral ecology and evolution, and much is known about their biology, physiology, and life-history (Andersson 1994; Sánchez-Tójar et al. 2018). Females are socially monogamous, but 25% of broods show they can be genetically promiscuous (Schroeder et al. 2016). On Lundy, they have on average 2-3 broods of 4-5 eggs per breeding season (Westneat et al. 2014). The sex ratio is stable, and the mean lifespan of recruits is three years (Alif et al. 2022). Although sparrows are territorial during the breeding season, during the non-breeding period they form gregarious groups that forage communally for seeds and at supplementary bird feeders (Summer-Smith 1963), both of which are available year-round on Lundy.

Most sparrows were first captured, and tissue sampled at their natal site during the breeding season (April to August) and a few during the post-fledging period (Schroeder et al. 2011; Girndt et al. 2019). We genotyped sparrow DNA at <22 microsatellite loci suitable for parentage assignment in sparrows (Dawson et al. 2012). Using the genetic data, we assembled a near-complete genetic pedigree (Schroeder et al. 2015, 2016), which at the time of writing spans twenty years, 2000–2019, and 8,379 individuals. We fitted all

133 sparrows with a unique combination of a coded metal ring and three coloured leg rings. We
134 also provided each sparrow with a subcutaneous Passive Identification Transponder (PIT
135 tag; TROVANID100: 12 × 2 mm and 0.1 g), which we have previously shown have no
136 detrimental effect on subsequent fitness (Schroeder et al. 2011). These tagged individuals
137 were then recorded when they visited a custom made 19.8cm x 19.8cm Radio Frequency
138 Identification antenna (RFID; DorsetID) mounted below a seed reservoir (Sánchez-Tójar et
139 al. 2017; Brandl et al. 2019), positioned centrally within our study site. The feeder was
140 open access, and explicitly not limited to a single bird feeding at one time, as is the case at a
141 hanging bird feeder (Youngblood 2019; Beck, Farine and Kempenaers 2020), taking into
142 consideration the gregarious feeding behaviour of house sparrows.

143

144 **Sociality measures**

145 To quantify the sociality of individual sparrows we used presence data from the RFID
146 antenna, collected during the non-breeding periods, November–January, of 2015/16 (15
147 weeks recording time) and 2016/17 (13 weeks recording time, hereafter referred to as two
148 events). An association between birds observed from these data can either reflect two or
149 more individuals that choose to maintain some social cohesion with one another. We
150 consider this to be a non-random association. Another option is that two individuals
151 without pre-established social cohesion coincide in time and space. We consider this
152 random mixing. The data records the presence of birds without distinguishing between
153 these two types of association. Hence, we derived a method to infer non-random
154 associations from these data. Further, dyadic interactions can also be aggressive
155 interactions, and our data cannot exclude these cases. Sparrows have long considered to be
156 a text-book model for signaling dominance hierarchies. Although, a recent meta-analysis
157 did not support the idea that the black bib of the house sparrows predicts dominance
158 status (Sánchez-Tójar et al. 2018). In sparrows' dominance hierarchies are typically linear,
159 while, not particularly steep, and there is no evidence for a correlation with reproductive
160 fitness (Sánchez-Tójar 2018).

161 The 'gambit of the group' is a common approach used to identify discrete groups among all
162 associating individuals (Whitehead and Dufault 1999; Figure 1A). However, given the

163 gregarious nature of sparrows and the high activity at our feeder, at which non-discrete
164 groups of sparrows accumulated, the gambit of the group approach overestimated
165 associations between individuals (Figure 1A; also see Ferreira et al. 2020), capturing both
166 random mixing and non-random associations. One solution to this would be to define a
167 non-random association as whenever two individuals overlapped by a defined period (Δ_t)
168 in the proximity of our bird feeder. However, in the sparrow system, again due to the near
169 constant visitations, this resulted in linear network structures, e.g., linking the first bird to
170 the second, then the second to the third, and so on for the whole observation period (Figure
171 1B). To account for the social behaviour, and dominance hierarchies, of sparrows, we
172 instead assumed that small groups and non-random social associations are established
173 before they attend the feeder (Summer-Smith 1963). Therefore we defined an association
174 simply as two individuals that arrived to feed within 150 seconds (Δ_t) of each other. Here,
175 an arrival is defined as the (re)appearance of the individual at the feeder after being absent
176 for a period of minimally >300 seconds (Δ_I). From our experience watching sparrows in
177 the field and on pre-recorded footage, arriving at our feeder (Plaza et al., 2019) to conclude
178 that Δ_t = 150 seconds was long enough to detect and link all individuals who arrive
179 together in a group (see Figure 1C), and the resulting data better samples non-random
180 associations between individuals.

181 From the resulting association matrices of the two events, 2015/16 and 2016/17, we built
182 a series of weighted, non-directional, social networks (hereafter, network/s), where the
183 vertices represent individual sparrows and interconnecting edges their associations. First,
184 we built individual networks for each of the 15 weeks in 2015/16, and 13 weeks in
185 2016/17, to estimate within-individual repeatability in social network metric, to validate
186 our sociality measures against the individual repeatability already demonstrated in this
187 system using both RFID and video data (Plaza et al. 2019). Then, we built a network for
188 each event to extract non-breeding sociality. Finally, we also built two bipartite networks
189 from each event (sub-graphs), which only considered association strength between
190 opposite-sex individuals.

191 From the first non-breeding networks we extracted three measures of sociality for each
192 individual using the 'iGraph' R package (Csardi and Nepusz 2006): We selected the sociality

193 measures to reflect aspects of an individual's social preference, following similar studies on
194 sociality (McDonald 2007; Beck, Farine and Kempenaers 2021). Degree represents the
195 number of associated individuals. Strength represents the quality of those relationships.
196 We calculated strength following (Farine 2013), using the sum of dyadic Simple Ratio
197 Indices (the association probability between a dyad, from 0, never associated, to 1, always
198 associated), which we transformed to give a measure of net association quality (Eq. 1,
199 where S denotes strength, $d_{(i)}$ and sum $SRI_{(i)}$ the degree and SRI of a given individual
200 respectively and N(V) = the number of vertices in a network)

201 $$(Eq.1) \quad S = d_{(i)} \frac{SRI_{(i)}}{N(V)}$$

202 We used eigenvector centrality (following McDonald 2007, hereafter centrality) to quantify
203 the influence of an individual to all others within the network (Newman 2004); Finally, we
204 extracted opposite-sex degree from the two bipartite sub-graphs, and which we used to
205 represent an individual's pool for mate choice as a fourth measure of sociality (following
206 Beck, Farine and Kempenaers 2021). We did not threshold our networks (following Farine
207 and Whitehead 2015) to maintain network structure.

208

209 **Fitness measures**

210 For each of the sparrows that survived to the following breeding period we used the
211 genetic pedigree to calculate two fitness measures, and for each of these, we calculated one
212 annual measure, and one across the lifetime of the sparrow. Both fitness measures are
213 based on the number of recruits, and we have shown that they correlate well with
214 reproductive value, thus represent fitness in an evolutionarily meaningful way (Alif et al.
215 2022). We defined recruits as offspring that survived and produced genetic offspring
216 themselves.

217 (1) ***Recruits***. For the number of annual recruits, we summed individual recruits within the
218 breeding year following the social events. We then again summed individual recruits across
219 a lifetime, or up to 2020 as a measure of lifetime recruits. Note that the latter category only

contained five sparrows that were still alive at the point of census, and as such, our recruitment data can be considered near complete.

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

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

Here, p_{ti} is the contribution of individual ($_i$) to population growth during a specific period t. Further, $\xi_{t(i)}$ is a measure of individual performance, here the number of surviving offspring of individual i at the end of the breeding period t. We added a value of one if the individual i itself survived to the next breeding period $t + 1$. The population size at time t is N_t at the beginning of each breeding cycle (here April). To estimate the individual's contribution to population growth, we use w_t, which represents the ratio of the population size at $t + 1$ to the population size at t. This de-lifed fitness p_{ti} is an annual value per individual, and we calculated it for all birds which produced at least one recruit. We then also summed p_{ti}, within individuals as a lifetime de-lifed fitness measure, p_i.

Individual repeatability in sociality

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

249 **Selection on sociality – annual fitness**

250 We quantified the association between sociality measures and fitness. As all four sociality
251 measures are inherently correlated, we modeled each separately to avoid collinearity
252 (Webster, Schneider and Vander Wal 2020). For each sociality measure, we ran two
253 models, with annual recruits and annual de-lifed fitness as the response variables. In the
254 models with annual numbers of recruits as response, we assumed a Poisson error
255 distribution with a log link function, and in the models explaining de-lifed fitness we
256 assumed a Gaussian error distribution. We mean-centered all social measures within each
257 year, eliminating between-year differences, and modelled them as fixed covariates. To test
258 for stabilizing or disruptive selection (Wolf et al. 2007), where averages are favored over
259 the extremes, we added each sociality variable also as quadratic effect. Bird identity was
260 modelled as a random effect on the intercept to account for pseudo-replication, and cohort
261 to account for environmental stochasticity. We modelled fixed effects for sex (male, 1 or
262 female, 0) and age (in calendar years) and age as a quadratic effect, to account for variation
263 in fitness as explained by demography (Schroeder et al. 2012). We added sex as an
264 interaction term with age to account for the extra-pair behaviour of older males (Girndt et
265 al. 2018).

266 **Selection on sociality – lifetime fitness**

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

270 **Statistical analyses**

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

Null models and dominance interactions

We ran a node-permutation null-model by randomizing bird identity against arrival time, without replacement, before constructing new networks and calculating mode network centrality measures from 1000 randomized permutations (Farine, 2017). We used these mean random measures to re-run all fitness models. Finally, to exclude the possibility that dominance was interacting with sociality measures, we tested for correlations between the sociality measures and between ELO ratings calculated from video observations taken within our events (Sánchez-Tójar 2018).

Results

Our data consisted of 150 individual birds making 410,114 visits to the RFID feeder within our study period (mean = 2,734 visits per bird, SD = 8,116), across both events. After constructing the networks, we identified 3,783 associations between 118 PIT tagged individuals during 2015/2016, and 874 associations between 69 individuals in 2016/2017. These networks contained 66.3% of 122 and 26.3% of 205 breeding birds in 2016 and 2017 respectively. Combined, we had 130 records for annual and lifetime fitness from 102 individuals, and where 33 were recorded in both years (for summary statistics see Table 1). The correlation between degree and opposite-sex degree implying that those with more opposite-sex associates also tend to also have more associates of either sex.

Individual repeatability in sociality

We confirmed individual repeatability by week in all four sociality measures between 15 weeks in 2015/16 and 13 weeks in 2016/17 (Table 1).

Selection on sociality – annual fitness

Opposite-sex degree had a statistically significant, negative linear relationship with the number of annual recruits and annual de-lifed fitness. Strength and centrality had a negative quadratic association with annual recruitment (Figure 2; Table 2; Table 3). Age and sex both also predicted annual recruits, with younger individuals and females

recruiting more offspring. Age also positively predicted annual de-lifed fitness (Table2; Table3). Older males had greater recruitment annually.

Selection on sociality – lifetime fitness

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

Null models and dominance interactions

We found no link between fitness and sociality, nor any evidence of selection from our null models (supplementary files, Figure 3). Likewise, dominance was not strongly correlated with sociality, implying that our method of assigning associations based on arrival time, rather than shared space at a bird feeder is not influenced by dominance (supplementary files).

Table 1. Summary statistics for fitness and summary statistics and repeatability for social measures for individual house sparrows on Lundy Island during two non-breeding events (November–January 2015/2016 and 2016/2017). Each measure is given as mean and standard deviation, as well as an R value which measures repeatability and a 95% CI.

Fitness Variable	Scale	2015/16 Mean, SD		2016/17 Mean, SD	
Recruits	Annual	2.65, 1.98		0.78, 1.07	
	Lifetime	5.34, 3.76		4.15, 3.86	
Sociality 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

Table 2. Model outputs, one for each of our four sociality measures (degree, strength, centrality, and opposite-sex degree), against annual recruits of house sparrows on Lundy Island, with a Poisson distribution. We inferred significance where the 95% CI did not span zero, positive effects on the response variable are highlighted in red, and negative in blue.

Annual recruits	Posterior mode 95% credible intervals			
Variable	Degree	Strength	Centrality	Opposite-sex degree
Fixed terms				
(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
Social 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
Social 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
Random terms				
*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

Table 3. Model outputs from GLMMs for each of our four sociality measures (Degree, Strength, Centrality and Opposite-sex degree), against lifetime recruits in the Lundy house sparrow system. We inferred significance where the 95%CI do not span zero, positive effects on the response variable are highlighted in red, and negative in blue. († Age in lifetime models denotes either lifespan, or age in 2020, whichever is greatest)

Lifetime recruits	Posterior mode, 95% credible intervals (lower – upper)			
Variable	Degree	Strength	Centrality	Opposite-sex degree
Fixed term				
(Intercept)	0.85 0—1.93	0.85 0.02—1.95	0.99 -0.06—1.87	0.8 -0.03—1.83
Social measure	0.1 -0—0.25	0.1 -0.09—0.3	0.12 -0.07—0.31	0.14 -0.05—0.25
Social 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
Random effects				
*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

Discussion

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

We constructed our networks by linking dyads of birds that arrived together to a bird feeder, but ignored the time that they spent there, to eliminate random associations. Other studies have also adapted similar approaches in high-density and open feeder systems, or have considered the same implicit problems (Gomes, Boogert and Cardoso 2021). Ferreira et al. (2020), for example, identified flocks arriving, but then defined associations by proximity at the feeder. Further research could optimize our approach for other systems, either by refining the time after which an individual is determined to have left the feeder (Δ_i), which we defined by watching a feeder with binoculars and thus, is likely to be specific to our system, or similarly, the time it takes all members of a group to interact with the feeder upon arrival (Δ_t).

Where previous studies on populations of wild birds have suggested links between aspects of sociality and annual fitness correlates (for examples see Firth and Sheldon 2016; Kohn 2017; Beck, Farine, and Kempenaers 2020), we also used lifetime measures, which better reflect the genetic contribution of the individual to population growth, and thus, fitness. This also allows us to describe how selection acts upon sociality across the population. We found that sociality had little influence on fitness at the annual scale, bar for opposite-sex association, which was linked to increased recruitment. Although not tested explicitly, our study corroborates that annual fitness benefits described elsewhere, particularly regarding mate choice (Oh and Badyaev 2010; Beck, Farine, and Kempenaers 2020, Beck, Farine, and Kempenaers 2021), directly translate into increased annual fitness. At the lifetime scale

however, our study also provides some insight into the evolution of social behaviors, which we found to be maintained at the population average through stabilizing selection.

Stabilizing selection in this case may be driven by factors such as high mate fidelity or changing sociality with age (Oh and Badyaev 2010; Albery et al. 2022), removing the need to constantly maintain opposite-sex associations over lifetime while maintaining individual fitness. However, those opposite-sex associations may be beneficial in an extra-pair context from the male perspective (Beck, Farine, and Kempenaers 2020), but support for sociality as a mechanism for 'good-genes' hypotheses are scarce (Hsu et al 2015) and require further research.

Our sociality measures were associated with de-lifed fitness and less so with recruitment at both annual and lifetime scales. This is probably because, although sociality may enhance mate choice, recruitment is also dependent on parental effects and relationships within the breeding season, which were not quantified here, although they have been suggested elsewhere (Bebbington et al. 2017; Riehl and Strong 2018), whereas de-lifed fitness also captures long-term survival. We found that older males recruited more offspring, likely by virtue of older males siring more extra-pair offspring (Girndt et al. 2018). Likewise, younger birds had lower annual de-lifed fitness, because younger birds had not recruited any offspring in previous years that would contribute to their current de-lifed fitness.

Overall, de-lifed fitness better represents fitness as it is a relative measure of the contribution to population growth (Alif et al. 2022). The number of recruits, while intuitively appealing, is not relative, and in good years, more birds may have a higher number of recruits, while in poor years, having one recruit may be an achievement. As such, this measure is not always comparable between years, and this might explain the discrepancy in our findings.

In conclusion, this study is the first to demonstrate a correlation between lifetime fitness measures and sociality, and present evidence for stabilizing selection on sociality in a wild population of passerine birds.

Acknowledgments

We would like to thank the Lundy Landmark trust and the Lundy Field Society for their ongoing support for our field work. This work was supported by the Quantitative Methods in Ecology and Evolution (QMEE) CDT funded by NERC (JD), a fellowship from the Volkswagen Foundation (JS), a grant from the German Research Foundation: Deutsche Forschungsgemeinschaft (JS), CIG PCIG12-GA-2012-333096 from the European Research Council (JS), and by Natural Environment Research Council grant NE/J024597/1 (TB). We also thank two anonymous reviewers for their helpful feedback.

The data used in this manuscript have been made available as supplementary files.

Bibliography

Albery GF, Clutton-Brock TH, Morris A, Morris S, Pemberton JM, Nussey DH, and Firth JA. Ageing red deer alter their spatial behaviour and become less social. Nat Ecol Evol (2022). https://doi.org/10.1038/s41559-022-01817-9

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

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

Aplin LM, Farine DR, Morland-Ferron J, and Sheldon BC. 2012. Social networks predict patch discovery in a wild population of songbirds. Proc. R. Soc. B. 279(1745): 4199–4205. doi.org/10.1098/rspb.2012.1591

Aplin, LM, Farine DR, Morand-Ferron J, Cole EF, Cockburn A, and Sheldon BC. 2013. Individual personalities predict social behaviour in wild networks of great tits (Parus major). Ecol. Lett. 16 (11): 1365–72. doi.org/10.1111/ele.12181.

Aplin, LM, J. Firth JA, Farine DR, Voelkl B, Crates RA, Culina A, Garroway CJ. 2015. Consistent individual differences in the social phenotypes of wild great tits, Parus major. Anim. Behav. 108: 117-127. doi.org/10.1016/j.anbehav.2015.07.016.

Aplin, LM, Farine DR, Mann RP, and Sheldon BC. 2014. Individual-level personality influences social foraging and collective behaviour in wild birds. Proc. R. Soc. B.. Sci. 281 (1789): 20141016. doi.org/10.1098/rspb.2014.1016.

Archie EA, Tung J, Clark M, Altmann J, and Alberts SC. 2014. Social affiliation matters: Both same-sex and opposite-sex relationships predict survival in wild female baboons. Proc. R. Soc. B. 281(1793): 20141261. doi.org/10.1098/rspb.2014.1261

Bebbington K, Kingma SA, Fairfield EA, Dugdale HL, Komdeur J, Spurgin LG, and Richardson DS. 2017. Kinship and familiarity mitigate costs of social conflict between Seychelles warbler neighbors. PNAS. 114(43): E9036 - E9045. doi.org/10.1073/pnas.1704350114.

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

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

Beck KB, Farine DR and Kempenaers B. 2021. Social network position predicts male mating success in a small passerine. Behav. Ecol. 32(5):856 – 864. doi.org/10.1093/beheco/arab034.

Birkhead TR and Biggins JD. 1987. Reproductive synchrony and Extra-pair copulation in birds. Ethology. 74(4): 320 - 334. doi.org/10.1111/j.1439-0310.1987.tb00942.x.

Blankenhorn W. 2010. The quantitative study of sexual and natural selection, in, Animal Behaviour: Evolution and Mechanisms. Kappeler P (Ed.). Springer. Germany.

Brandl HB, Farine DR, Funghi C, Schuett W, and Griffith SC. 2019. Early-life social environment predicts social network position in wild zebra finches. Proc. R. Soc. B. 286: 20182579—20182579. doi.org/10.1098/rspb.2018.2579.

Cameron EZ, Setsaas TH and Linklater WL. 2019. Social bonds between unrelated females increase reproductive success in feral horses. PNAS. 106(33):13850 - 13853. doi10.1073pnas.0900639106

Carter KD, Brand R, Carter JK, Shorrocks B, and Goldizen AW. 2013. Social networks, long-term associations and age-related sociability of wild giraffes. Anim. Behav. 86(5):901 - 910. doi.org/10.1016/j.anbehav.2013.08.002.

Croft DP., James R and Krause J. 2008. Exploring Animal Social Networks. Princeton University Press, NJ.

Coulson T, Benton TG, Lundberg P, Dall SRX, Kendall BE and Gaillard JM. 2006. Estimating individual contributions to population growth: Evolutionary fitness in ecological time. Proc. R. Soc. B. 273 (1586): 547–55. doi.org/10.1098/rspb.2005.3357.

Cresswell W. 1994. Flocking is an effective anti-predation strategy in redshanks, Tringa totanus. Anim. Behav. 47(2): 433 - 442. doi.org/10.1006/anbe.1994.1057.

Cresswell W. and Quinn JL. 2011. Predicting the optimal prey group size from predator hunting behaviour. J. Anim. Ecol. 80(2):310-319. doi.org/10.1111/j.1365-2656.2010.01775.x.

Csardi G and Nepusz T. 2006. The igraph software package for complex network research. Inter J. Complex Syst. 1695(5): 1 - 9.

Dawson DA., G.J. Horsburgh GJ, A.P. Krupa AP, Stewart IRK, Skjelseth S, Jensen H, Ball AD, Spurgin LG, Mannarelli ME, Nakagawa S, Schroeder J, Vangestel C, Hinten GN and Burke T. 2012. Microsatellite resources for Passeridae species: A predicted microsatellite map of the house sparrow Passer domesticus. Mol. Ecol. Res. 12(3): 501 – 523. doi:10.1111/j.1755-0998.2012.03115.x.

Dimitriadou S, Croft DP and Darden SK. 2019. Divergence in social traits in Trinidadian guppies selectively bred for high and low leadership in a cooperative context. Sci Rep 9(17194):. doi.org/10.1038/s41598-019-53748-4

Dobson F, Murie J and Viblanc V. 2020. Fitness Estimations for Ecological Studies: An Evaluation in Columbian Ground Squirrels. Front. Ecol, Evol. 8. doi.org/10.3389/fevo.2020.00216

Endler JA. 1986. Natural Selection in the Wild. Princeton University Press, New Jersey.

Falconer DS and Mackay TFC. 1996. Introduction to Quantitative Genetics, Edinburgh.

Farine DR, and Whitehead H. 2015. Constructing, conducting and interpreting animal social network analysis. J. Anim. Ecol. 84(5):1144 - 1163. doi.org/10.1111/1365-2656.12418.

Farine DR. 2017. A guide to null models for animal social network analysis. Methods Ecol. Evol. 8(10): 1309 – 20. doi.org/10.1111/2041-210X.12772.

Farine DR, and Sheldon BC. 2015. Selection for territory acquisition is modulated by social network structure in a wild songbird. J. Evol. Biol. 28(3): 547 - 556. doi.org/10.1111/jeb.12587.

Farine, DR. 2013. Animal Social Network Inference and Permutations for Ecologists in R using asnipe. Meth. Ecol. Evol. 4(12): 1187 – 1194. doi/full/10.1111/2041-210X.12121.

Ferreira AC, Covas R, Silva LR, Esteves SC, Duarte IF, Fortuna R, Theron F, Doutrelant C and Farine DR. 2020. How to make methodological decisions when inferring social networks. Ecol. Evol. 10 (17): 9132 – 9143. doi.org/10.1002/ece3.6568.

Firth JA, Cole EF, Ioannou CC, Quinn JL, Aplin LM, Culina A, McMahon K, and Sheldon BC. 2018. Personality shapes pair bonding in a wild bird social system. Nat. Ecol. Evol. 2(11):1696 - 1699. doi.org/10.1038/s41559-018-0670-8.

Firth JA, and Sheldon BC. 2016. Social carry-over effects underpin trans-seasonally linked structure in a wild bird population. Ecol. Let. 19(11):1324 - 1332. doi.org/10.1111/ele.12669.

Firth JA, Sheldon BC, and Farine DR. 2016. Pathways of information transmission among wild songbirds follow experimentally imposed changes in social foraging structure. Biol. Lett. 12(6). doi.org/10.1098/rsbl.2016.0144.

Forstmeier W, Martin K, Bolund E, Schielzeth H and Kempenaers B. 2011. Female extrapair mating behavior can evolve via indirect selection on males. PNAS. 108(26): 10608 - 10613. doi.org/10.1073/pnas.1103195108.

Franks DW, Ruxton GD, and James R. 2010. Sampling animal association networks with the gambit of the group. Behav. Ecol. Sociobiol. 64(3): 493 - 503. doi.org/10.1007/s00265-009-0865-8.

Girndt A, Chng CWT, Burke T, and Schroeder J. 2018. Male age is associated with extra pair paternity, but not with extra-pair mating behaviour. Sci. Rep. 8:8378. doi.org/10.1038/s41598-018-26649-1

Girndt A, Cockburn G, Sánchez-Tójar A, Hertel M, Burke T and Schroeder J. 2019. Male age and its association with reproductive traits in captive and wild house sparrows. J. Evol. Biol. 32(12):1431 - 1443. doi.org/10.1111/jeb.13542.

Grant PR, and Grant BR. 2019. Adult sex ratio influences mate choice in Darwin's finches. PNAS. 116(25): 12372 - 12382. doi.org/10.1073/pnas.1903838116.

Gomes ACR, Boogert NJ, Cardoso GC. 2021. Network structure and the optimization of proximity-based association criteria. Meth. Ecol. Evo. 12(1):88 – 100. doi.org/10.1111/2041-210X.13387.

Hadfield JD. 2010. MCMC methods for multi-response generalized linear mixed models: The MCMCglmm R package. J. Stat. Softw. 33 (2):1 - 22. doi.org/10.18637/jss.v033.i02.

Hillemann F, Cole EF, Sheldon BC, and Farine DR. 2020. Information use in foraging flocks of songbirds: no evidence for social transmission of patch quality. Anim. Behav. 165: 35–41. doi.org/10.1016/j.anbehav.2020.04.024.

Hsu YH. Schroeder J, Winney I, Burke T and Nakagawa S. 2015. Are extra-pair males different from cuckolded males? A case study and a meta-analytic examination. Molecular Ecology. 24(7):1558 – 1571. https://doi.org/10.1111/mec.13124

Kohn GM. 2017. Friends give benefits: autumn social familiarity preferences predict reproductive output. Anim. Behav. 132: 201 – 208. doi.org/10.1016/j.anbehav.2017.08.013.

Korsten P, Van Overveld T, Adriaensen F and Matthysen E. 2013. Genetic integration of local dispersal and exploratory behaviour in a wild bird. Nat. Comm. 4: 2362. doi.org/10.1038/ncomms3362.

Krause JU, and Ruxton GD. 2002. Living in groups. Oxford Series in Ecology and Evolution. Oxford: Oxford University Press.

Kruuk LEB. 2004. Estimating genetic parameters in natural populations using the "animal model." Proc. R. Soc. B. 359(1446):873 - 890. doi.org/10.1098/rstb.2003.1437.

Kurvers RHJM, Prox L, Farine DR, Jongeling C, and Snijders L. 2020. Season-specific carryover of early life associations in a monogamous bird species. Anim. Behav. 164:25–37. doi.org/10.1016/j.anbehav.2020.03.016.

Lea AJ, Blumstein DT, Wey TW, and Martin JGA. 2010. Heritable victimization and the benefits of agonistic relationships. PNAS. 107(50): 21587–21592. doi.org/10.1073/pnas.1009882107.

Le Galliard JF, Fitze PS, Ferrière R, and Clobert J. 2005. Sex ratio bias, male aggression, and population collapse in lizards. PNAS.102(50): 18231–18236.

Maldonado-Chaparro AA, Montiglio PO, Forstmeier W, Kempenaers B and Farine DR. 2018. Linking the fine-scale social environment to mating decisions: a future direction for the study of extra-pair paternity. Biol. Rev. 93(3): 1558—1577. doi.org/10.1111/brv.12408.

Mayer C and Pasinelli G. 2013. New support for an old hypothesis: Density affects extra-pair paternity. Ecol. Evol. 3(3):694 - 705. doi.org/10.1002/ece3.489.

McDonald DB. 2007. Predicting fate from early connectivity in a social network. PNAS. 104(26):10910–10914. doi.org/10.1073/pnas.0701159104.

McDonald GC, Engel N, Ratão SS, Székely T and Kosztolányi A. 2020. The impact of social structure on breeding strategies in an island bird. Sci. Rep. 10(1): 13872. doi.org/10.1038/s41598-020-70595-w.

Moiron M., A Charmantier and A Bouwhuis. 2022. The quantitative genetics of fitness sin a wild seabird. Evolution. Doi:10.1111/evo.14516 [online ahead of print]

Nakagawa S, and Schielzeth H. 2010. Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. Biol. Rev. 85(4): 935 - 956. 10.1111/J.1469-185x.2010.00141.X

Oh KP and Badyaev AV. 2010. Structure of social networks in a passerine bird: Consequences for sexual selection and the evolution of mating strategies. Am. Nat. 176(3): E80—E89. doi.org/10.1086/655216.

Plaza M, Burke T, Cox T, Carroll AF, Girndt A, Halford G, Martin DA, Sánchez-Fortún M, Sanchez-Tojar A, Somerville J, Schroeder J. 2019. Social network node-based metrics can function as proxies for animal personality traits. J. Evol. Biol. 33(11): 1634 - 1642. doi.org/10.32942/OSF.IO/YVQ9D.

Proops L. Troisi CA, Kleinhappel TK and Romero T. 2021. Non - random associations in group housed rats (Rattus norvegicus). Sci. Rep. 11(1):15349. doi.org/10.1038/s41598-021-94608-4.

Psorakis I, Roberts SJ, Rezek I and Sheldon BC. 2012. Inferring social network structure in ecological systems from spatiotemporal data streams. J. R. Soc. Interface. 9(76): 3055 – 3066. doi.org/10.1098/rsif.2012.0223.

Psorakis I, Voelkl B, Garroway CJ, Radersma R, Aplin LM, Crates RA, Culina A, Farine DR, Firth JA, Hinde CA, Kidd LR, Milligan ND, Roberts SJ, Verhelst B and Sheldon BC. 2015. Inferring social structure from temporal data. Behav. Ecol. Sociobiol. 69: 857 - 866. doi.org/10.1007/s00265-015-1906-0.

R Core Team. 2022. R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing. http//www.R-project.org/.

Reid JM, Nietlisbach P, Wolak ME, Keller LF and Arcese P. 2019. Individuals expected genetic contributions to future generations, reproductive value, and short-term metrics of fitness in free-living song sparrows (Melospiza meolodia). Evolution Letters. 3(3):271 – 285. doi/pdf/10.1002/evl3.118

Riehl C, and Strong MJ. 2018. Stable social relationships between unrelated females increase individual fitness in a cooperative bird. Proc. R. Soc. B. 285(20180130). doi.org/10.1098/rspb.2018.0130.

Sánchez-Tójar A, Winney I, Girndt A, Simons MJP, Nakagawa S, Burke T, and Schroeder J. 2017. Winter territory prospecting is associated with life-history stage but not activity in a passerine. J. Avian Biol. 48(3):407 - 416. doi.org/10.1111/jav.01055.

Sánchez-Tójar A, S Nakagawa, Sánchez-Fortún M, Martin DA, Ramani S, Girndt A, Bókony V, Kempenaers B, Liker A., Westneat DF, Burke T and Schroeder J. 2018. Meta-analysis challenges a textbook example of status signalling and demonstrates publication bias. ELife. 7: e37385. doi.org/10.7554/eLife.37385

Sánchez-Tójar A. 2018. The evolution of social dominance in house sparrows. http://nbn-resolving.de/urn:nbn:de:bsz:352-2-9850l4uzuvk43

Schroeder J, Cleasby IR, Nakagawa S, Ockendon N and Burke T. 2011. No evidence for adverse effects on fitness of fitting passive integrated transponders (PITs) in wild house sparrows Passer domesticus. J. Avian Biol.42(3):271 - 275. doi.org/10.1111/j.1600-048X.2010.05271.x.

Schroeder J, Nakagawa S, Cleasby IR, and Burke T. 2012. Passerine birds breeding under chronic noise experience reduced fitness. PLoS One. 7(7): E39200. doi.org/10.1371/journal.pone.0039200.

Schroeder J, Burke T, Mannarelli ME, Dawson DA and Nakagawa S. 2012A. Maternal effects and heritability of annual productivity. J. Evol. Biol. 24(1):149 - 156. doi: 10.1111/j.1420-9101.2011.02412.x.

Schroeder J, Nakagawa S, Rees M, Mannarelli ME and Burke T. 2015. Reduced fitness in progeny from old parents in a natural population. PNAS. 112(13): 4021 - 4025. doi.org/10.1073/pnas.1422715112.

Schroeder J, Hsu YH, Winney I, Simons M, Nakagawa S and Burke T. 2016. Predictably philandering females prompt poor paternal provisioning. Am. Nat. 180(2): 219 – 230. doi.org/10.1086/687243.

Silk JB, Alberts SC, and Altmann J. 2003. Social Bonds of Female Baboons Enhance Infant Survival. Science, 302(5648): 1227–1231. doi.org/10.1126/science.1088474

Silk JB. 2007. The adaptive value of sociality in mammalian groups. Philos. Trans. R. Soc. Biol. Sci.362(1480): 539 - 59. doi.org/10.1098/rstb.2006.1994.

Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL, Moscovice LR, Wittig RM, Seyfarth RM and Cheney DL. 2009. The benefits of social capital: Close social bonds among female baboons enhance offspring survival. Proc. R. Soc. B.. 276 (1670): 3099–3104. doi.org/10.1098/rspb.2009.0681.

Silk JB, Beehner JC, Bergman, TJ, Crockford C, Engh AL, Moscovice LR,Wittig RM, Seyfarth, RM and Cheney DL. 2010. Strong and consistent social bonds enhance the longevity of female baboons. Curr. Biol. 20(15): 1359–1361. doi.org/10.1016/j.cub.2010.05.067.

Silk, MJ, Croft DP, Tregenza T and Bearhop S. 2014. The importance of fission-fusion social group dynamics in birds. Ibis. 156(4):701 - 715. doi.org/10.1111/ibi.12191.

Simons MJP, Winney I, Nakagawa S, Burke T and Schroeder J. 2015. Limited catching bias in a wild population of birds with near-complete census information. Ecol. Evol. 5(16):3500 - 3506. doi.org/10.1002/ece3.1623.

Summer-Smith D. 1963. The House Sparrow. Collins. UK.

Stanton MA and Mann J. 2012. Early Social Networks Predict Survival in Wild Bottlenose Dolphins. PLoS One. 7(10):E47508. doi.org/10.1371/journal.pone.0047508.

Strickland KD. Mitchell J, Delmé C and Frère CH. 2021. Repeatability and heritability of social reaction norms in a wild agamid lizard. Evolution. 75(8): 1953–65. doi.org/10.1111/evo.14298.

Thompson NA, and Cords M. 2018. Stronger social bonds do not always predict greater longevity in a gregarious primate. Ecol. Evl. 8(3): 1604–1614. doi.org/10.1002/ece3.3781

Thys B, Eens M, Aerts S, Delory A, Iserbyt A and Pinxten R. 2017. Exploration and sociability in a highly gregarious bird are repeatable across seasons and in the long-term but are unrelated. Anim. Behav. 123: 339–48: doi.org/10.1016/j.anbehav.2016.11.014.

Voelkl B, Firth JA, and Sheldon BC. 2016. Nonlethal predator effects on the turn-over of wild bird flocks. Sci. Rep. 6: 33476. doi.org/10.1038/srep33476.

Webber QRM, Schneider DC and Vander Wal E. 2020. Is less more? A commentary on the practice of 'metric hacking' in animal social network analysis. Anim. Behav., 168: 109–120. doi.org/10.1016/j.anbehav.2020.08.011.

Westneat DF, Bókony V, Burke T, Chastel O, Jensen H, Kvalnes T, Lendvai ÁZ, Liker A, Mock D, Schroeder J, Schwagmeyer PL, Sorci G and Stewart IRK. 2014. Multiple aspects of plasticity in clutch size vary among populations of a globally distributed songbird. J. Anim. Ecol. 83(4): 876–887. doi.org/10.1111/1365-2656.12191

Wey T, Blumstein DT, Shen W and Jordán F. 2008. Social network analysis of animal behaviour: a promising tool for the study of sociality. Anim. Behav. 75(2): 333 – 44. doi.org/10.1016/j.anbehav.2007.06.020.

Whitehead H and Dufault S. 1999. Techniques for Analyzing Vertebrate Social Structure Using Identified Individuals: Review and Recommendations. Adv. Study Behav. 28: 33 - 74. doi.org/10.1016/S0065-3454(08)60215-6.

Wolf M., van Doorn GS, Leimar O, Weissing FJ. 2007. Life-history trade-offs favour the evolution of animal personalities. Nature, 447(7144): 581 - 584.

Youngblood M. 2019. A Raspberry Pi-based, RFID-equipped birdfeeder for the remote monitoring of wild bird populations. Ring. Migr. 34(1): 25 – 32. doi.org/10.1080/03078698.2019.1759908

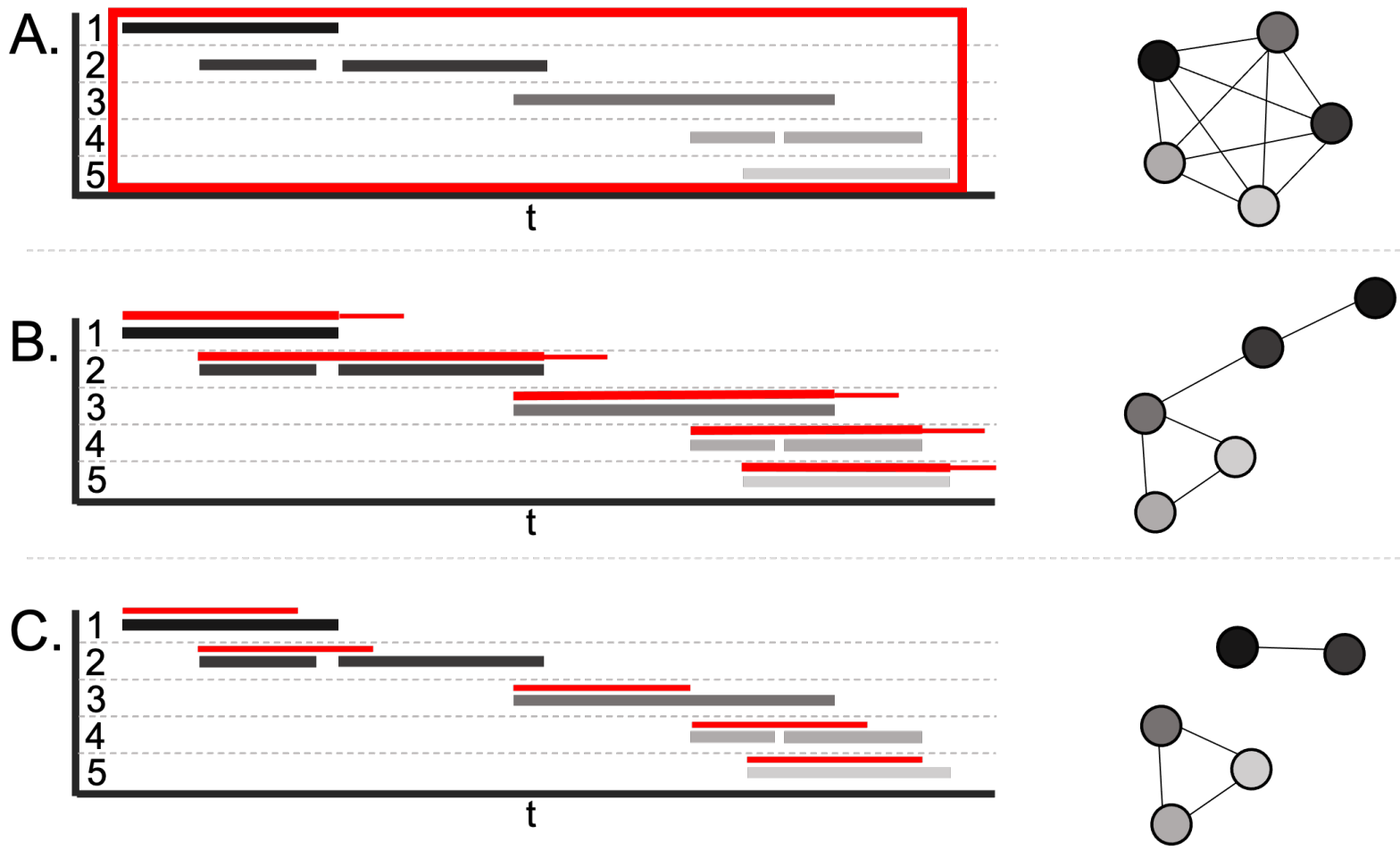
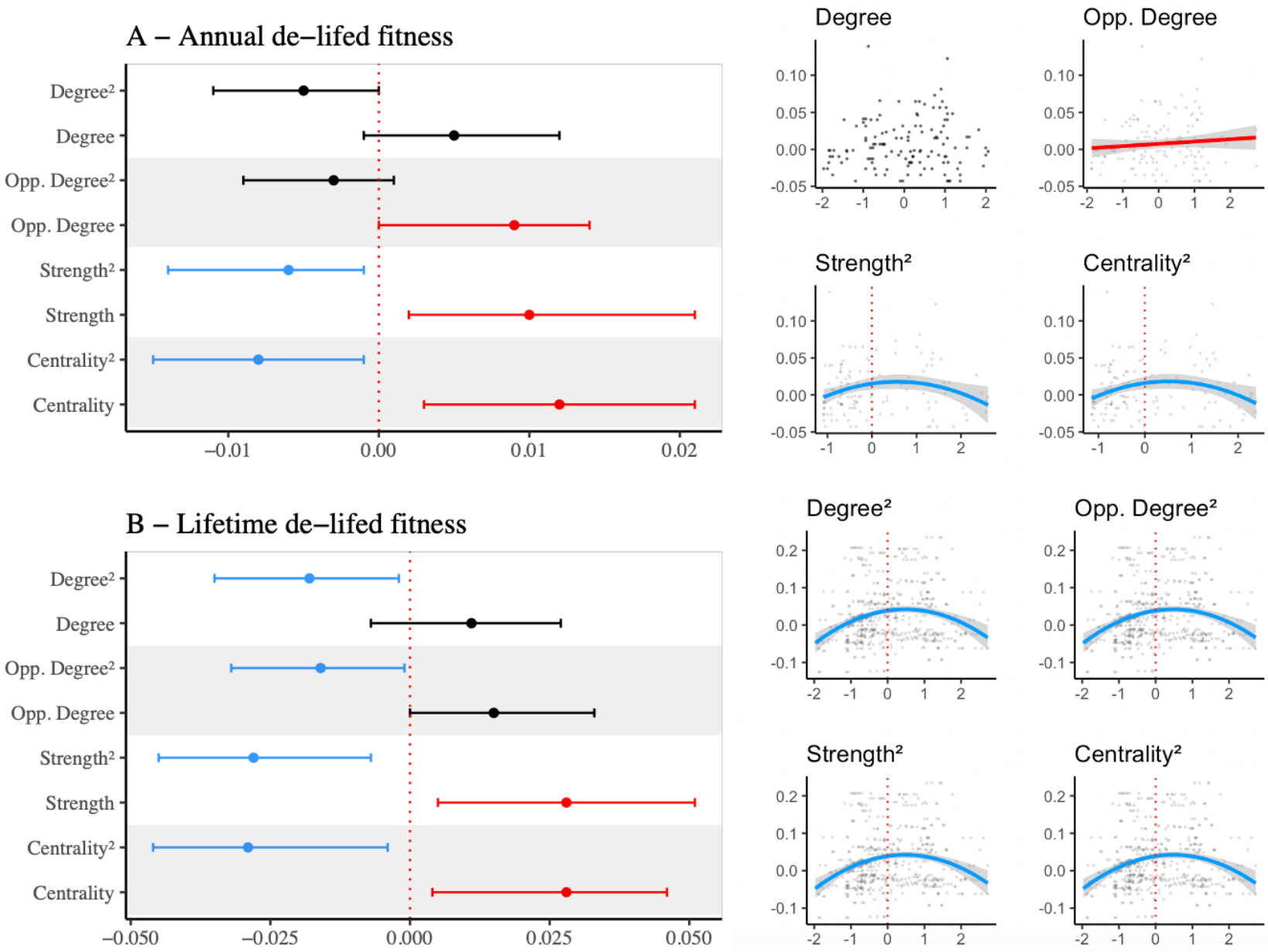

A.
1
2
3
4
5
t
B.
1
2
3
4
5
t
C.
1
2
3
4
5
t

Figure 1. Three versions of a simulated event (A, B and C) show the interval over which five individuals (1–5, black/grey bars) spent at a resource over time (t), and the derived social networks from each approach: A = gambit of the group, which links all individuals in a discrete group equally; B = time-window overlap (by Δ_t), which links individuals who overlap at a resource; and C = arrival time (developed for this study), which links individuals who arrive together to a resource. Red bars denote the time period during which individuals are considered to be associated: A, all individuals within a group; B, where they are physically present at the same time (thick red bar), or shortly after they depart to account for birds which were present, but not currently being recorded by the antenna, in that case, over-lapping by Δ_t (thin red bar, typically a few seconds); or, C, where they arrive within Δ_t of each other, but the subsequent time spent at a 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 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 link all individuals which arrive together, while ignoring those already present at the resource, which has the potential to link 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 resource, after which they can be recorded as arriving again.


A – Annual de–lifed fitness
Degree²
Degree
Opp. Degree²
Opp. Degree
Strength²
Strength
Centrality²
Centrality
–0.01
0.00
0.01
0.02
B – Lifetime de–lifed fitness
Degree²
Degree
Opp. Degree²
Opp. Degree
Strength²
Strength
Centrality²
Centrality
–0.050
–0.025
0.000
0.025
0.050
Degree
Opp. Degree
Strength²
Centrality²
Degree²
Opp. Degree²
Strength²
Centrality²

693

Figure 2. De-lifed fitness as response variables against social measures from eight linear mixed models, at two scales, from the Lundy Island house sparrows: Explanatory variables for Annual de-lifed fitness (A); and Lifetime de-lifed fitness (B), where ^{2} denotes a quadratic function, also shown in the four adjacent panels for A and B, and their 95% credible intervals. Credible intervals are given as solid bars for each explanatory variable, where a solid point denotes the posterior mode. Black bars denote no effect on the response variable; red denote a positive and blue, a negative, relationship with the response. In adjacent panels, quadratic functions of each response variable presented in A and B (on the Y axis: A Centrality, Degree, Opp. Degree, Strength, and B Centrality, Degree, Opp. Degree, Strength). Blue curves represent a negative interaction with fitness measures (on the X axis). Measures with no effect are not shown in figure. We found no link to sex, and age was also subject to stabilizing selection, (given in supplementary files, table 4).