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Increased opposite sex association is linked with fitness benefits, otherwise sociality is subject to stabilising selection in a wild passerine.

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Abstract

Animal sociality, an individual's propensity to association with others, has consequences for fitness, and particularly mate choice. For example, directly, by increasing the pool of prospective partners, and indirectly through increased survival. Individuals benefit from both over the short-term as these benefits are associated with mating status and subsequent fecundity, but whether animal sociality also translates into fitness is unknown. Here, we quantified social associations and their link with annual and lifetime fitness, measured as the number of recruits and in de-lifed fitness. We measured this in birds visiting a feeding station over two non-breeding periods, using social network analysis and a multi-generational genetic pedigree. We find high individual repeatability in sociality. We found that individuals with an average sociality had the highest fitness, and that birds with more opposite-sex associates had higher fitness, but this did not translate to improved lifetime fitness. For lifetime fitness, we found evidence for stabilizing selection on between sex sociality measures, suggesting that such benefits are only short-lived in a wild population.

Keywords: sociality, social network, selection, social behaviour, genetic pedigree, fitness

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Background

The extent to which an individual chooses to associate with others – its sociality – has life-history consequences and is therefore expected to be subject to selection (Krause and Ruxton 2002). Sociality functions as an emergent trait of behavioural preference and personality (Aplin et al. 2014; Plaza et al. 2020). Thus, some individuals are consistently more inclined to socialise than others, as is demonstrated in mammals (Silk et al. 2009; Proops et al. 2021; Strickland et al. 2021) and birds (Croft et al. 2009; Aplin et al. 2015; Thys et al. 2017; Plaza et al. 2020; Beck, Valcu, and Kempenaers 2020), but not exclusively (Krause et al. 2000; Dimitriadou, Croft & Darden 2019). Sociality is mediated by the social environment, i.e. the sociality of others (Ellis et al. 2017; Firth et al. 2017; Firth, Sheldon, and Brent 2017) and by the physical environment (Cresswell 1994; Grabowska-Zhang et al. 2016). Thus, sociality can only evolve where the benefits outweigh the costs (Krause and Ruxton 2002; Silk 2007; Silk et al. 2014). For example, communal foraging during the non-breeding period can facilitate information transfer between individuals (Aplin et al. 2012; Hillemann et al. 2020) and reduce predation risk (Cresswell and Quinn 2011). But during the breeding season these benefits also incur costs associated with competition for resources, mates (Le Galliard et al. 2005; Grant and Grant 2019; Kurvers 2020; but also see Lea et al. 2010) and offspring paternity (Birkhead and Biggins 1987; Forstmeier et al. 2011; Mayer and Pasinelli 2013). Social individuals may also increase their reproductive value, or fitness, by maximising the opportunity for mate choice through being in a more central social network position (McDonald 2007; Oh and Badyaev 2010; Beck, Farine, and Kempenaers 2021). Thus, although some benefits can be obtained during the breeding period, most of these tend to be short-term and beneficial in a specific context, for example in communal reproductive groups (Bebbington et al. 2017; Riehl and Strong 2018). Most permanent benefits are instead obtained during the non-breeding period, when group cohesion is stronger, and carried over into the next breeding season (Firth and Sheldon 2016; Kohn 2017; Maldonado-Chaparro et al. 2018; Beck, Farine, and Kempenaers 2020), and thus also need to be quantified across years rather than in annual reproductive success measures.

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Sociality, like any behaviour that varies between, but not within, individuals can be subject to selection (Plaza et al 2020). Directional (or linear) selection results in a relationship between a trait and some measure of fitness, stabilising selection favors traits at the population average, rather than those at the extremes, which is disruptive selection (Wolf et al. 2007). However, the association between lifetime fitness and individual sociality, and its potential to be driven by cumulative short-term benefits has not been studied yet.

With the recent development of powerful and more accessible tools to construct and analyse networks of associated individuals, hereafter social networks (Wey et al. 2008; Farine and Whitehead 2015; Farine 2017), the study of sociality has become popular in ecology and evolution. Yet, to describe the association between fitness and sociality, any potential study must first overcome two problems: First, the definition of a social association varies between studies and is seldom clearly defined (Figure 1; Psorakis et al. 2012, 2015). Second, precise measures of individual lifetime fitness are difficult to quantify because this requires wild animals to be monitored throughout their whole lives, observe all their breeding attempts, and follow the fates of offspring to determine recruitment. Thus, the fitness consequences of sociality are often only assessed through annually measured reproductive parameters, proxies for fitness (for example, paired status, eggs laid, chicks fledged etc., and hereafter fitness proxies), rather than more exact measures (e.g. offspring recruited, or genetic contributions to a population, hereafter fitness measures), which require a well resolved and multi-generational genetic pedigree (Kruuk 2004; Korsten et al. 2013).

Our study system, an island population of house sparrow *Passer domesticus* where we can monitor all individuals from birth to death, without capture bias (Simons et al. 2015), is well placed to overcome both problems. First, we have sociality data, collected across two non-breeding periods, from birds that are electronically registered visiting a feeder. The subsequently inferred sociality measures exhibit within-individual repeatability in this wild population, but also in captivity; thus, our measure of sociality is biologically meaningful (Plaza et al. 2020). Second, we have lifetime recruitment data available, with a well resolved, genetic, multi-generational pedigree and, because our population is closed, can use these to compute precise fitness estimates (Schroeder et al. 2015).

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Thus, here we tested the following predictions for non-breeding sociality and its association with fitness: First, we confirmed that the sociality traits we measured were meaningful, by testing that sociality varied less within- than between individuals. Then we tested for directional, disruptive, or stabilizing selection, by testing for the association of those sociality measures with two measures of fitness at the annual and lifetime scales.

Methods

Study system

We used data from the house sparrow (hereafter, sparrow/s) study system, a systematic, 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. Most sparrows were first captured at their natal site during the breeding season (April to August) and fewer during the post-fledging period (Schroeder et al. 2011; Girndt et al. 2019). We fitted all sparrows with a unique combination of a coded metal ring and three plain coloured leg rings. We collected tissue samples when the sparrow chicks were two and twelve days old, and then where possible, twice per year post-fledging. We genotyped sparrow DNA at <23 microsatellite loci suitable for parentage assignment in sparrows (Dawson et al. 2012). Using the genetic data, we assembled a near-complete genetic pedigree, which at the time of writing spans twenty years, 2000–2019, and 8,379 individuals (Schroeder et al. 2015, 2016). We also provided each sparrow with a subcutaneous Passive Identification Transponder (PIT tag; TROVANID100: 12 × 2 mm and 0.1 g), which previously we have shown has no detrimental effect on subsequent fitness (Schroeder et al. 2011). These tagged individuals were then recorded visiting a custom made 19.8_{cm} x 19.8_{cm} Radio Frequency Identification antenna (RFID; DorsetID) mounted on a seed reservoir (Sánchez-Tójar et al. 2017; Brandl et al. 2019) positioned centrally within our study site.

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Social network construction

We used presence data from the RFID antenna, collected during the non-breeding periods, November–January, of 2015/16 and 2016/17 (hereafter referred to as two events). An association observed from this data can either reflect two or more individuals that opt to maintain some social cohesion with one another (we consider this to be an "honest" association), or to occur between individuals without pre-established social cohesion but who coincidentally occupy the same time and space (hereafter, random mixing). Our data record the coarse presence of birds at a bird feeder without distinguishing between these two types of association. Hence, we derived a method to infer honest associations and to distinguish these from the random mixing of individuals at our bird feeder.

A common approach to this problem is to draw associations among all individuals within a discrete group or flock, the 'gambit of the group' (Whitehead and Dufault 1999; Figure 1A). However, with the high activity at our feeder at which discrete groups of sparrows accumulated, this approach overestimates associations between individuals (Figure 1A; also see Ferreira et al. 2020), capturing both random mixing and honest associations. One solution to this would be to define the class of association according to whether two individuals overlapped by some defined time period (Δ^t) in the proximity of our bird feeder; however, in our system, this results in linear network structures, e.g. linking the first bird to the second, then the second to the third, and so on, ultimately failing to account for the social structures of visiting groups, and linking visiting groups by sparrow that linger at the feeder (Figure 1B). We instead defined associations between individuals that arrived within 150 seconds (Δ^t) of each other, and only after the arriving individual had previously been absent for a period of >300 seconds (Δ^I). We watched many hours of footage of sparrows at feeders (Plaza et al., 2020) to conclude that that Δ^t = 150 seconds is long enough to detect and link all individuals who arrive together in a group (see Figure 1C), and the resulting data is likely to represent honest association between individuals rather than random mixing, as the arriving individual clearly choose to associate with the already present individual.

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From the resulting association matrices from two events during the non-breeding season, 2015/16 and 2016/17, we built one weighted, non-directional, social network for each event, where a vertex represented an individual and an interconnecting edge an association. We then also built two bipartite networks from the same data (sub-graphs), which only considered associations between opposite-sex individuals.

From the first two networks we extracted three measures of sociality using the 'iGraph' R package (Csardi and Nepusz 2006): degree, strength, and centrality. Degree, the number of associates, was calculated as the sum of associated individuals. Strength was calculated using dyadic Simple Ratio Indices (the association probability between a dyad, from 0, never associated, to 1, always associated), multiplied by degree, and divided by the number of potential associates in the network (count of vertices) and multiplied by 10. We also calculated eigenvector centrality (following McDonald 2007, hereafter centrality) to quantify the influence of an individual to all others within the network (Newman 2004). Finally, we then extracted opposite-sex degree from the two bipartite sub-graphs (following Beck, Farine and Kampenaers 2021) – the number of opposite-sex associates.

To test the repeatability of the four sociality measures, and to validate the biological significance of our approach to assign associations, we further subset all four networks (two main networks and two bipartite sub-graphs) into 15 sub-graphs in 2015/16, and 13 sub-graphs in 2016/17, each representing one week.

Fitness measures

For each of the sparrows in our networks that survived to the following breeding period, we used our genetic pedigree to calculate two measures of fitness, both of which represent reproductive value (Alif et al. 2021). We calculated both fitness measures at the annual and lifetime scale. We defined recruits as offspring that survived and produced genetic offspring. First, we summed individual recruits within the breeding year following the social events (annual recruits). We then also summed individual recruits across a parent's lifetime, or up to 2020 (lifetime recruits to date).

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As a second measure of fitness, we used de-lifed fitness (p_{ti}), which estimates an individual's genetic contribution (Coulson et al. 2006), as

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

De-lifed fitness is a retrospective measure of realised fitness, calculated by removing (or, de-lifing) an individual, and any of its offspring, from the pedigree and recalculating the resulting change in the population growth. Here, p 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.

Model structure

First, we validated the sociality measures by confirming individual repeatability. We modelled degree, opposite-sex degree, strength, and centrality, respectively, as response variables in four Gaussian linear mixed models with only an intercept, and 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 the repeatability (Nakagawa and Schielzeth 2010).

Then, to quantify the association between sociality measures and fitness, we ran four models, one for each sociality measure, for each of our four fitness measures. In the eight models explaining annual and lifetime numbers of recruits, we used a Poisson log link function, and in the eight models explaining p_{ti} and p_i we used a Gaussian error. We mean-centered degree, opposite-sex degree, strength, and centrality, and modelled these as fixed

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covariates, but as sole social measure in each model to account for collinearity between them (Webster, Schneider & Vander Wal 2020).

In the models concerning the annual fitness variables, we added fixed effects for sex (male, 1 or female, 0) and age (in calendar years) to compensate for variation in fitness as explained by age and sex (Schroeder et al. 2012). We added sex as an interaction term with age to account for older males being more likely to engage in extra-pair behaviour (Girndt et al. 2018). Finally, to test for evidence for stabilising or disruptive selection, we added each sociality variable also as a quadratic effect to our models. In all annual models, bird identity was modelled as a random effect on the intercept to account for pseudoreplication, because our data combined two networks, which in some cases contained the same individuals, and cohort (the year the bird was hatched) to account for environmental stochasticity.

We modelled lifetime recruits and lifetime de-lifed fitness in the same way as the annual ones, but instead of age we used lifespan, or age at year 2020 if they were still alive then. Because each bird was only represented once in this dataset, we only modelled cohort as a random effect, and we averaged social measures within individuals and events.

We used Bayesian Markov Monte-Carlo methods using the package MCMCglmm for R (Hadfield 2010) to run all models. We ran the repeatability models over 13,000 iterations using the package default priors. We defined 'inverse Wishart' priors for all fitness models and ran each over 343,000 iterations, with a burn-in of 3,000 and a thinning interval of 200. We visually checked the posterior trace plots for all model outputs and ensured that autocorrelation was below 0.1 and the effective sample sizes were above 1,000. The fixed effect on the response variable was considered statistically significant when the 95% credible interval (CI) of its posterior distribution did not span zero.

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

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constructing the networks, we identified 3,783 associations between 118 individuals during the event in 2015/2016, and 874 associations between 69 individuals during the event in 2016/2017. These networks contained 66.3% and 26.3% of breeding birds in 2016 and 2017, respectively. Combined, we had 135 records for annual and lifetime fitness from 102 individuals, and where 33 were recorded in both years (for summary statistics see Table 1).

We confirmed individual repeatability in all four sociality measures between weeks in both events (Table 1). Social measures were associated with fitness at both, the annual and lifetime scales. We found a negative quadratic effect between strength and annual and lifetime de-lifed fitness, and the same for strength (Figure 2; Table 2; Table 3). This suggests that selection favors the population average for both social traits (Figure 2).

Opposite-sex degree however was linked with increased annual de-lifed fitness and with the annual number of recruits, suggesting that individuals with more opposite-sex associations have higher annual fitness However, this did not translate into lifetime fitness, as opposite-sex degree showed a negative quadratic effect with lifetime de-lifed fitness, but not recruits over a lifetime (Figure 2, Table 3).

Table 1. Summary statistics for long-term fitness and social measures for individual house sparrows on Lundy Island during two non-breeding events (November–January 2015/2016 and 2016/2017).

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

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Table 2. Model outputs, one for each of our four sociality measures (degree, strength, centrality, and opposite-sex degree), against annual recruits with Poisson link. 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.

Annual recruits	Posterior mode 95% credible intervals (lower – upper)			
Variable	Degree	Strength	Centrality	Opposite sex degree
Fixed terms				
(Intercept)	**3.08** **1.22—6.11**	**3.53** **1.08—6.21**	**3.29** **1.22—6.26**	**3.85** **1.16—6.39**
Social measure	0.16 -0.02—0.33	0.22 -0.01—0.43	0.17 -0.03—0.41	**0.17** **0.03—0.38**
Sex (male)	-0.78 -1.43—0.04	**-0.64** **-1.52—-0.01**	**-0.71** **-1.51—-0.04**	**-0.69** **-1.48—-0.07**
Age	**-0.83** **-1.31—-0.31**	**-1.00** **-1.36—-0.33**	**-0.95** **-1.33—-0.32**	**-1** **-1.37—-0.36**
Social measure^2	-0.06 -0.24—0.08	-0.08 -0.29—0.09	-0.16 -0.31—0.11	-0.04 -0.16—0.10
Age*Sex (male)	0.21 -0.02—0.4	**0.25** **0—0.53**	0.22 -0.02—0.49	**0.19** **0—0.48**
Random terms	-	-	-	-
*Bird ID	**0** **0—0.13**	**0** **0—0.12**	**0** **0—0.13**	**0** **0—0.12**
*Cohort	**2.64** **0.10—15.83**	**2.45** **0.03—16.22**	**2.30** **0.01—18.10**	**2.64** **0.13—18.51**
Residuals	**0** **0—0.23**	**0** **0—0.28**	**0** **0—0.27**	**0** **0—0.24**

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Table 3. Model outputs from GLMMs for each of our four sociality measures (Degree, Strength, Centrality and Opposite-sex degree), against Lifetime recruits (Poisson,) 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. (†) Note that age in lifetime models is 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)	0.84 -0.02—1.88	0.66 -0.01—1.87	0.91 -0.08—1.96	0.96 0—1.94
Social measure	0.07 -0.07—0.22	0.13 -0.06—0.32	0.10 -0.10—0.30	0.10 -0.04—0.25
Sex (male)	0.25 -0.30—1.03	0.45 -0.34—1.00	0.28 -0.37—0.95	0.18 -0.27—0.96
†Age	0.12 -0—0.23	**0.08** **0—0.24**	0.12 -0—0.23	**0.13** **0—0.23**
Social measure^2	-0.03 -0.18—0.11	-0.08 -0.23—0.12	-0.03 -0.25—0.11	-0.02 -0.16—0.12
†Age*Sex (male)	-0.06 -0.20—0.06	-0.06 -0.21—0.06	-0.06 -0.21—0.06	-0.08 -0.20—0.05
Random effects	-	-	-	-
*Cohort	**NA** **0.06—2.76**	**0.51** **0.11—2.63**	**0.49** **0.13—2.79**	**0.67** **0.13—2.94**
Residuals	**NA** **0.02—0.29**	**0.10** **0.01—0.28**	**0.13** **0—0.28**	**0.11** **0.01—0.28**

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Discussion

We found evidence for annual fitness benefits for having more opposite-sex associates, but also evidence for, if considering lifetime fitness, stabilising selection on sociality in a wild population of birds. Our study species, sparrows are highly gregarious during the non-breeding period, moving and foraging in dense flocks; therefore, we defined associations between individuals that arrived together at a bird feeder after a period of absence. We confirmed high repeatability in all four social measures (Plaza et al. 2020) and, thus, captured associations more honestly than if we grouped birds that simply overlapped at the feeder. Other studies have also adapted similar gambit-of-the-group approaches in high-density systems. Ferreira et al. (2020), for example, identified gathering events, but then also proximity between the individuals using a bird feeder. Further research could 14ptimize our approach, either by refining the time after which an individual is determined to have left the feeder (Δ^{i}), or similarly, the time it takes all members of a group to interact with the feeder upon arrival (Δ^{t}). We considered our social measures to be an aspect of an individual's personality (Plaza et al, 2020), and as such this might also contribute to nonrandom mate choice (Munson et al. 2020; Dingemanse, Class & Holtmann 2021).

We measured sociality over two non-breeding periods, and found evidence for fitness benefits in the following breeding season. Previous studies have documented benefits of sociality using fitness proxies particularly that sociality improves mate choice (Oh and Badyaev 2010; Beck, Farine, and Kempenaers 2021) and may facilitate male extra-pair paternity (Beck, Farine, and Kempenaers 2020). Our study corroborates that these indirect benefits indeed directly translate into annual fitness. At the annual scale this might suggest a role in mate choice, which is inherently dependent on the demography of individuals within a network. However, we also found evidence for stabilising selection, in opposite sex degree when testing for lifetime fitness, and for strength and centrality for both, annual and life-time fitness.

Our social measures were associated with delifed fitness and less so with recruitment annually and over the lifetime of a sparrow. This is probable because, although sociality may enhance mate choice, recruitment is also dependent on parental effects and

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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 some aspect of long-term survival at the individual scale, but also of their progeny. We found that older males recruited more offspring, likely by virtue of older males siring more extra-pair offspring than younger males (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.

However, more generally, de-lifed fitness better represents actual fitness as it is a relative measure of the contribution to population growth. The number of recruits, while an intuitively appealing measure, is not relative, and in good years, more birds may have a higher number of recruits, while in poor year, having one recruits may be an unusual 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 evidence for stabilising selection on sociality in a wild population.

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The data used in this manuscript have been made available on the dryad repository.

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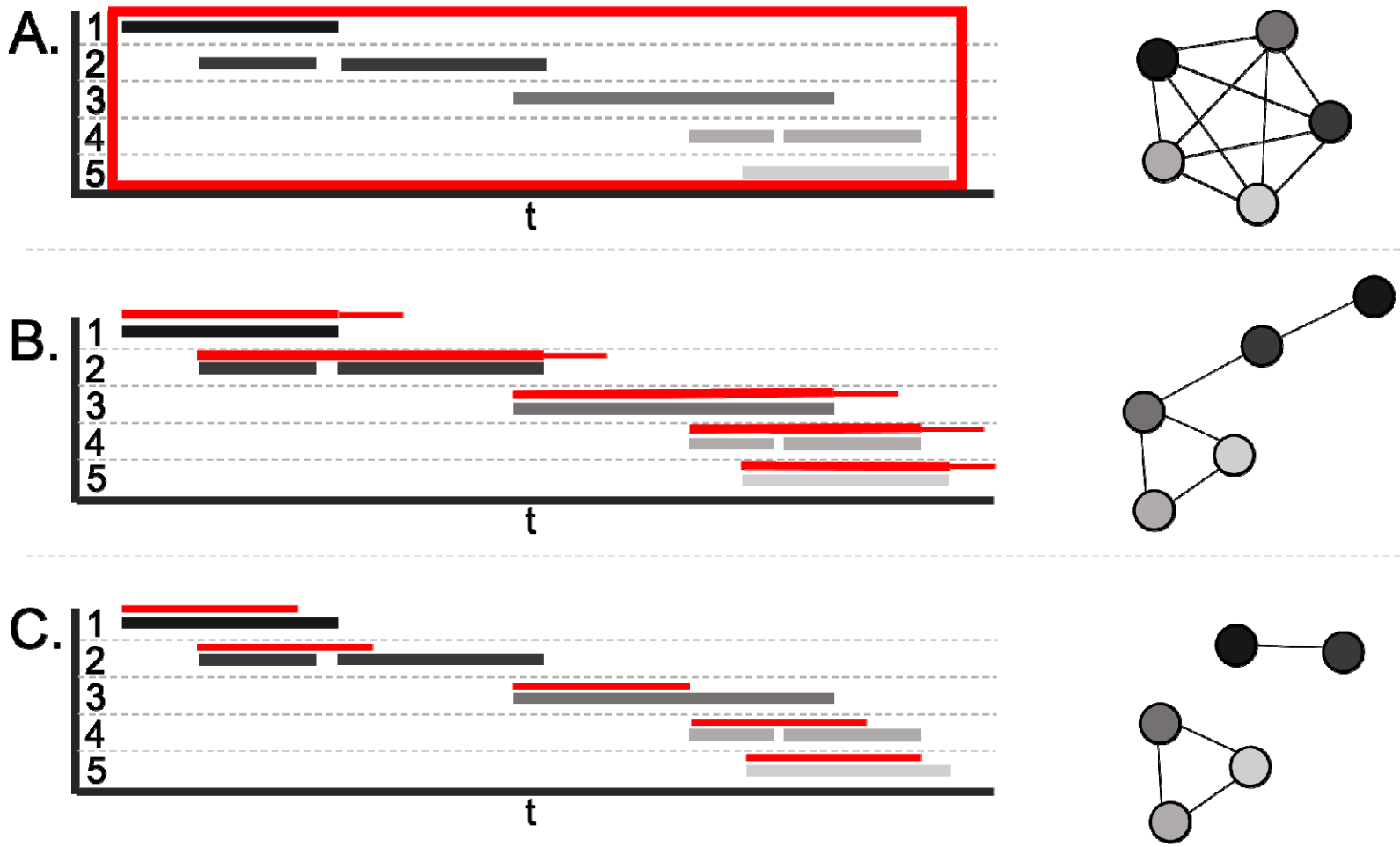

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Figure 1. Three versions of a simulated event (A, B & C) show the interval over which five individuals (1–5, black/grey bars) spent at a resource over time (t), and the derived social networks from each approach: A = gambit of the group, which links 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.

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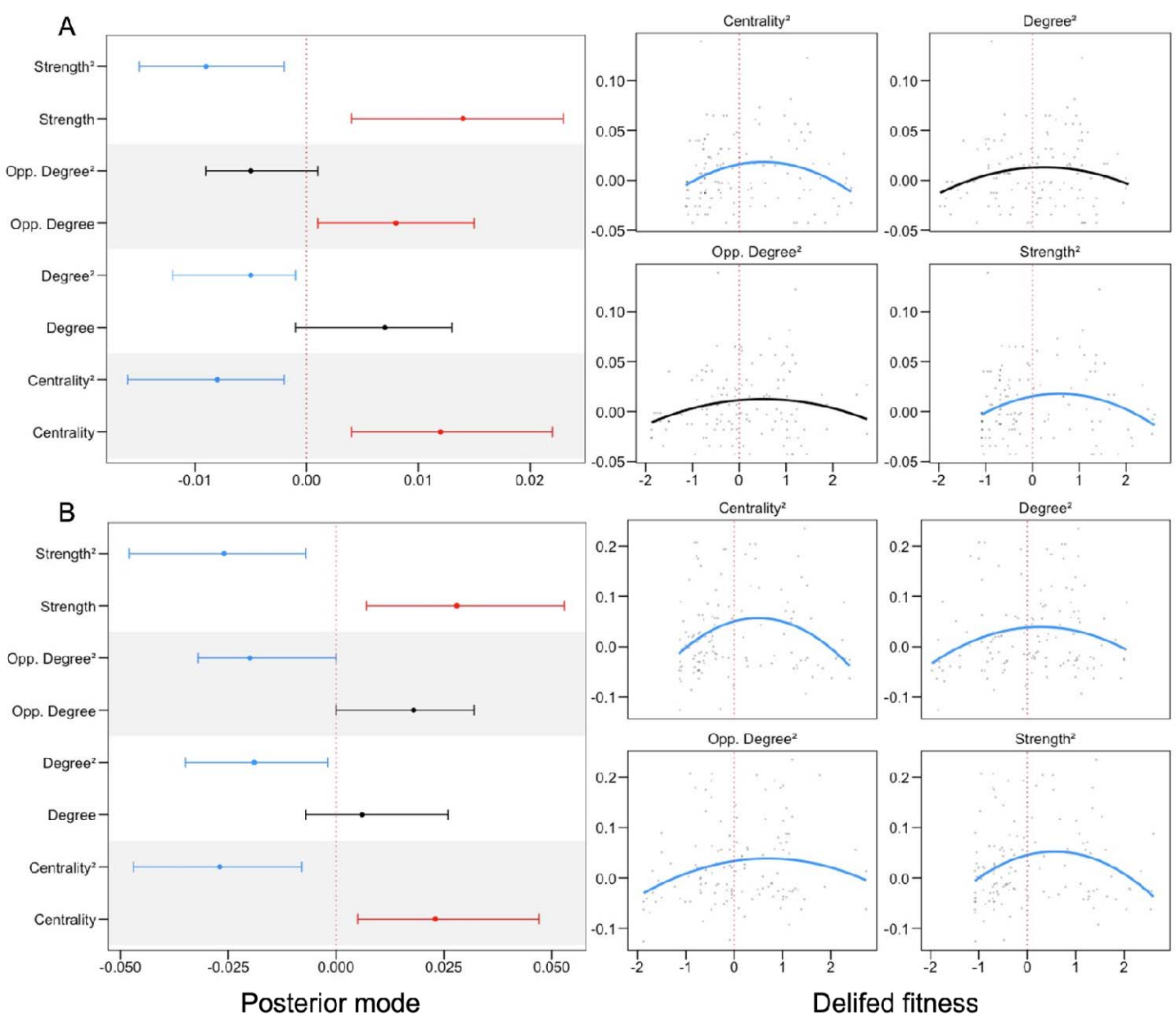

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Figure 2. Four long-term fitness measures as response variables against social measures from 8 linear mixed models, at two scales, from the Lundy Island house sparrows: Explanatory variables for Annual delifed fitness (A); and Lifetime delifed fitness (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, and black, no interaction with fitness measures (on the X axis).

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