

1 Wild songbirds exhibit consistent individual differences in inter- 2 specific social behaviour

3 F. Hillemann¹, E. F. Cole¹, D. R. Farine^{1,2,3,4}, B. C. Sheldon¹

4 1 Edward Grey Institute of Field Ornithology, Department of Zoology, University of Oxford, Oxford, U.K.

5 2 Department of Collective Behaviour, Max Planck Institute of Animal Behavior, Konstanz, Germany

6 3 Centre for the Advanced Study of Collective Behaviour, University of Konstanz, Konstanz, Germany

7 4 Department of Biology, University of Konstanz, Konstanz, Germany

8

9

10 **ABSTRACT**

- 11 1. Natural populations and communities consist of individuals that differ in their
12 phenotypes. There is increasing evidence in community ecology that consistent
13 intraspecific variation in behaviour changes the outcome of ecological interactions.
- 14 2. Differences in intra- and inter-specific interactions are expected to play a major role in
15 determining patterns of species coexistence and community structure. However, the
16 question of whether individuals vary in their propensity to associate with heterospecifics
17 has been neglected.
- 18 3. We used social network analysis to characterise pattern of heterospecific associations
19 in wild mixed-species flocks of songbirds, and assessed whether individuals adopt
20 consistent social strategies in their broader, heterospecific, social environment. We
21 quantified heterospecific foraging associations using data from a large automatically
22 monitored PIT-tagged population of birds, involving more than 300 000 observations of
23 flock membership, collected over three winters, for two tit species (Paridae), blue tits,
24 *Cyanistes caeruleus*, and great tits, *Parus major*.
- 25 4. We assessed individual consistency in interspecific social preferences over both short-
26 term (week-to-week) and longer-term (year-to-year) timescales for a total of 4610
27 individuals, and found that blue tits and great tits exhibited marked and consistent
28 intraspecific differences in heterospecific social phenotypes in terms of both absolute

29 and relative number of associates. Further, we found that these consistent differences
30 were significantly greater than expected from spatial and temporal differences in
31 population densities.

32 5. Heterospecific associations represent a major component of the social environment for
33 many species, and our results show that individuals vary consistently in their social
34 decisions with respect to heterospecifics. These findings provide support for the notion
35 that intraspecific trait variation contributes to patterns at community and ecosystem
36 levels.

37

38 **Key words:** *Cyanistes caeruleus*, mixed-species group, Paridae, *Parus major*, repeatability,
39 social behaviour, social network analysis, social phenotype

40

41

42 **INTRODUCTION**

43 The social environment is an important component of individuals' lives. How individuals
44 interact with conspecifics has been shown to have implications for their susceptibility to
45 disease (Silk et al. 2018), access to resources (Aplin et al. 2012), and reproductive success
46 and survival (Alberts 2019). Many potential mechanisms might mediate a sociality-fitness
47 link, including access to resources, agonistic support, and anti-predator benefits (Ostner &
48 Schülke 2018). While much of our current understanding of the costs and benefits of group
49 living results from research on single-species groups (Krause & Ruxton 2002), social groups
50 can take many different forms, and frequently include individuals from different species
51 (Goodale et al. 2017). Mixed-species groups are widespread across animal communities
52 (amphibians: Glos et al. 2007, birds: Sridhar et al. 2009, fish: Lukoschek & McCormick 2000,
53 mammals: Stensland et al. 2003), and offer opportunities for studying the causes of social
54 behaviour without confounding effects of kin-selection or mate-choice (Farine et al. 2012).
55 Many of the key processes thought important for group-living in single-species contexts have

56 been suggested to also apply to the formation of mixed-species groups (Dhondt 2012,
57 Sridhar & Guttal 2018). For example, both grouping and use of heterospecific social
58 information have been shown to provide anti-predator benefits (Magrath et al. 2015; Meise
59 et al. 2018; Goodale et al. 2019) and foraging benefits (Dolby & Grubb 1998; Farine et al.
60 2015) to members of mixed-species groups. In turn, interactions with heterospecifics could
61 influence the positions of individuals within their social networks, and thereby contribute to
62 ecological and evolutionary processes arising via the social environment (see Cantor et al.
63 2019 for a review).

64

65 Ecological research on species coexistence has traditionally focussed on averaged
66 differences between species, thus ignoring the importance of intraspecific variation among
67 individuals for species interactions (Bolnick et al. 2011; Violle et al. 2012; Hart et al. 2016). It
68 has become increasingly apparent that individual-level processes are of vital importance for
69 understanding community dynamics and other emerging properties of individual interactions.
70 To study social behaviour in mixed-species groups, Farine et al. (2012) suggested a
71 paradigm shift, from a species-level perspective to treating interactions between individuals
72 as the basic unit of analysis (*sensu* Hinde 1976). Such a bottom-up approach accounts for
73 the effect of inter-individual differences in traits and has long been applied to study sociality
74 in single-species groups, thus providing a theoretical and analytical basis for analysing
75 heterospecific sociality. Social Network Analysis (SNA) has become an important method for
76 quantifying individuals' social decisions (such as partner choice), interaction pattern among
77 individuals, and the emerging social structure of groups and populations (Cantor et al. 2019).
78 To our knowledge, only two studies have analysed dyadic interactions to explore the role of
79 individual-level decisions in shaping heterospecific groups and both focus on within-species
80 variation in measures of social behaviour (Farine et al. 2012; Farine & Milburn 2013). These
81 studies show that a bottom-up approach is useful when exploring hypotheses regarding
82 individual variation in heterospecific association propensity. Yet, neither of these studies

83 explored whether individuals differ consistently in their propensity to associate with
84 heterospecifics.
85
86 Considering individuals' social decisions in a broader, multi-species context will allow a
87 better understanding of the link between individual-level decisions, fitness-related outcomes,
88 and the structure of mixed-species social communities (Farine et al. 2012). For example,
89 how individuals are positioned within their social environment can predict their reproductive
90 success (Formica et al. 2011; Farine & Sheldon 2015). Specifically, the propensity for great
91 tits, *Parus major*, to acquire a breeding territory has been shown to be higher, not only for
92 birds that dispersed into the population earlier, but also when individuals dispersed early
93 relative to their competitors (Farine & Sheldon 2015). For selection to act via the social
94 environment, individuals must vary consistently in their social environment (McDonald et al.
95 2017). Hence, a key first step in relating fitness consequences to social network position is
96 to understand the distribution and consistency of individual variation in behaviour by
97 characterising individual interaction patterns and social phenotypes. Consistency in social
98 behaviour is often assumed, but only a few studies have shown that individuals can express
99 consistent social phenotypes, by repeatedly measuring and comparing their behaviour
100 over larger time spans (Blumstein et al. 2013; Jacoby et al. 2014; Aplin et al. 2015; Menz et
101 al. 2017; O'Brien et al. 2018). Whether individuals also express consistent social strategies
102 in a multi-species context is yet to be explored.

103

104 In this study, we test whether individual members of wintering mixed-species flocks of
105 songbirds have consistent interspecific social preferences. Over three winters, we recorded
106 associations among two tit species (Paridae) fitted with individual passive integrated
107 transponder (PIT) tags, recorded by a grid of automated feeding stations fitted with radio
108 frequency identification (RFID) antennae. This large-scale observational study provided a
109 unique opportunity to assess individual consistency in interspecific social preferences over
110 both short-term (week-to-week) and longer-term (year-to-year) timescales. We used SNA to

111 quantify measures of gregariousness and heterospecific flocking propensity for 2775
112 individual blue tits, *Cyanistes caeruleus*, and 1835 great tits, observed over three years, and
113 then assessed the individual consistency of these traits using repeatability analyses. We
114 then used network randomisation approaches (Farine 2017) to calculate repeatability
115 estimates after accounting for spatio-temporal differences in the distribution, and thus broad
116 social environments, among individuals. By comparing the two sets of repeatability
117 estimates, we were able to separate consistency in social decision making from consistency
118 in behavior caused by spatial factors.

119

120 **METHODS**

121 *Study system*

122 This study was conducted from December 2011 to March 2014, in the context of a long-term
123 research project studying the social behaviour of tits in Wytham Woods, Oxfordshire, U.K.
124 (51°46'N, 01°20'W). Blue tits and great tits, as well as some coal tits, *Parus ater*, marsh tits,
125 *Poecile palustris*, and European nuthatches, *Sitta europaea*, were individually tagged with a
126 unique British Trust for Ornithology (BTO) metal leg band, and a plastic leg ring carrying a
127 passive integrated transponder (PIT tag, IB Technologies, UK). Birds were ringed as
128 nestlings or as adults caught at nest-boxes during the breeding season, or using mist-nets in
129 winter. Sex and age (first year/adult) were identified using plumage coloration or breeding
130 records. The proportion of the population being tagged was very high, estimated over 90%
131 for the first year of the study (see Aplin et al. 2013 for a formal analysis).

132

133 Tits form mixed-species foraging flocks with fission-fusion dynamics outside the breeding
134 season, which mainly consist of Parid species, but can be joined by nuthatches,
135 treecreepers, and woodpeckers (Hinde 1952; Ekman 1989). In this study, we consider
136 heterospecific interactions between blue tits and great tits, the most abundant species in this

137 population, that together account for 90.6 ± 0.8 % (mean \pm SEM) of individuals recorded
138 across the three winters under study.

139

140 *Data collection*

141 We collected data on social behaviour of individual birds by recording their visits to feeding
142 stations equipped with radio-frequency identification (RFID) antennae (Dorset ID,
143 Netherlands). We deployed a total of 65 sunflower-seed bird feeders with two access points
144 were deployed throughout the study area in an even grid of approximately 250 x 250 m (see
145 Supplementary Material Figure S1). These feeding stations opened automatically before
146 sunrise and shut down after dusk on Saturday and Sunday (hereafter *weekends*), and
147 remained closed on weekdays. Each time a bird visited the feeder, the identity of the bird
148 detected by the RFID antenna would be logged automatically onto the RFID logger, and we
149 downloaded these data from each feeder weekly. Data for this study was collected during
150 three separate seasons of 14 weekends each, over three winters: 3 December 2011 to 27
151 February 2012 (Year 1), 1 December 2012 to 3 March 2013 (Year 2), and 30 November
152 2013 to 2 March 2014 (Year 3). These time periods correspond to those used to assess
153 individual differences social phenotypes of great tits in a single-species context (by Aplin et
154 al. 2015). Number of individuals observed in each season is given in Table 1.

155

156 *Detecting groups*

157 We followed the same protocol as previous studies on this system (e.g., Aplin et al. 2013,
158 2015; Farine et al. 2012, 2015) to process the datastream of spatiotemporal detections of
159 PIT-tagged birds at feeders. We used a Gaussian mixture model (GMM) to identify gathering
160 events, or flocks (Psorakis et al. 2012). The GMM works by identifying short-term bursts of
161 activity of individuals repeatedly visiting a feeder. When birds visit a feeder, they briefly
162 perch to collect a seed that they then take to nearby vegetation to process (see
163 Supplementary Material Video S1). These visits generate temporal waves in the number of
164 detections that the GMM identifies. The advantage of the GMM approach is that it can

165 identify flocks of differing sizes, and modelling shows that the resulting networks are more
166 robust than other approaches (Psorakis et al. 2015). We applied this method to the data at
167 each feeder on each day, and aggregated data from all of the flocks into one group by
168 individual matrix for each of the 42 weekends in our study period. Detection of groups was
169 done using the gmmevents function in the asnipe package (Farine 2013) in R v.3.4.4 (R
170 Core Team, 2012)

171

172 *Constructing social networks*

173 Dyadic association strength was calculated using the simple ratio index. The simple ratio
174 index generates a value between 0 and 1, which represents to probability of observing two
175 individuals together given that at least one individual was in a given flock (Hoppitt & Farine
176 2017). This represents an unbiased estimate of the proportion of times two individuals spend
177 together (Whitehead 1995). We combined association strengths for each dyad for each
178 weekend to produce a social network. We generated 42 weekend social networks. In
179 addition, we combined data on flock membership over whole winters to produce on social
180 network for each season (3 winter). Social networks were constructed using the asnipe
181 package (Farine 2013) in R v.3.4.4 (R Core Team, 2012).

182

183 *Measures of social phenotype*

184 We calculated the following individual-level measures of social behaviour for great tits and
185 blue tits: i) measures of gregariousness: unweighted degree (total number of associates of
186 any species), weighted degree (overall association strength for all species interactions), and
187 average foraging group size, and ii) a relative measure of heterospecific flocking propensity
188 that is independent from an individual's gregariousness: a variant of the 'external-internal'
189 (E-I) index (Krackhardt & Stern 1988). The E-I index quantifies the relationship between links
190 in two exclusive categories and was originally proposed for friendship links to organisational
191 subunits (i.e., external: friendship links between subunits, internal: friendship links within
192 subunits). Analogously, we calculated the E-I index by subtracting the number of ties to

193 conspecifics from the number of heterospecific associations, and dividing this by the total
194 number of associations. Values range from 1 to -1, with 1 specifying that the focal only
195 associates with heterospecifics, -1 indicating strong homophily (focal individual only has ties
196 to conspecifics); the index will be zero if links are distributed equally between conspecifics
197 and heterospecifics.

198

199 *Repeatability Analysis*

200 We calculated the proportion of phenotypic trait variation that can be attributed to inter-
201 individual variation, where repeated samples corresponded to replicated networks. To
202 assess consistency in social phenotypes over short and long time periods, we calculated
203 within-year (week-to-week) and between-year repeatability in measures of great tit and blue
204 tit behaviour. Our approach to analysing repeatability of heterospecific social behaviour
205 follows methods previously used to calculate individual differences in the social phenotypes
206 of great tits in a single-species context (Aplin et al. 2015). We calculated repeatability scores
207 using linear mixed-effects models, as the proportion of variance that can be explained by the
208 individual random effect (intra-class correlation coefficient, ICC; Nakagawa & Schielzeth
209 2010). Our models accounted for the global population size and network density of the
210 sampling period (weekend or season, respectively). For all models, with the exception of the
211 E-I index, we square-rooted the response variables to conform to normality. We estimated a
212 95% range confidence intervals of the repeatability scores using restricted maximum
213 likelihood Markov chain Monte Carlo sampling, using the R package MCMCglmm with
214 default priors (Hadfield 2010).

215

216 *Comparing observed repeatability results to null expectations*

217 As is often the case for social networks, we can expect strong influences of i) resource
218 distribution and other spatial features on group formation (Farine & Sheldon 2019), and ii)
219 local population density (Farine et al. 2015), on social metrics. We therefore used network
220 randomisation approaches (Farine 2017) to control for the spatio-temporal distribution of

221 individuals to isolate the social component of individuals' decisions from environmental
222 factors. We designed a null model that randomised identities in each step (1000
223 randomisations in total), but controlled for the spatio-temporal distribution of individuals and
224 species identity. Within each network, we randomly swapped identities among individuals
225 (node permutations), but restricted swaps to be between individuals of the same species
226 that had the majority of their visits recorded at the same feeding station during the data
227 collection for that network. Such restricted node permutations were necessary in order to
228 maintain the total amount of variance in the model constant when applied to randomised
229 datasets by maintaining a consistent social network structure, while randomising the link
230 within individuals across different networks. We estimated the repeatability values for each
231 of the 1000 resulting randomised networks using the same mixed-model approach described
232 above. From the distribution of null repeatability values, we extracted the 95% to represent
233 the expected range of individual behaviour without social preferences, i.e. the repeatability
234 arising from their spatiotemporal occurrence only. To calculate what proportion of the
235 repeatability was accounted for by the permuted data, we divided the mean of the
236 randomised estimates by the observed repeatability estimate.

237

238 *Ethical Note*

239 This work was part of an ongoing long-term research project at Wytham Woods, which was
240 approved by the local ethical review panel at the Department of Zoology, University of
241 Oxford. All catching, handling, and ringing of birds was conducted by experienced BTO
242 licence holders.

243

244 **RESULTS**

245 We quantified heterospecific associations in 342 510 observations of flock membership, or
246 grouping events, recorded over three years. Great tits were on average observed in $13.57 \pm$
247 10.26 (mean \pm SD) sampling periods (weekends), and blue tits in 11.37 ± 10.03 sampling

248 periods, across the three years. The majority of birds were recorded in one winter only (1876
249 blue tits and 1270 great tits), but 629 blue tits and 356 great tits were observed in two years,
250 and 270 blue tits and 209 great tits were recorded in all three years of data collection.

251

252 Blue tits and great tits exhibited considerable intraspecific variation in measures of social
253 behaviour (see Table1). On average, individuals had an annual total of 120 associates, but
254 some individuals were recorded foraging with more than 600 other individuals in one year.

255 Birds also varied markedly in the average strength to their associations, with some

256 individuals being three-times more strongly connected to their associates than the

257 population's mean edge strength. Blue tits and great tits were on average seen with ten

258 other group members, but some individuals' annual mean foraging group sizes reached up

259 to 40. The relative number of heterospecific to conspecific group members (E-I index) also

260 varied considerably for individuals, with some preferentially associating with conspecifics

261 (negative values of E-I index) and others preferentially associating with heterospecifics

262 (positive values of E-I index). Table 1 summarises the spread of inter-individual differences

263 in measures of social behaviour, and provides number of individuals included in each year.

264

265 Individuals from both species were significantly repeatable in their heterospecific social

266 behaviour on both short (week-to-week) and long (year-to-year) timescales (Figure 1, Table

267 S1). Across the three years of the study, the average week-to-week repeatability scores

268 ranged from 0.49 to 0.62 for heterospecific degree, from 0.43 to 0.61 for heterospecific edge

269 strength, from 0.45 to 0.63 for heterospecific average foraging group size, and from 0.38 to

270 0.51 for E-I index. Table S1 in the Supplementary Material lists repeatability scores

271 separately for blue tits and great tits. Year-to-year repeatability estimates were similar to, or

272 slightly higher than within-year scores for degree, edge strength, and group size, but the

273 between-year consistency in relative number of conspecific and heterospecific associates

274 (E-I index) was moderately low for both blue tits and great tits, with $R=0.38$ and $R=0.25$,

275 respectively.

276

277 All repeatability scores were significantly higher than expected by chance. The observed
278 repeatability values were outside the 95% range of estimates calculated from 1000
279 permuted datasets for each measure, despite the spatially constrained null model
280 sometimes explaining a large share of individuals' repeatability scores (see Table S1 in the
281 Supplementary Material). For example, where individuals foraged explained 85-90% of blue
282 tits' week-to-week consistency in average group size, whereas the permuted data only
283 accounted for about 50% of the week-to-week repeatability in blue tits' association strength.
284 In both blue tits and great tits, the proportion of the individual week-to-week repeatability that
285 can be explained by the spatio-temporal distribution of birds was largest for group size,
286 slightly lower for E-I index, and smallest for degree and edge strength. In other words, how
287 individuals are distributed in space and time contributed relatively more to the consistency in
288 measures of social behaviour for some phenotypes than for others. The repeatability
289 estimates for degree, edge weight, and group size were usually higher when considering
290 year-to-year repeatability, compared to week-to-week repeatability. In contrast, the year-to-
291 year repeatability of individuals' relative number of conspecific to heterospecific group
292 members was lower than its short-term consistency, from week-to-week.

293

294 **DISCUSSION**

295 We show that individual great tits and blue tits differ consistently in their propensity to
296 associate with heterospecifics. In part, the repeatability in heterospecific associations was
297 driven by spatial variation in population densities and grouping tendencies, with 40-90% of
298 the within-year variation and 20-80% of the between-year repeatability in individual
299 behaviour explained by the spatio-temporal distribution of individuals. These high values
300 suggest that individuals may be making decisions about heterospecific associations as a
301 parameter of their habitat choice. Further, we identified a significant social component to the
302 consistency in measures of heterospecific social behaviour over and above the variation

303 explained by space alone, suggesting that individuals make choices about who to associate
304 with on a flock-by-flock basis, or over timescales of minutes. Our results demonstrate that
305 social phenotypes translate into the heterospecific social environment, with individuals
306 showing marked inter-individual variation in overall gregariousness, and connectedness to
307 heterospecifics in multi-species networks. Given the growing evidence for the effects of
308 individuals' social environment on modulating evolutionary and ecological processes (Cantor
309 et al. 2019), the importance of decisions about the heterospecific social associations could
310 be widely under-appreciated.

311

312 While blue tits and great tits were consistent in measures of their heterospecific social
313 behaviour over both short (weekend-to-weekend) and long (year-to-year) timescales,
314 repeatability scores for degree, edge weight, and group size tended to be higher when
315 measured across years, compared to within years. Similarly, between-year repeatability
316 estimates of great tit social phenotypes in a single-species context were higher than their
317 within-year estimates (Aplin et al. 2015). Annual averages of behavioural measures might
318 provide a more accurate description of individual phenotypes than parameters extracted
319 from weekend-long social networks. It is also possible that more consistent individuals have
320 a higher probability of year-to-year survival. These hypotheses are not mutually exclusive
321 and require further investigation.

322

323 Direct comparisons of repeatability values, for example between great tits and blue tits, or
324 between different years, are not straightforward, because the calculation of between-
325 individual variance will depend on population sizes of both species, and therefore
326 opportunities to associate with conspecifics and heterospecifics. Yet, compared to
327 repeatability of different behaviours observed in other studies (reviewed in Bell et al. 2009),
328 blue tits and great tits showed a high consistency in their heterospecific social behaviour.
329 For example, repeatability scores reported for migration, mate preference, and parental
330 behaviours were on average less than 0.3, whereas week-to-week repeatability values

331 observed in this study ranged from 0.4 to 0.6, with. Consistent individual differences in social
332 network position were previously shown in only a few populations where social behaviour
333 was studied in a conspecific context (e.g., Jacoby et al. 2014; Menz et al. 2017; O'Brien et
334 al. 2018), including a study on our system, which noted inter-individual differences and
335 reported similar repeatability in great tit social strategies (group size: $R = 0.43-0.64$, degree:
336 $R = 0.46-0.61$, association strength: $R = 0.41-0.64$) in a single-species context (Aplin et al.
337 2015). Here, we extend findings of studies on single-species systems by showing that
338 individuals vary in their heterospecific social associations in much the same way as was
339 previously reported within species.

340

341 A major ecological and evolutionary question is how social groups form. While we found that
342 individual-level repeatability was significantly larger than expected by chance, the null
343 distribution of repeatability values (from the spatially-constrained permuted datasets) were
344 also consistently larger than 0, and within the range of what are considered moderate to high
345 repeatability values for behaviour (Bell et al. 2009). Different metrics of individuals'
346 heterospecific social phenotypes can thus be explained by differences in spatial choices and
347 within-location social choices to varying relative amounts. Our results suggest that social
348 choices explain a relatively larger proportion of measures of sociability that represent the
349 outcome of repeated measures of associations among the same individuals (e.g., average
350 association strength), while the distribution of individuals, or their choice of location, explains
351 relatively more of the measures that represent cumulative observations (e.g., E-I index). The
352 high levels of repeatability in measures represented by cumulative observations suggest that
353 individuals may be choosing these environments via larger-scale social decisions, such as
354 those involving the decision of where to disperse. Studies on dispersal have found that the
355 presence (Doligez et al. 2003) and behaviour (Seppänen & Forsman 2007) of
356 heterospecifics can play a major role in shaping individual-level dispersal and habitat choice
357 decisions. Thus, the social environment that individuals experience depends on social
358 choices made at different temporal and spatial scales.

359

360 Our findings open up many new questions regarding the evolutionary ecology of behaviour
361 in natural populations. Heterospecific associations might have long-term impacts on
362 individual fitness-related traits, going beyond the immediate drivers arising from foraging and
363 anti-predator benefits. For example, a recent analysis on our study system suggest that
364 great tit breeding performance is affected by their heterospecific breeding neighbourhoods
365 (Roth 2019). How differences in individual association pattern can shape the local structure
366 of populations is demonstrated by carry-over effects of social behaviour. For example,
367 associations among wild zebra finches, *Taeniopygia guttata* during the nesting period predict
368 pattern of interactions in subsequent years (Brandl et al. 2019), while winter social networks
369 among great tits translate to breeding neighbourhoods during spring (Firth & Sheldon 2016).
370 The patterns of local structure arising from interactions among individuals can then translate
371 into local communities, and, in turn, these communities can generate repeatable hierarchical
372 social structures (Farine & Sheldon 2019). Thus, carry-over effects of social structure arising
373 from heterospecific social associations warrants much greater attention.

374

375 Our study contributes to the emerging picture that a bottom-up approach integrating the
376 different components, or scales, of social decision-making is needed to gain full
377 understanding of how social communities are formed and maintained. Individuals are not
378 only considering conspecifics when making decisions about which groups to join, but also
379 heterospecifics. This insight opens opportunities to address new questions, such as whether
380 non-random social associations form between individuals of different species, how these
381 emerge and are maintained, and their consequences across different ecological and
382 evolutionary processes. Future work should also explore the underlying causes and fitness
383 consequences of individual differences in the propensity to associate with heterospecifics,
384 and test how such processes can influence the evolution of social groups.

385

386 **ACKNOWLEDGEMENTS**

387 We are grateful to all members of the EGI's (Edward Grey Institute of Field Ornithology)
388 Wytham Tit Project and Social Networks Group for their help with the data collection in the
389 field. The work was supported by grants from the European Research Council (AdG 250164)
390 and the BBSRC (BB/L006081/1) awarded to BCS, DRF was funded by the Max Planck
391 Society and the DFG Centre of Excellence 2117 "Centre for the Advanced Study of
392 Collective Behaviour" (ID: 422037984), and FH was funded by a NERC studentship award,
393 ref. 1654580. Many thanks to Raul Costa-Pereira for much appreciated input, and to Josh
394 Firth for help with the analysis and valuable discussion throughout the preparation of the
395 manuscript.

396

397 **AUTHOR CONTRIBUTIONS STATEMENT**

398 All authors conceived the idea of the study, FH and DRF analysed the data; FH led the
399 writing of the manuscript. All authors contributed critically to the drafts and gave final
400 approval for publication.

401

402 **DATA AVAILABILITY STATEMENT**

403 Data and code used for analyses will be available from the figshare repository.

404

405 REFERENCES

- 406 Aplin LM, Farine DR, Morand-Ferron J, & Sheldon BC. 2012. Social networks predict patch
407 discovery in a wild population of songbirds. *Proceedings of the Royal Society B:*
408 *Biological Sciences*, 279, 4199-4205.
- 409 Aplin LM, Farine DR, Morand-Ferron J, Cole EF, Cockburn A, & Sheldon BC. 2013.
410 Individual personalities predict social behaviour in wild networks of great tits (*Parus*
411 *major*). *Ecology Letters*, 16, 1365-1372.
- 412 Aplin LM, Farine DR, Mann RP, & Sheldon BC. 2014. Individual-level personality influences
413 social foraging and collective behaviour in wild birds. *Proceedings of the Royal Society*
414 *B: Biological Sciences*, 281, 20141016.
- 415 Aplin LM, Firth JA, Farine DR, Voelkl B, Crates RA, Culina A, Garroway CJ, Hinde CA, Kidd
416 LR, Psorakis I, Milligan ND. 2015. Consistent individual differences in the social
417 phenotypes of wild great tits, *Parus major*. *Animal Behaviour*, 108, 117-127.
- 418 Alberts SC. 2019. Social influences on survival and reproduction: Insights from a long-term
419 study of wild baboons. *Journal of Animal Ecology*, 88, 47-66.
- 420 Bell AM, Hankison SJ, & Laskowski KL. 2009. The repeatability of behaviour: a meta-
421 analysis. *Animal behaviour*. 77, 771-783.
- 422 Bolnick DI, Amarasekare P, Araújo MS, Bürger R, Levine JM, Novak M, Rudolf VH,
423 Schreiber SJ, Urban MC, Vasseur DA. 2011. Why intraspecific trait variation matters in
424 community ecology. *Trends in Ecology & Evolution*, 26, 183-192.
- 425 Brandl HB, Farine DR, Funghi C, Schuett W, Griffith SC. 2019 Early-life social environment
426 predicts social network position in wild zebra finches. *Proceedings of the Royal Society*
427 *B: Biological Sciences*, 286, 20182579.
- 428 Cantor M, Maldonado-Chaparro A, Beck K, Carter G, He P, Hillemann F, Klarevas-Irby J,
429 Lang SD, Ogino M, Papageorgiou D, Prox L, & Farine DRF. 2019. Animal social
430 networks: revealing the causes and implications of social structure in ecology and
431 evolution. *EcoEvoRxiv*, May 14.
- 432 Dhondt AA. 2012. Interspecific competition. *Oxford Avian Biology Series*. Oxford University
433 Press, Oxford.
- 434 Dolby AS, Grubb TC. 1998. Benefits to satellite members in mixed-species foraging groups:
435 an experimental analysis. *Animal Behaviour*, 56, 501-509.

- 436 Doligez B, Cadet C, Danchin E, Boulinier T. 2003. When to use public information for
437 breeding habitat selection? The role of environmental predictability and density
438 dependence. *Animal Behaviour*, 66, 973-88.
- 439 Ekman J. 1989. Ecology of non-breeding social systems of Parus. *Wilson Bulletin*, 101, 263-
440 288.
- 441 Farine DR, Garroway CJ, Sheldon BC. 2012. Social network analysis of mixed-species
442 flocks: exploring the structure and evolution of interspecific social behaviour. *Animal*
443 *Behaviour*, 84, 1271–1277.
- 444 Farine DR. 2013. Animal social network inference and permutations for ecologist in R using
445 asnipe. *Methods in Ecology and Evolution*, 4, 1187-1194.
- 446 Farine DR, & Milburn PJ. 2013. Social organisation of thornbill-dominated mixed-species
447 flocks using social network analysis. *Behavioral Ecology and Sociobiology*, 67, 321-330.
- 448 Farine DR, Aplin LM, Sheldon BC, Hoppitt W. 2015 Interspecific social networks promote
449 information transmission in wild songbirds. *Proceedings of the Royal Society B:*
450 *Biological Sciences*, 282, 20142804.
- 451 Farine DR, Sheldon BC. 2015. Selection for territory acquisition is modulated by social
452 network structure in a wild songbird. *Journal of Evolutionary Biology*, 28, 547-556.
- 453 Farine DR. 2017. A guide to null models for animal social network analysis. *Methods in*
454 *Ecology and Evolution*, 8, 1309-1320.
- 455 Farine DR & Sheldon BC. 2019. Stable multi-level social structure is maintained by habitat
456 geometry in a wild bird population. *bioRxiv*, 1 Jan 2019, 085944.
- 457 Firth JA & Sheldon BC. 2016 Social carry-over effects underpin trans-seasonally linked
458 structure in a wild bird population. *Ecology Letters*, 19, 1324-1332.
- 459 Glos J, Dausmann KH, Linsenmair EK. 2007. Mixed-species social aggregations in
460 Madagascan tadpoles—determinants and species composition. *Journal of Natural*
461 *History*, 41, 1965-1977.
- 462 Goodale E, Beauchamp G, Ruxton GD. 2017. *Mixed-species groups of animals: behaviour,*
463 *community structure, and conservation.* New York, NY: Academic Press.
- 464 Goodale E, Ruxton GD, & Beauchamp G. 2019. Predator Eavesdropping in a Mixed-Species
465 Environment: How Prey Species May Use Grouping, Confusion, and the Cocktail Party
466 Effect to Reduce Predator Detection. *Frontiers of Ecology and Evolution*. 7-141.

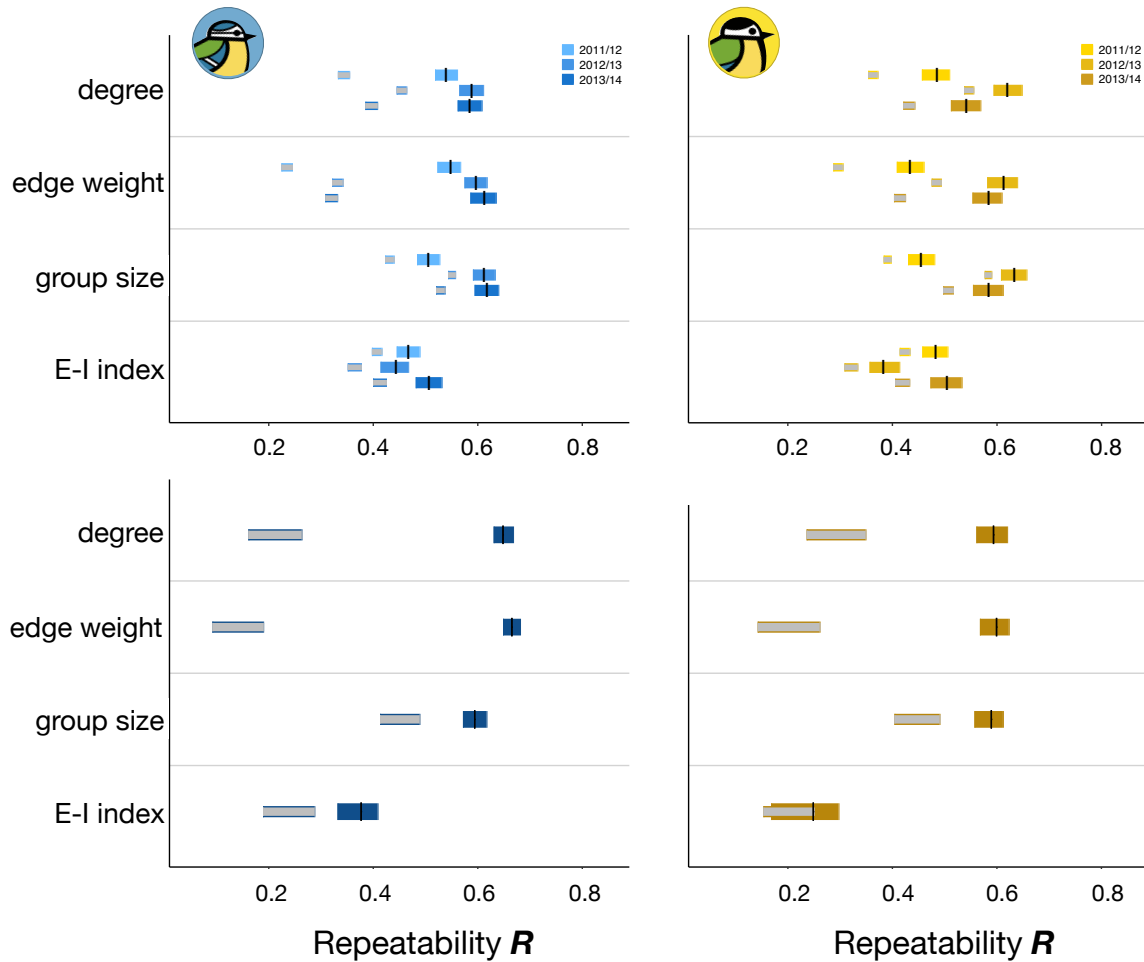
- 467 Hart SP, Schreiber SJ, Levine JM. 2016. How variation between individuals affects species
468 coexistence. *Ecology Letters*, 19, 825-838.
- 469 Hinde RA. 1952. The behaviour of the Great Tit (*Parus major*) and some other related
470 species. *Behaviour*, 2, 1–201.
- 471 Hoppitt WJ, Farine DR. 2018. Association indices for quantifying social relationships: how to
472 deal with missing observations of individuals or groups. *Animal Behaviour*, 136, 227–
473 238.
- 474 Krackhardt D, Stern RN. 1988. Informal networks and organizational crises: an experimental
475 simulation. *Social Psychology Quarterly*, 51, 123–140.
- 476 Lukoschek V, McCormick MI. 2000. A review of multi-species foraging associations in fishes
477 and their ecological significance. In *Proceedings of the 9th International Coral Reef*
478 *Symposium*, vol. 1, pp. 467–474. Ministry of Environment, Indonesia: Indonesian
479 Institute of Sciences, International Society for Reef Studies Bali.
- 480 Magrath RD, Haff TM, Fallow PM, Radford AN. 2015. Eavesdropping on heterospecific
481 alarm calls: from mechanisms to consequences. *Biological Reviews*. 90, 560–586.
- 482 McDonald GC, Farine DR, Foster KR, & Biernaskie JM. 2017. Assortment and the analysis
483 of natural selection on social traits. *Evolution*, 71, 2693-2702.
- 484 Menz CS, Goldizen AW, Blomberg SP, Freeman NJ, Best EC. 2017. Understanding
485 repeatability and plasticity in multiple dimensions of the sociability of wild female
486 kangaroos. *Animal Behaviour*, 126, 3-16.
- 487 O'Brien PP, Webber QM, & Vander Wal E. 2018. Consistent individual differences and
488 population plasticity in network-derived sociality: An experimental manipulation of
489 density in a gregarious ungulate. *PloS one*, 13, 0193425.
- 490 Ostner J & Schülke O. 2018. Linking Sociality to Fitness in Primates: A Call for Mechanisms.
491 In *Advances in the Study of Behavior*, 50, 127-175. Academic Press.
- 492 Psorakis I, Roberts SJ, Rezek I, & Sheldon BC. 2012. Inferring social network structure in
493 ecological systems from spatio-temporal data streams. *Journal of the Royal Society*
494 *Interface*, 9, 3055-3066.
- 495 Psorakis I, Voelkl B, Garroway CJ, Radersma R, Aplin LM, Crates RA, Culina A, Farine DR,
496 Firth JA, Hinde CA, Kidd LR. 2015. Inferring social structure from temporal data.
497 *Behavioral Ecology and Sociobiology*, 69, 857-866.
- 498 R Core Team. 2012. R: A language and environment for statistical computing. Vienna,
499 Austria: R Foundation for Statistical Computing.

- 500 Roth AM. 2019. Exploring the Intersection between Animal Personality and Sociality. DPhil
501 Thesis, Oxford University Research Archive, Oxford, UK.
- 502 Seppänen JT, Forsman JT. 2007. Interspecific social learning: novel preference can be
503 acquired from a competing species. *Current Biology*, 17, 1248-1252.
- 504 Silk MJ, Weber NL, Steward LC, Hodgson DJ, Boots M, Croft DP, Delahay RJ, & McDonald
505 RA. 2018. Contact networks structured by sex underpin sex-specific epidemiology of
506 infection. *Ecology Letters*, 21, 309-318.
- 507 Sridhar H, Beauchamp G, Shanker K. 2009. Why do birds participate in mixed-species
508 foraging flocks? A large-scale synthesis. *Animal Behaviour*, 78, 337-347.
- 509 Sridhar H & Guttal V. 2018. Friendship across species borders: factors that facilitate and
510 constrain heterospecific sociality. *Philosophical Transactions of the Royal Society B*,
511 373, 20170014.
- 512 Stensland E, Angerbjorn A, Berggren P. 2003 Mixed-species groups in mammals.
513 *Mammalian Reviews*, 33, 205–223.
- 514 Violle C, Enquist BJ, McGill BJ, Jiang LI, Albert CH, Hulshof C, Jung V, Messier J. 2012.
515 The return of the variance: intraspecific variability in community ecology. *Trends in*
516 *Ecology & Evolution*, 27, 244-252.
- 517 Whitehead H. 1995. Investigating structure and temporal scale in social organizations using
518 identified individuals. *Behavioural Ecology*, 6, 199–208.
- 519

520 **TABLES AND FIGURES**

521 Table 1. Number of individual great tits and blue tits included in each winter data collection
 522 period, and spread of metrics of social behaviour. Annual mean values across all individuals
 523 are provided, and 1st and 3rd quartile in brackets.
 524

		Blue tit	Greáútit
N individuals	2011-12	1631	1085
	2012-13	1306	813
	2013-14	1154	842
Degree	2011-12	131.2 [71.0, 183.0]	169.9 [106.0, 226.0]
	2012-13	101.9 [49.0, 145.0]	115.1 [65.0, 158.0]
	2013-14	93.6 [50.5, 133.0]	111.3 [62.0, 156.0]
Strength	2011-12	3.8 [1.2, 5.8]	5.0 [3.4, 6.8]
	2012-13	3.2 [0.9, 5.1]	4.2 [1.9, 6.2]
	2013-14	2.9 [1.1, 4.4]	3.4 [1.7, 5.0]
Group size	2011-12	11.6 [9.0, 14.0]	11.6 [9.5, 13.8]
	2012-13	10.3 [6.9, 13.2]	9.9 [6.9, 13.0]
	2013-14	8.8 [6.1, 11.1]	8.7 [6.2, 10.9]
E-I index	2011-12	-0.05 [-0.18, 0.68]	-0.06 [-0.20, 0.07]
	2012-13	-0.10 [-0.24, 0.04]	0.02 [-0.10, 0.13]
	2013-14	-0.06 [-0.19, 0.08]	-0.05 [-0.19, 0.10]



526

527 Fig. 1: Repeatability scores for week-to-week (top row) and between-year (bottom row)
 528 heterospecific social behaviour in great tits (left) and blue tits (right). Black lines show the R
 529 score estimates, and yellow or blue bars indicating the 95% range, which was obtained
 530 using restricted maximum likelihood Markov chain Monte Carlo sampling. Grey bars
 531 represent the 95% range of the repeatability values calculated from 1000 spatially-controlled
 532 data randomisations. All measures of social behaviour were significantly repeatable
 533 (confidence intervals do not overlap with zero; $p < 0.001$ in all cases), and observed values
 534 are significantly higher than the repeatability scores from the randomised data ($p = 0.027$ for
 535 E-I index between-year repeatability in great tits, and $p < 0.001$ elsewhere). Underlying data
 536 can be found in Table S1 in the Supplementary Material.

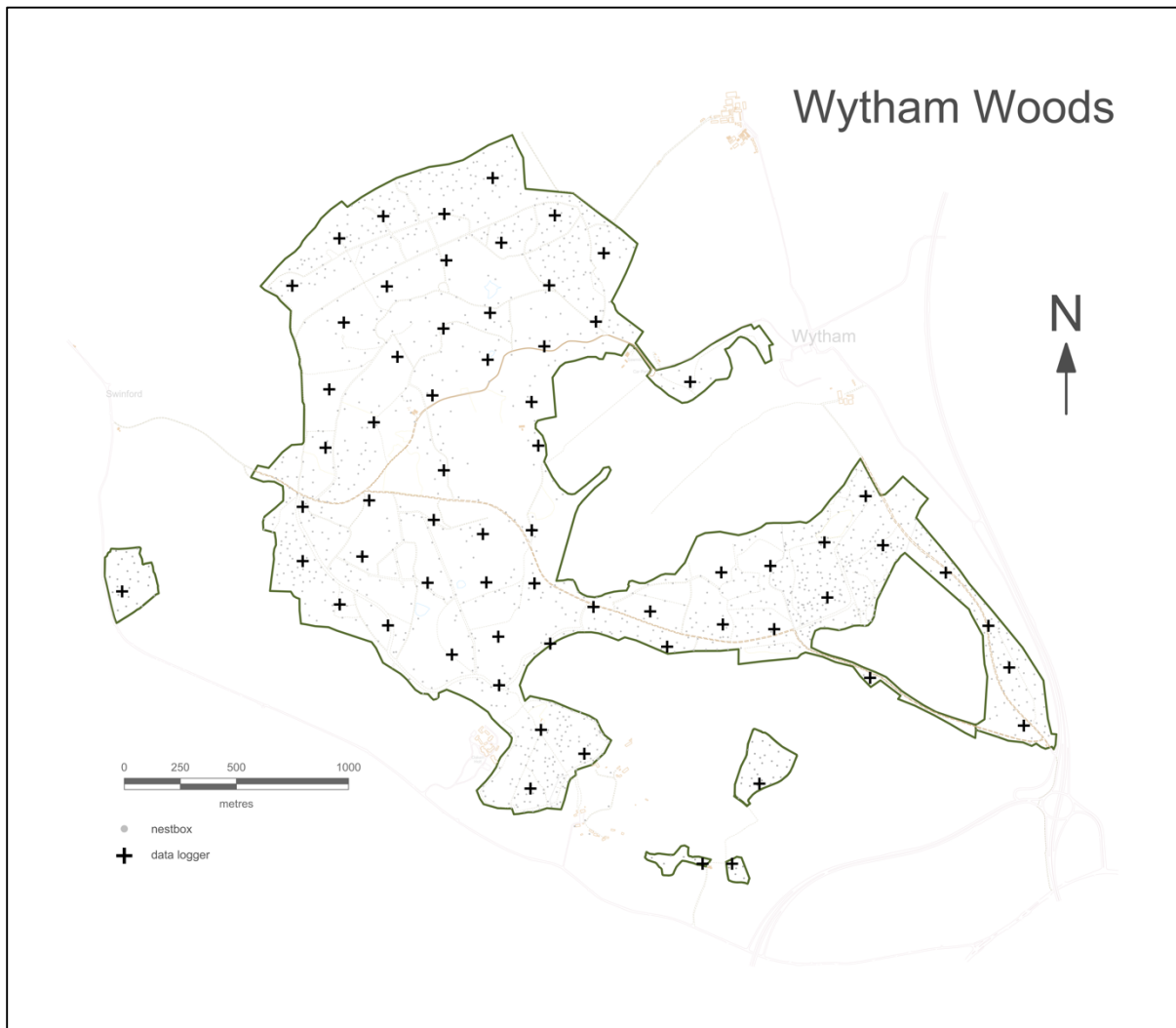
537

538 SUPPLEMENTARY MATERIAL

539 Table S1: Repeatability scores (R_{obs}) and 95% range of confidence, as per restricted
 540 maximum likelihood Markov chain Monte Carlo sampling, for degree (total number of
 541 associations), edge weight (association strength), average group size, and E-I index. All
 542 measures are significantly repeatable and observed values are significantly higher than
 543 expected repeatability scores (R_{ran}) from 1000 permutations of the data ($p=0.027$ for E-I
 544 index between-year repeatability in great tits, and $p<0.001$ elsewhere). The spatially
 545 constrained null model accounts for different proportions of the within-individual consistency
 546 in heterospecific social behaviour.

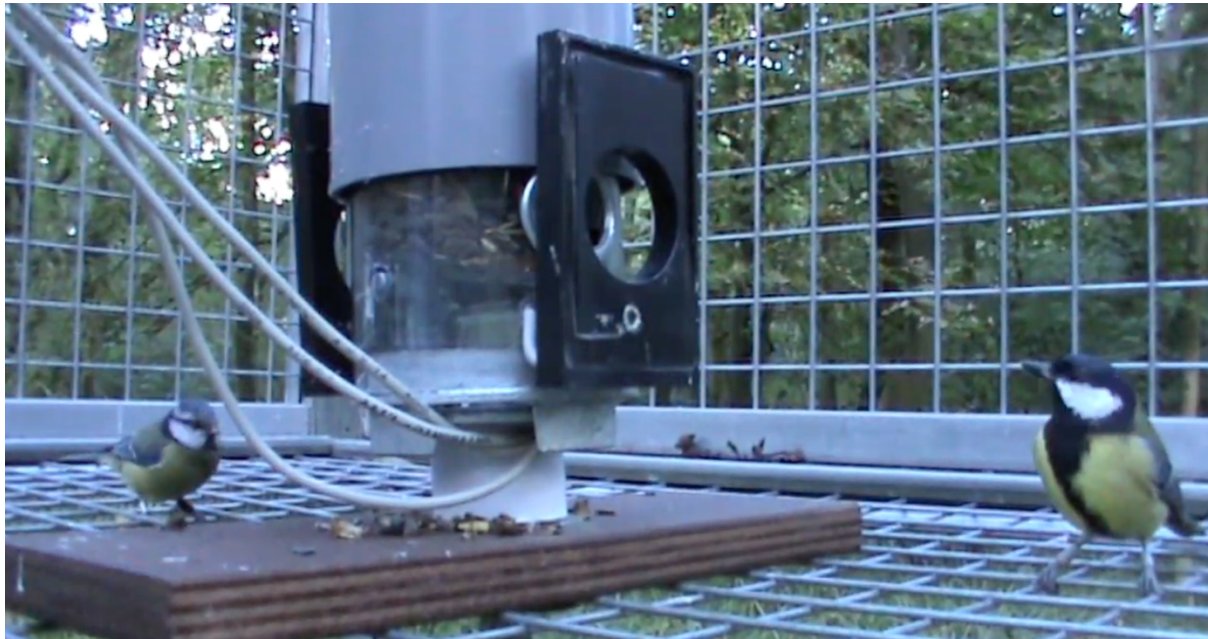
547

Species	Metric	Season	R_{obs} [$R_{obs,low}$ - $R_{obs,up}$]	[$R_{ran,low}$ - $R_{ran,up}$]	$R_{ran,mean}/R_{obs}$
Blue tit	Degree	2011-12	0.54 [0.52-0.56]	[0.33-0.35]	63.66 %
		2012-13	0.59 [0.56-0.61]	[0.44-0.46]	77.20 %
		2013-14	0.58 [0.56-0.61]	[0.38-0.41]	67.83 %
		year-to-year	0.65 [0.63-0.67]	[0.16-0.27]	32.67 %
	Edge weight	2011-12	0.55 [0.52-0.57]	[0.22-0.24]	42.79 %
		2012-13	0.60 [0.57-0.62]	[0.32-0.34]	55.57 %
		2013-14	0.61 [0.59-0.63]	[0.31-0.33]	52.20 %
		year-to-year	0.67 [0.65-0.68]	[0.09-0.19]	21.14 %
	Group size	2011-12	0.51 [0.48-0.53]	[0.42-0.44]	85.27 %
		2012-13	0.61 [0.59-0.63]	[0.54-0.56]	89.91 %
		2013-14	0.62 [0.59-0.64]	[0.52-0.54]	85.62 %
		year-to-year	0.59 [0.57-0.61]	[0.41-0.49]	75.86 %
	E-I index	2011-12	0.47 [0.44-0.49]	[0.40-0.42]	87.05 %
		2012-13	0.44 [0.41-0.47]	[0.35-0.38]	82.10 %
		2013-14	0.51 [0.48-0.53]	[0.40-0.42]	81.38 %
		year-to-year	0.38 [0.33-0.41]	[0.19-0.29]	63.20 %
Great tit	Degree	2011-12	0.49 [0.46-0.51]	[0.35-0.37]	74.78 %
		2012-13	0.62 [0.59-0.65]	[0.54-0.55]	88.11 %
		2013-14	0.54 [0.51-0.57]	[0.42-0.44]	79.76 %
		year-to-year	0.59 [0.56-0.62]	[0.23-0.34]	49.23 %
	Edge weight	2011-12	0.43 [0.41-0.46]	[0.29-0.30]	68.27 %
		2012-13	0.61 [0.58-0.64]	[0.48-0.49]	78.98 %
		2013-14	0.58 [0.55-0.61]	[0.40-0.42]	70.87 %
		year-to-year	0.60 [0.57-0.62]	[0.14-0.26]	33.61 %
	Group size	2011-12	0.45 [0.43-0.48]	[0.38-0.40]	85.86 %
		2012-13	0.63 [0.61-0.66]	[0.58-0.59]	92.06 %
		2013-14	0.58 [0.55-0.61]	[0.50-0.52]	86.74 %
		year-to-year	0.59 [0.56-0.61]	[0.40-0.49]	75.85 %
	E-I index	2011-12	0.48 [0.46-0.51]	[0.41-0.43]	87.73 %
		2012-13	0.38 [0.36-0.41]	[0.31-0.33]	83.89 %
		2013-14	0.50 [0.47-0.53]	[0.41-0.43]	83.05 %
		year-to-year	0.25 [0.19-0.30]	[0.15-0.25]	80.94 %



548

549 Figure S1: Map of the study site, Wytham Woods (Oxfordshire, UK). Black crosses show the
550 location of the 65 automated RFID feeding stations, which record feeder visits of PIT-tagged
551 birds. These data loggers are distributed in a grid of each approximately 250 x 250 m, and
552 open and close simultaneously on two days per week during the winter months, thus
553 providing a snapshot of the spatio-temporal distribution of birds.



554

555 Video V1: Link to Video demonstrating the collection of social association data at automated
556 feeding station. Birds (*Paridae* spp.) with PIT-tags moulded into plastic rings on their legs
557 perch on the RFID antennae when taking a seed from one of the feeder's two access holes,
558 and typically process the unhusked seeds in the nearby vegetation.