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Napper, C.J. and Hatchwell, B.J. orcid.org/0000-0002-1039-4782 (2016) Social dynamics in nonbreeding flocks of a cooperatively breeding bird: causes and consequences of kin associations. *Animal Behaviour*, 122. pp. 23-35. ISSN 0003-3472

<https://doi.org/10.1016/j.anbehav.2016.09.008>

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1 **Social dynamics in non-breeding flocks of a cooperatively**
2 **breeding bird: causes and consequences of kin associations**

3

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11 Word count (main text only): 9111

12 Word count (text + references): 11070

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14 Kin selection is regarded as a key process in the evolution of avian cooperative breeding, and kinship
15 influences helper decisions in many species. However, the effect of kinship on non-breeding social
16 organisation is still poorly understood despite its potential fitness implications. Here, we investigated
17 the origins and consequences of kin associations in non-breeding flocks of long-tailed tits *Aegithalos*
18 *caudatus*, an atypical cooperative breeder where helpers are failed breeders that redirect care towards
19 relatives living in kin neighbourhoods. We found that kinship is an important factor in initial grouping
20 decisions; all members of a nuclear family initially joined the same flock and failed breeders chose to
21 flock with their relatives. Flocks that merged during the non-breeding season also contained relatives.
22 In contrast to these findings of positive kin association, when long-tailed tits switched flocks they
23 tended to disperse into flocks with fewer relatives, although such switches often occurred with kin. In
24 a playback experiment, we found no evidence that aggression shown towards members of other flocks
25 was affected by kinship, indicating that kin associations result from a preference to flock with
26 relatives rather than a constraint on flocking with non-relatives. Finally, using social network analysis,
27 we show that fine-scale non-breeding associations among individuals were positively related with
28 kinship, and that these non-breeding associations were reflected in helping decisions in the subsequent
29 breeding season, in addition to the previously reported effects of kinship and proximity. We conclude
30 that long-tailed tits prefer to associate with kin when not breeding, and suggest that by doing so they
31 gain either nepotistic benefits within flocks or future indirect benefits during breeding.

32

33 *Keywords:* *Aegithalos caudatus*; cooperative breeding; helper; kin neighbourhood; kin selection;
34 long-tailed tit; relatedness; social network; winter flock.

35

36 Cooperatively breeding birds typically live in groups that include close relatives (Hatchwell, 2009;
37 Riehl, 2013) and kin selection is generally regarded as a major driver of helping behaviour (Dickinson
38 & Hatchwell, 2004; West, Griffin, & Gardner, 2007). Indeed, an effect of kinship on the alloparental
39 investment of helpers has been extensively documented (e.g. Curry, 1989; Dickinson, 2004; Wright,
40 McDonald, te Marvelde, Kazem, & Bishop, 2010), but much less is known about the effect of kinship
41 on social interactions in contexts other than breeding, possibly because interactions outside the
42 breeding season are often deemed to be less important in the evolution of sociality. Nevertheless, kin-
43 based winter sociality has been suggested to distinguish species that breed cooperatively from those
44 that do not (Ekman, 1989; Noske, 1991), and to act as an intermediate stage in the transition from
45 asociality to cooperative breeding (Drobniak, Wagner, Mourocq, & Griesser, 2015). Furthermore,
46 individuals that delay dispersal to associate with close kin during the winter have been shown to
47 derive nepotistic benefits relative to immigrants in western bluebirds *Sialia mexicana* (Dickinson,
48 Euaparadorn, Greenwald, Mitra, & Shizuka, 2009; Dickinson, Ferree, Stern, Swift & Zuckerberg
49 2014) and Siberian jays *Perisoreus infaustus* (Ekman, Bylin, & Tegelstrom, 2000). However, few
50 other studies have examined the role that relatedness plays in social interactions both within and
51 between groups outside of the breeding season, even though such interactions may have important
52 consequences for the cooperative behaviour of individuals during subsequent breeding events.

53 Most cooperatively breeding bird species spend the non-breeding season in stable family
54 groups that form when mature offspring delay dispersal and remain on their parents' territory (Covas
55 & Griesser, 2007; Ekman, Hatchwell, Dickinson, & Griesser, 2004; Emlen, 1982). Helping can also
56 occur within extended family networks or 'kin neighbourhoods' (Dickinson & Hatchwell, 2004). In
57 such systems, non-breeding group membership is often less stable than in typical cooperative
58 breeders, with individuals dispersing between groups and groups merging or disbanding. Dispersive
59 behaviour is generally thought to disrupt the kin structure of a population (Emlen, 1997; Gardner &
60 West, 2006; Perrin & Goudet, 2001), raising the question of how kin neighbourhoods develop in
61 dispersive species. Several potential mechanisms exist, the most obvious of which is localised natal
62 dispersal that results in relatives living in close proximity to each other (Dickinson et al., 2009;
63 Preston, Briskie, Burke, & Hatchwell, 2013; Sharp, Simeoni, & Hatchwell, 2008). There is also

64 growing evidence for the coordinated dispersal of kin in cooperative breeders (e.g. Koenig, Hooge,
65 Stanback, & Haydock, 2000; Pollack & Rubenstein, 2015; Ridley, 2012; Williams & Rabenold,
66 2005), including among species that help within kin neighbourhoods (Sharp, Baker, Hadfield,
67 Simeoni, & Hatchwell, 2008). Of course, there may also be costs of associating with relatives,
68 especially if it entails kin competition over resources (Griffin & West, 2002) or a risk of inbreeding
69 (Pusey, 1987). Therefore, for certain categories of individuals, such as juveniles of one particular sex,
70 there may also be countervailing selection for dispersal away from relatives, resulting in sex-biased
71 natal dispersal (Greenwood, 1980). Alternatively, inbreeding may be avoided via active
72 discrimination against kin as social or sexual partners within kin neighbourhoods that comprise male
73 and female relatives (Dickinson, Akçay, Ferree & Stern 2016; Riehl & Stern, 2015).

74 Besides the immediate benefits of living alongside relatives (Ekman et al., 2004), if helping
75 decisions are influenced by familiarity as well as kinship, non-breeding social associations in kin
76 neighbourhoods may also have important fitness consequences during subsequent breeding events.
77 Within kin neighbourhoods, individuals may interact with both relatives and non-relatives, so that
78 shared group membership may be insufficient for effective kin discrimination, even though this may
79 be needed for individuals to maximise their inclusive fitness (Cornwallis, West & Griffin, 2009). The
80 effects of kinship and familiarity on helping behaviour are hard to distinguish in species that live in
81 discrete family groups because helpers are usually both related to and associated with any potential
82 recipients of their help. However, distinguishing the effects of these factors may be more
83 straightforward when helping occurs within kin neighbourhoods comprising both kin and non-kin
84 (e.g. Kraaijeveld & Dickinson, 2001; McGowan, Fowlie, Ross, & Hatchwell, 2007).

85 We investigated the origins and consequences of kin associations in non-breeding flocks of
86 long-tailed tits, *Aegithalos caudatus*. Long-tailed tits have a kin-selected cooperative breeding system
87 where redirected helping occurs within kin neighbourhoods. Birds do not delay dispersal or breeding
88 to help; instead, at the beginning of each breeding season all birds attempt to breed in pairs. Helpers
89 are breeders whose own nests have failed and whose care is redirected to the brood of another pair.
90 Helping is typically kin-directed and usually occurs between brothers, although a small minority of
91 helpers are female and a small proportion care at the nests of non-relatives (Hatchwell, Gullett, &

92 Adams, 2014; Nam, Simeoni, Sharp, & Hatchwell, 2010; Russell & Hatchwell, 2001). Following
93 breeding, long-tailed tits form mixed-sex flocks usually comprising 5-25 birds. Flock members forage
94 together during the day and roost together in linear huddles at night, thereby gaining thermoregulatory
95 benefits (Hatchwell, Sharp, Simeoni & McGowan, 2007). Flocks occupy large non-exclusive ranges
96 that typically contain both adults and juveniles from multiple families as well as unrelated immigrants
97 that disperse between flocks during their first winter. These immigrants include both sexes, although
98 in our study population the majority are females due to female-biased natal dispersal (Sharp, Simeoni,
99 McGowan, Nam & Hatchwell, 2011). Most birds flock with at least one close relative ($r \geq 0.25$)
100 during the non-breeding season (Ezaki, Miyawaza & Sakikawa, 1991; Hatchwell, Anderson, Ross,
101 Fowlie, & Blackwell, 2001; McGowan et al., 2007), but how these patterns of kinship arise is not well
102 understood. Likewise, while it is known that the ranges of related flocks overlap more than those of
103 unrelated flocks (Hatchwell, Anderson et al., 2001), and that siblings often disperse together (Sharp,
104 Baker, et al., 2008; Sharp, Simeoni, et al., 2008), flock membership is not fixed with both adults and
105 juveniles switching between flocks, and flocks coalescing or disbanding through the non-breeding
106 season; the influence of relatedness on these flock mergers and switches has not been examined.
107 Finally, although several factors determining a failed breeder's propensity to help have been described
108 previously, including condition (Meade & Hatchwell, 2010), relatedness (Russell & Hatchwell 2001)
109 and date (MacColl & Hatchwell 2002), the potential influence of prior association during the non-
110 breeding season is unknown.

111 In this paper, we first examined whether flock membership, flock mergers and flock switches
112 were influenced by the relatedness of flock members. We then used a playback experiment to test
113 whether observed kin associations were caused by differential aggression towards unrelated intruders.
114 Third, we used social network analysis to study the effect of kinship on fine-scale social interactions
115 among individual birds. Finally, we investigated the effect of these associations on helping behaviour
116 in the following breeding season.

117

118 **METHODS**

119

120 *Study System*

121

122 *Field Observations*

123 We have studied a population of long-tailed tits occupying a 3 km² site in the Rivelin Valley,
124 Sheffield, UK (53°23'N, 1°34'W) since 1994. At the start of each breeding season, pairs (mean = 49
125 *per annum*) were located and colour-ringed (>95% of all adults are ringed by the end of each breeding
126 season). Long-tailed tits are single-brooded; their nests were found by following pairs and
127 subsequently monitored closely until they failed or broods fledged. During the nestling period, nests
128 were observed for approximately one hour every other day and the identities of all provisioning adults
129 (parents and any helpers) recorded. Nestlings in accessible nests were colour-ringed when 11 days
130 old. Flocks were observed during the non-breeding seasons of 1996-1997 (October-March, 35
131 observation days), 1997-1998 (May-February, 56 days), 1998-1999 (May-February, 57 days), 2011-
132 2012 (May-March, 87 days) and 2012-2013 (May-March, 80 days). Flocks were followed for up to
133 4h, until contact was lost or until all birds in the group were identified. All flock members could
134 rarely be identified in a single observation period, so we assumed that sighting of two or more known
135 flock members was a reliable indicator of flock identity. Flock size was defined as the number of
136 ringed birds in each flock. This is a minimum estimate because most flocks also contained a small
137 number of unringed immigrants that dispersed into our study site in their first winter. Flock position
138 was recorded every two minutes on to large-scale maps (scale 1 cm: 50 m) in 1996-1999, and every
139 minute using a Garmin Geko 201 GPS in 2011-2013. Map registrations were converted to map
140 coordinates for analysis at a resolution of 10 m.

141

142 *Pedigree Construction*

143 We used social pedigrees derived from 19 years of field observations to estimate dyadic
144 relatedness among individuals in our population. Long-tailed tits can use social pedigree information
145 provided by calls that they learn from carers to recognise kin (Sharp, McGowan, Wood, & Hatchwell,
146 2005), and these cues provide a reliable estimate of genetic relatedness because brood parasitism and

147 extra-pair paternity are infrequent (Hatchwell, Ross, Chaline, Fowlie, & Burke, 2002). A cross-
148 fostering experiment ($N = 9$ broods) produced seven cross-fostered recruits in 1996 – 1998
149 (Hatchwell, Ross, Fowlie & McGowan, 2001), these were considered as relatives of their foster
150 family rather than their biological family. Dyads were classified as first-order relatives ($r = 0.5$),
151 second-order relatives ($r = 0.25$), third order relatives ($r = 0.125$) or unrelated ($r = 0$). Social pedigrees
152 were inevitably incomplete because our population is open, with immigrants dispersing into the study
153 site during their first winter. Therefore, we performed sibship reconstructions for these immigrants as
154 well as parentage analyses for all birds that were first ringed as adults, as detailed below.

155 Blood samples (approx. 10 μ l per bird) were taken from 84.8% of observed flock members (N
156 = 495) by brachial venipuncture under UK Home Office Licence. Genomic DNA was extracted from
157 blood, amplified and genotyped at twenty microsatellite loci: Ase18, Ase37, Ase64, Hru2, Hru6,
158 LOX1, Pca3, Pma22, Ppi2, CAM01, CAM03, CAM15, CAM17, CAM23, P2DP8, Pca4, Tgu_01-040,
159 Tgu_04-012, Tgu_05-053 and Tgu_013-017; mean number of alleles = 14.6, range = 2 – 53 (Adams,
160 Robinson, Mannarelli, & Hatchwell, 2015; Simeoni et al., 2007). Birds were sexed using standard
161 molecular genetic techniques (Griffiths, Double, Orr, & Dawson, 1998).

162 The great majority of birds ringed as adults were likely to be immigrants, but some may have
163 fledged unringed from inaccessible nests in the study site. To ensure that we did not misclassify these
164 birds as immigrants, we performed a parentage analysis using the likelihood approach in CERVUS v.
165 3.0 (Kalinowski, Taper, & Marshall 2007). Allele frequencies were estimated using all genotyped
166 individuals in all years (1994-2012, $N = 2755$) to maximise accuracy in estimating the frequency of
167 rare alleles and to ensure non-zero allele frequencies. For each year, CERVUS was run with the
168 following simulation parameters: 100,000 offspring, the true number and sampled proportion of
169 candidate parents, 96.3% loci typed (calculated from allele frequency data), 10 as the minimum
170 number of loci typed and a mistyping rate of 0.01. We classified all birds that were first ringed as
171 adults as ‘offspring’ and all breeders and helpers from the previous year as ‘candidate parents’; this is
172 justified because natal dispersal in long-tailed tits occurs during an individual’s first year (McGowan,
173 Hatchwell, & Woodburn, 2003; Sharp, Baker, et al., 2008) so any immigrants in a given year are
174 likely to have hatched in the previous year. We then carried out parentage analyses with known sexes,

175 but no prior information about how the sexes were paired, using critical LOD scores for 99%
176 confidence derived from the simulations. To ensure the reliability of parentage assignments in our
177 pedigree matrix, parent-offspring relationships were considered to be genuine only if the parents were
178 known to have been paired and to have fledged unringed chicks in the year in question. This resulted
179 in 12 (2.4%) of the birds we observed in flocks being assigned to a natal nest within the study site
180 (one bird from 1997-1998 flocks, seven birds from three nests in 2011-2012 flocks and four birds
181 from two nests in 2012-2013 flocks).

182 Long-tailed tits often disperse with relatives (Sharp, Simeoni, et al., 2008), so to determine
183 whether sibling groups existed among immigrants we reconstructed sibships using KINGROUP v.2
184 for all years from 1994 to 2012. All immigrants in a given year were considered to be potential
185 siblings and we tested for the presence of full siblings using the ‘descending ratio’ algorithm
186 (Konovalov et al., 2004), and the allele frequencies used in the parentage analysis described above.
187 The results from sibship reconstruction were considered to match those of likelihood ratio tests if the
188 score for a dyad was $P < 0.05$. Sibling relationships were added to our social pedigrees only if all
189 siblings in a given group were mutually significantly matched in the analysis. This resulted in two
190 sibgroups in flocks in 1996-1997 (two groups of two birds), three sibgroups in 1997-1998 (three
191 groups of two birds), four sibgroups in 1998-1999 (four groups of two birds), eight sibgroups in 2011-
192 2012 (five groups of two birds, one group of three birds and two groups of four birds) and four
193 sibgroups in 2012-2013 (three groups of two birds and one group of seven birds). These sibgroups
194 were in addition to those sibgroups assigned to nests within the study site in the parentage analysis.

195

196 *Flock Dynamics*

197

198 *Flock Membership*

199 To investigate whether kinship influenced flock membership, we first recorded whether all
200 individuals associated with a successful nest (parents, offspring and any helpers) initially joined the
201 same flock. Secondly, we investigated whether failed breeders that did not become helpers joined
202 flocks containing relatives. To do this, we determined how many nearby flocks were available for a

203 failed breeder to join on the day they were first observed in a flock; flocks were considered nearby if
204 they were within the maximum distance (1260 m) travelled by any failed breeder to join a flock from
205 their last known breeding attempt. We fitted generalised linear mixed models (GLMMs) with a
206 binomial error structure and logit link function using the ‘lmer’ function in the R package ‘lme4’
207 (Bates & Maechler, 2010) to determine the role of kinship in flock-joining decisions. Whether or not a
208 flock was ‘joined’ (1 or 0) was the response term; ‘relatedness’, ‘distance’ and an interaction between
209 these two variables were fitted as predictor variables, and the ‘ID’ of the failed breeder was fitted as a
210 random term. ‘Relatedness’ was defined as the proportion of each flock that was related to the failed
211 breeder at three levels ($r = 0.5$, $r \geq 0.25$ and $r \geq 0.125$) calculated using pedigree information
212 supplemented by parentage and sibship analyses (see above). ‘Distance’ was the distance between a
213 bird’s last breeding attempt and the location of the flock on the day that they were first observed in it.
214 Failed breeders were included only if they did not help, had a choice of nearby flocks to join, and
215 were first observed in a flock in May or June of 1997, 1998, 2011 or 2012 so that only initial flocking
216 decisions were considered. Lastly, if a failed breeder appeared in the dataset in multiple years, we
217 used the observation from their first year only.

218 From the three global models (one for each measure of relatedness), we generated candidate
219 models containing all possible combinations of the predictors. These were then ranked using AICc
220 and models within two AICc of the top model were deemed to be supported. If multiple models were
221 supported, a final model was obtained by averaging parameter estimates according to their Akaike
222 weights (Burnham & Anderson, 2002) using the R package ‘MuMIn’ (Barton, 2012). The relative
223 importance of each explanatory variable in the final model was calculated as a sum of all the model
224 weights in which that variable appears, so that if a variable appeared in all models it would have a
225 relative importance of one. All statistical analyses were carried out in the R environment, v 2.12.0 (R
226 Development Core Team, 2010).

227

228 *Flock Mergers*

229 Two flocks were considered to have merged if they joined to form a permanent new flock,
230 with no members remaining in their original flocks. Flocks occasionally coalesced briefly as they

231 foraged in a shared part of their ranges, before splitting again; these ‘temporary mergers’ were
232 excluded from analysis. All flock mergers occurred soon after broods fledged, when unringed birds
233 were rare in the study site, so flock size was defined here as the total number of birds in each flock on
234 the merger date, including any unringed birds. To investigate the effect of kinship on flock mergers,
235 we compared the relatedness (at three levels: $r = 0.5$, $r \geq 0.25$ and $r \geq 0.125$, as above) of
236 neighbouring flocks that merged with those that did not. If an individual was related to multiple birds
237 in another flock, we defined relatedness from its closest relative in that flock. Flocks were considered
238 to be neighbours if they were within 480m (the greatest observed distance between flocks that
239 merged) on the merger date and if no other flocks occupied the space between them. Too few flock
240 mergers were observed for statistical analysis.

241

242 *Flock Switches*

243 Individuals observed in multiple flocks over the course of the non-breeding season were
244 considered to have switched flocks. Direct observations of flock switches were rare, so switches were
245 assumed to have occurred on the midpoint between the dates the bird was last observed in their
246 original flock and first identified in a new flock. Birds that switched between the same two flocks
247 within a month of each other were considered to have switched together, unless they were known to
248 have switched at different times. Occasionally, birds switched back and forth between the same two
249 flocks, remaining in the new flock only for a short period of time (median duration of temporary
250 switches = 23.5 days, range = 3 - 149; note that this is the maximum duration of switches and most
251 birds that switched temporarily were observed in their new flock only once). These ‘temporary
252 switches’ were excluded from analysis. If a bird switched flocks more than once during the study, we
253 used only their first switch; this excluded 9 birds that switched flocks in more than one season. To
254 determine whether flock switches were influenced by kinship, we compared a bird’s relatedness to
255 members of its original flock and to its new flock on its switch date using Wilcoxon signed-rank tests
256 in R (R Development Core Team, 2010). Relatedness was defined as the proportion of each flock that
257 was related to the individual at three levels ($r = 0.5$, $r \geq 0.25$ and $r \geq 0.125$), as above. Flock size was
258 defined here as the total number of ringed birds in each flock on the switch date. Tests were

259 performed using all switches, and also separately for each sex, age class (adult or juvenile) and status
260 in the previous breeding season (successful breeder, failed breeder or helper).

261

262 *Playback Experiment*

263

264 A playback experiment was used to investigate behaviour involved in flocking decisions,
265 specifically testing whether the response of flocks towards the calls of non-flock members was
266 influenced by kinship. We used the short-range ‘churr’ call that is often produced when long-tailed
267 tits meet an unfamiliar flock or individual. This call is highly individual-specific (Sharp & Hatchwell,
268 2005) and during breeding pairs react less aggressively towards the playback of churr calls of relatives
269 than those of non-relatives (Sharp et al., 2005). Churr calls were recorded from individually marked
270 breeding adults close to their nests in 2011 and 2012 at a distance of <15 m. Recordings were made
271 onto a Tascam DR-100 with a sampling frequency of 44.1 kHz and 24-bit accuracy using a
272 Sennheiser MKH60P48 microphone fitted with a standard basket windshield and windjammer.
273 Spectrograms were produced for all recordings using Avisoft SASLab Pro (version 5.1.20) and the
274 ‘cleanest’ churr call was selected for each individual. All selected calls were of similar amplitude to
275 each other and to those produced in the field. A highpass frequency filter of 1kHz was applied to
276 minimise background noise without altering the minimum frequency of calls. A 1-minute sequence of
277 36 randomly spaced copies of the call was then created and this sequence was looped five times to
278 create a 5-minute sequence for playback.

279 Playback experiments were conducted during the non-breeding season of 2011-2012 (3 trials)
280 and 2012-2013 (5 trials). Focal flocks were located and each experienced two treatments: the churr
281 calls of a relative ($r \geq 0.25$ to at least one flock member; mean number of flock members bird was
282 related to = 3.375, range = 1 - 6), and the churr calls of a randomly selected non-relative ($r < 0.125$ to
283 all flock members). Relatedness was determined using social pedigrees. All calls used for playbacks
284 were from birds that were alive but living in a different flock to the one subject to playback. Trials
285 consisted of a control period of five minutes of no playback followed by five minutes of playback.
286 Calls were broadcast using an iPod touch and an X-mini II portable speaker, and all flocks were

287 within 20 m of the speaker at the start of playback. To measure flock responses, we recorded the
288 closest approach to the speaker, the time spent within 20 m of the speaker, and the rate of churr and
289 triple calls (a non-aggressive contact call) during the whole trial and during playback. Treatment order
290 was randomised and the observer, who stood >20 m from the speaker, was blind to which treatment
291 was taking place. Trials of kin and non-kin playback to a focal flock took place a week apart.

292 Wilcoxon signed-rank tests were used to determine whether flocks responded differently to
293 calls of relatives and non-relatives. The difference between treatments in closest approach to the
294 speaker, time spent within 20 m of the speaker and net vocal response per flock member (the
295 difference in call rate between the control and playback periods when controlled for flock size) was
296 used to examine responses. There was no significant difference between years so data were pooled for
297 analyses. All analyses were performed in R version 2.12.0 (R Core Development Team, 2010).

298

299 *Analysis of Individual Associations*

300

301 *Social Network Analysis*

302 Direct physical interactions between identifiable individuals are rarely observed, so two birds
303 were considered associated if they were seen together in the same flock on the same day. This ‘gambit
304 of the group’ (Franks, Ruxton & James, 2010) is appropriate for this species because all flock
305 members forage and roost together so the assumption that each individual is associated with every
306 other individual is met. Weighted association indices were calculated for each dyad using the half
307 weight index (HWI) in the program SOCPROG 2.4 (Whitehead, 2009). This index was chosen
308 because it is the most appropriate when individuals are located infrequently, creating a bias in favour
309 of sighting only one individual from a dyad in a given sampling period (Cairns & Schwager, 1987).

310 The HWI is defined as:

$$311 \quad \text{HWI} = y_{ab}/(y_{ab} + y_0 + 0.5(y_a + y_b)),$$

312 where y_{ab} = number of sampling periods in which both bird ‘a’ and bird ‘b’ were seen in the same
313 group, y_a = number of sampling periods in which bird ‘a’ was observed but bird ‘b’ was not, y_b =

314 number of sampling periods in which bird 'b' was observed but bird 'a' was not and y_0 = number of
315 sampling periods in which birds 'a' and 'b' were seen in different groups. Only birds present in the
316 study site for the entire non-breeding season were included in the weighted network to ensure that
317 mortality/dispersal did not affect analyses. Birds were also excluded from the weighted network if
318 they were observed on fewer than three sampling days (14 birds in 1996-1997, 8 birds in 1997-1998,
319 2 birds in 1998-1999, 19 birds in 2011-2012 and 17 birds in 2012-2013) because rarely observed birds
320 tended to have low maximum association strengths.

321 To determine whether dyads associated more or less frequently than expected by chance, we
322 compared the observed weighted association matrix with randomly permuted association matrices
323 using the SOCPROG program. Random observations of individuals in different groups were swapped
324 so that the total number of groups each individual was seen in and the number of individuals in each
325 group were kept constant (Bejder, Fletcher & Bräger, 1998; Manly, 1995). Association matrices were
326 permuted sequentially beginning with the observed matrix and so were not independent. Therefore,
327 we performed 1,000 permutations each containing 1,000 trial flips (after which P -values stabilised to
328 within 0.01) to assess the significance of the differences in the standard deviation (SD) and coefficient
329 of variance (CV) between the observed matrix and the permuted matrices. We also assessed the
330 significance of the difference in the proportion of non-zero edges (i.e. associations) in the observed
331 matrix and permuted matrices. Significantly higher SD and CV of real data compared to random data
332 indicates preferred associations and a lower proportion of non-zero indices in the observed data
333 compared to the permuted data indicates that individuals avoid each other. P -values were calculated
334 based on the proportion of permuted CV or SD values that are lower than the observed values, for
335 example, $P = 0.70$ indicates that the real value is larger than 70% of the random ones. If the real value
336 fell within the top or bottom 2.5% of the random distribution ($P > 0.975$ or $P < 0.025$), we rejected the
337 null hypothesis that the real value could have arisen by chance.

338

339 *Social Association and Relatedness*

340 To determine whether social association was influenced by kinship, we examined the
341 significance of correlations between matrices of dyadic association and dyadic relatedness using

342 Mantel tests with 1,000 permutations in SOCPROG. This approach was used to investigate
343 associations among all birds, between males, between females (although there were too few females
344 in our networks to perform this test in 1996-1997) and between the sexes. We repeated these tests
345 while controlling both measures for a third matrix of the distance between nests in the previous
346 breeding season to control for an effect of philopatry causing related individuals to live in close
347 spatial proximity and therefore to be more likely to be associated by chance.

348

349 *Social Association and Helping*

350 To study the effect of non-breeding associations on helping decisions, we first identified
351 helpers that (a) were in the weighted network in the winter prior to helping, (b) helped at a nest at
352 which at least one member of the breeding pair was also in the network, and (c) had a choice of active
353 nests (i.e. contained nestlings on the day they started helping) where at least one member of each pair
354 was in the network. If a helper helped at multiple nests in the year in question, we considered only
355 their first helping decision; 5/22 helpers considered in this analysis helped at a second nest after their
356 first choice nest had been depredated. We fitted generalised linear mixed models (GLMMs) with a
357 binomial error structure and logit link function using the ‘lmer’ function in the R package ‘lme4’
358 (Bates & Maechler, 2010) to determine whether association in the previous winter influenced which
359 pair the helper chose to assist. Whether a nest was ‘helped’ or not was used as the response term in
360 this analysis; ‘association strength’, ‘kinship’ and ‘distance’ were fitted as predictor variables and
361 ‘helper ID’ was fitted as a random effect. Association strength was defined here as the association
362 index between the potential helper and the most closely associated member of a breeding pair; kinship
363 was defined as the relatedness between the potential helper and the brood; and distance was measured
364 between the helper’s last known breeding attempt and the nest in question. From this global model we
365 generated a set of candidate models containing all possible combinations of the predictor variables
366 which were then ranked using AICc. There were no models within two AICc of the top model so we
367 calculated parameter estimates from this model (Burnham & Anderson, 2002). GLMM analysis was
368 carried out in R v2.12.0 (R Development Core Team, 2010). Finally, we used Mantel tests with 1000

369 permutations to assess the correlation between the distance between two individuals' nests and their
370 association strength in the previous non-breeding season's social network.

371

372 **RESULTS**

373

374 *Flock Dynamics*

375

376 The number of flocks in our study area varied within and between years. In 1996-1997, there
377 were just four flocks (containing 63 ringed birds) that retained their separate status from October to
378 March. In 1997-1998, two of the six initial flocks merged shortly after fledging, leaving five flocks (N
379 = 93 birds) that remained distinct for the rest of the season. Likewise, in 1998-1999, two of 11 flocks
380 observed at the start of the non-breeding season merged soon after fledging, leaving 10 flocks (N =
381 117 birds) that persisted until March. The study population was generally larger during the second
382 period of non-breeding observations: in 2011-2012, there were initially 20 flocks, but mergers in early
383 June resulted in 13 flocks (N = 177 birds) that retained separate status for the rest of the year. In 2012-
384 2013, following mergers and one disbandment, 13 initial flocks (N = 156 birds) became 10 flocks that
385 remained distinct until the following season. Average flock size across all years was 16.45 ± 10.6 SD
386 (N = 42; range = 2 - 42) ringed birds (this is a minimum flock size due to the presence of some
387 unringed birds). The non-breeding ranges of flocks that remained after flocks had merged or
388 disbanded (Fig. 1) illustrate the extensive overlap in flock home ranges previously described by
389 Hatchwell, Anderson et al. (2001).

390

391 *Flock Membership*

392 At the end of each breeding season, all birds associated with a successful nest (parents,
393 offspring and any helpers) flocked together (with one exception in 2011 where the female and helpers
394 joined a different flock to the male and fledglings following disruption caused by depredation of some
395 offspring during fledging). Typical fledged brood size is 7.8, so this means that juveniles usually had

396 several first-order relatives in their initial flock. Failed breeders either joined a family group or
397 formed a new flock if there were no families nearby. The average distance between the last breeding
398 attempt of a failed breeder and the flock it joined was 373 m (range = 40 – 1260 m, $N = 90$; five failed
399 breeders were observed joining flocks in two years, but appear only once in the GLMM analyses).
400 Most failed breeders (78.8%, $N = 85$) had a choice of flocks within a range of 1260 m, and they
401 generally joined closer flocks (Table 1, Fig. 2a). Failed breeders were also most likely to join a flock
402 when they were more closely related to its members (Table 1, Fig. 2b). This was true for all three
403 levels of relatedness, but kinship had the strongest effect on the flock membership decisions of failed
404 breeders when only first-order relatives ($r = 0.5$) were considered (Table 1). There was also an
405 interaction between distance and kinship; birds were most likely to join flocks with their relatives if
406 they joined closer flocks, probably due to the effect of philopatry (Table 1). This apparent preference
407 for flocking with relatives resulted in 77.8% ($N = 36$) of failed breeders with a relative present in a
408 nearby flock joining a flock containing at least one relative ($r \geq 0.125$). The remaining 49 failed
409 breeders had no nearby relatives and hence joined flocks with non-kin ($r < 0.125$).

410

411 *Flock Mergers*

412 We observed nine mergers between eight pairs and one trio of flocks. Five mergers occurred
413 between flocks with members related at the level of $r = 0.5$, eight occurred between flocks related at r
414 ≥ 0.125 and just one was between unrelated flocks. Of the 19 flocks involved in mergers, only seven
415 had a choice of neighbouring flocks within the maximum distance of 480 m. The mean \pm SD
416 relatedness of focal flocks to the flock they merged with (as measured by the proportion of the flock
417 that were relatives at the $r \geq 0.125$ level) was 0.638 ± 0.377 ($N = 7$) and their relatedness to the flocks
418 they did not merge with was 0.429 ± 0.437 ($N = 7$). The small sample size precludes further analysis.

419

420 *Flock Switches*

421 Most birds remained in the same flock for the whole of the non-breeding season; 85.1%
422 of all birds ($N = 604$) were observed in one flock only (although some of these will have died or

423 dispersed from the study site at some stage). We observed 147 switches, but after exclusion of
424 temporary switches and repeated switches by the same bird, we analysed 69 switches between non-
425 breeding flocks. Across all years, there was no significant difference in the probability of switching
426 according to sex (females 15.3%, $N = 274$; males 10.7%, $N = 327$; chi-square test: $\chi^2_1 = 2.55$, $P =$
427 0.12), or age (adults 13.7%, $N = 342$; juveniles 11.9%, $N = 236$; $\chi^2_1 = 0.286$, $P = 0.59$). In addition,
428 the probability of switching was not significantly associated with the status of adults at the end of the
429 previous breeding season (successful breeders 15.6%, $N = 96$; failed breeders 13.4%, $N = 164$; helpers
430 14.0%, $N = 43$; chi-square test: $\chi^2_2 = 0.24$, $P = 0.89$). Flock switches took place throughout the non-
431 breeding season, although they were most common soon after fledging (Fig. 3a). This pattern of flock
432 switches is similar to the timing of disappearances of ringed birds from our study population during
433 the non-breeding season (Fig. 3b), although the latter must include mortality as well as dispersal
434 events.

435 In general, birds switched to flocks containing fewer relatives (Table 2). The proportion of
436 first-order relatives in a flock had a greater influence on an individual's switching decision than the
437 proportion of relatives with $r \geq 0.25$ or 0.125 in a flock. Closer scrutiny of flock switches showed that
438 juveniles tended to switch flocks to one containing fewer opposite-sex relatives, but only when
439 considering first-order kin (Table A1). Finally, any sex differences in switching behaviour in relation
440 to kinship were of marginal significance, but males ($r = 0.5$) moved to flocks where they were less
441 closely related to other birds (Table 2, Table A1). The sex ratio of ringed birds in original and
442 destination flocks did not differ significantly (Table A2), suggesting that flock switches were not
443 driven by a lack of potential mates in the current flock.

444 Individuals moved between flocks together in 57.1% ($N = 147$) of all observed switches, with
445 a mean \pm SD group size of 2.8 ± 1.69 birds ($N = 30$ groups; range = 2 - 9). Males (65.6%, $N = 32$) and
446 females (56.8%, $N = 37$) were equally likely to switch flock in a group (chi-square test: $\chi^2_1 = 0.26$, $P =$
447 0.613), but juveniles (76.9%, $N = 26$) tended to switch flocks with others more often than adults
448 (51.2%, $N = 43$; chi-square test: $\chi^2_1 = 3.50$, $P = 0.061$). Of the birds that switched flock in a group,
449 61.9% ($N = 42$) did so with at least one first-order relative and 71.4% ($N = 42$) switched flock with at
450 least one relative ($r \geq 0.125$). In these group switches, birds did not preferentially switch with relatives

451 from their flock of origin; indeed, for those birds that switched permanently, relatedness to birds they
452 switched flock with (mean $r = 0.146 \pm 0.136$ SD, $N = 42$) was significantly lower than their
453 relatedness to all members of their flock of origin (mean $r = 0.228 \pm 0.206$ SD, $N = 42$; Wilcoxon
454 Test $V = 85$, $N = 42$, $P < 0.001$). Switching groups typically included both sexes (18/30; 60%), the
455 remainder being all male (26.7%) or all female (13.3%) groups. When siblings dispersed together (N
456 = 14 sibling groups) there was no indication of sex-bias either; seven sibling groups were mixed sex
457 and seven were single sex (five male, two female).

458

459 *Playback Experiments*

460

461 In all trials, flocks responded immediately to the start of playback by approaching the speaker
462 (mean \pm SD closest approach = 8.31 ± 4.69 m, $N = 16$ trials, 8 flocks), but often lost interest and
463 resumed foraging while the playback was still being broadcast (mean \pm SD duration < 20 m from the
464 speaker = 194 ± 114 s, $N = 16$ trials). Flocks also responded aggressively, with more churr calls
465 (Wilcoxon signed-rank test: $V = 1$, $N = 16$ trials, $P < 0.001$) and fewer triple calls ($V = 105$, $N = 16$, P
466 = 0.011 ; Fig. 4) relative to the control period. Thus, there was a rapid, aggressive, but short-lived
467 response to the simulated presence of a non-flock member. However, there was no differential
468 response towards calls of relatives versus non-relatives; the flock's vocal response to playback, the
469 closest approach to the speaker and the time spent within 20m of the speaker did not differ
470 significantly between the two treatments (Table 3).

471

472 *Individual associations*

473

474 We observed a total of 606 birds in flocks across all years, but only those present throughout
475 a non-breeding season and observed on at least three occasions were included in analyses, giving a
476 sample of 164 birds in weighted networks (15 in 1996-1997, 34 in 1997-1998, 44 in 1998-1999, 53 in
477 2011-2012, and 18 in 2012-2013). Unsurprisingly, given their flocking behaviour, long-tailed tits

478 exhibit significant pairwise associations and avoidances. In all years, the CV and SD of observed
479 association indices were higher than those of at least 99.9% of random permutations, and the number
480 of non-zero edges in observed networks was significantly lower than in random networks (Table 4).
481 On average, individuals had 8.22 associates ($N = 164$ birds, range = 0 - 18) and the average
482 association strength between associated birds was 0.394 ($N = 673$ links, range = 0.059 - 1.000).

483

484 *Social Association and Relatedness*

485 Across all years, 69.5% ($N = 164$) of birds had a relative ($r \geq 0.125$) in the population.
486 Relatedness and social association were closely linked, with the pedigree relatedness matrix and half
487 weight association matrix being significantly correlated in all years (Fig. 5, Table 5). Overall, the
488 mean \pm SD association strength of relatives ($r \geq 0.125$) was 0.406 ± 0.289 , while for non-relatives ($r <$
489 0.125) it was 0.061 ± 0.160 . Mean \pm SD association strength between first-order relatives ($0.513 \pm$
490 0.243) was much higher than for second (0.118 ± 0.213) or third-order relatives (0.124 ± 0.143),
491 suggesting that the link between social networks and kinship is driven mainly by the association of
492 close kin. When analysing the sexes separately, the strength of links between males, between females
493 and between the sexes increased with kinship, with the exception of males in 1996-1997 and females
494 in 2011-2012 (Table 5). These patterns persisted when both matrices were controlled against a third
495 matrix of distances between last known nests in the previous breeding season, although correlations
496 among females tended to be either non-significant or weaker than those for males (Table 5).

497

498 *Social Association and Helping*

499 In the breeding seasons following our observations of non-breeding flocks, 26 birds from our
500 weighted networks helped at a nest where at least one member of the breeding pair was also in the
501 network; 84.6% ($N = 26$) of these helpers assisted a bird they had previously been associated with.
502 However, 75.3% ($N = 73$) of failed breeders that we had observed in networks did not help even
503 though they had an associate in the population with an active nest after their own nest had failed.
504 Furthermore, 31.5% of these non-helpers were related to that associate, indicating that the presence of
505 an associated relative with an active nest does not necessarily lead to helping. We also observed eight

506 failed breeders helping an unrelated pair, six (75%) of which were known to be associated with at
507 least one member of that pair in the previous non-breeding season. Finally, 22 helpers in our weighted
508 networks had a choice of previous associates to help. GLMM analysis showed that association
509 strength was a significant predictor of which associate they chose to help (Fig. 6), as was relatedness
510 to the brood and the distance from the helper's last breeding attempt; birds were most likely to help
511 associated relatives whose nests were closest to their own (Table 6).

512

513 **DISCUSSION**

514 The non-breeding flock dynamics of long-tailed tits were strongly influenced by kinship. This
515 was evident in initial grouping decisions, where all individuals associated with a successful nest
516 flocked together and failed breeders joined flocks containing relatives, when available. Likewise, the
517 few mergers observed were mostly of related flocks. On the other hand, flock-switches tended to
518 result in dispersal to flocks with fewer relatives, although it was common for birds to switch flocks in
519 groups with their relatives, especially for juveniles. When we investigated non-breeding social
520 interactions at the individual level using social network analysis, associations were again influenced
521 by kinship, especially for males. A playback experiment indicated that these flocking decisions were
522 not a function of nepotistic behaviour by members of the destination flock, because we observed no
523 difference in flock responses to the calls of kin and non-kin. Finally, social links in non-breeding
524 flocks were positively associated with helping decisions in the subsequent breeding season, in
525 addition to the previously reported effects of kinship and distance.

526 Our finding that all individuals associated with a successful nest (parents, offspring and
527 helpers) initially flocked together is unsurprising because adult long-tailed tits provision fledglings
528 until they are independent, about three weeks after fledging. More interesting is that failed breeders
529 chose to flock with relatives even if they were not associated with them in the preceding breeding
530 season and had travelled further from their last breeding attempt to do so, indicating that kin
531 association is not simply a function of extended parental care and philopatry. This kin association that
532 we observed outside the breeding season replicates the kin preference of failed breeders in helping

533 decisions (Russell & Hatchwell, 2001; Nam et al., 2010; Hatchwell et al., 2014). In both cases, kin
534 associations are not simply a function of birds having only relatives to interact with, but rather appears
535 to result from an active choice of relatives as associates in both breeding and non-breeding contexts.
536 This study also confirms previous results showing a substantial proportion of unrelated birds within
537 non-breeding flocks of long-tailed tits. Importantly, our finding that unrelated failed breeders could
538 join a flock even though they had not helped any flock members supports McGowan et al.'s (2007)
539 conclusion that helping is not payment for group membership in long-tailed tits.

540 Flock mergers mostly involved related flocks, reinforcing the kin structure that already exists
541 due to their initial family-based formation. Long-tailed tit flocks do not occupy stable, exclusive
542 territories during the non-breeding season and the ranges of related flocks are more likely to overlap
543 than those of unrelated flocks (Hatchwell, Anderson et al., 2001), perhaps predisposing them to
544 merge. Such mergers have been recorded in many species, usually in the context of fission-fusion
545 social dynamics (Aureli et al., 2008), but the degree of group cohesion and the frequency and
546 permanence of fission-fusion events is extremely variable across species, as is the role of kinship. In
547 some cases, relatedness is strongly associated with such events (e.g. Archie, Moss & Alberts, 2006;
548 Holekamp, Smith, Strelhoff, Van Horn & Watts, 2012), while in others the effect of relatedness is less
549 pronounced (e.g. Lee, Lee & Hatchwell, 2010; Wolf & Trillmich, 2008), or even absent (e.g. Arnberg,
550 Shizuka, Chaine & Lyon, 2015; Liker et al., 2009). In the only previous study of mergers of non-
551 breeding groups in cooperatively breeding birds, small breeding groups of apostlebirds *Struthidea*
552 *cinerea* merge to form larger non-breeding flocks, but the effect of relatedness on mergers is unknown
553 (Griesser et al., 2009).

554 Permanent flock switches were frequent and, in contrast to initial grouping decisions,
555 resulted in movement to flocks containing fewer relatives. Sharp, Baker et al. (2008) reported
556 that many birds in our population, especially females, disperse beyond the study site boundary,
557 but mean natal dispersal distance within the study site was <500m, so many dispersers would be
558 expected to move to adjacent flocks. The timing of switches that we observed also coincided
559 with disappearances from the study site (Fig. 3) so switches are presumably such short-distance
560 dispersal events. If inbreeding avoidance is a major driver of dispersal, juveniles are predicted to

561 be more dispersive than adults (Greenwood, 1980; Pusey, 1987). We could not directly compare
562 the frequencies of flock switches by adults and juveniles, because many juveniles disperse
563 beyond the boundaries of our study site while adults do not, and because the mortality rate of
564 juveniles is much higher than that of adults (Sharp, Baker, et al., 2008). However, the fact that
565 destination flocks for juveniles that switched contained fewer relatives than flocks of origin is
566 consistent with the idea that switches reduce the risk of inbreeding.

567 On the other hand, dispersal is usually assumed to dilute population kin structure, but we
568 found two ways in which kin structure is maintained by dispersing long-tailed tits. First, they
569 often dispersed with relatives; and second, even after dispersing and attempting to breed
570 independently, failed breeders joined non-breeding flocks containing relatives. Several other
571 cooperative breeders disperse in coalitions (e.g. Koenig et al., 2000; Ridley, 2012; Williams &
572 Rabenold, 2005) and our finding that it is common for long-tailed tits to switch flock with
573 relatives within our study site complements previous work by Sharp, Simeoni, et al. (2008) who
574 found that related immigrants often enter our study population together. In contrast to other
575 cooperative species where dispersing relatives are usually of the same sex, it is notable that long-
576 tailed tits frequently switched flocks with opposite-sex relatives. Therefore, although flock
577 switching by long-tailed tits may well be a strategy to reduce the risk of inbreeding, it does not
578 remove that risk entirely because dispersers often moved with opposite-sex kin and destination
579 flocks usually contained kin. Dickinson et al. (2016) have recently shown in western bluebirds,
580 another kin neighbourhood cooperative breeder, that males pairing within or nearby their winter
581 group risked breeding with kin but actively avoided related females as partners, implying
582 effective inbreeding avoidance through kin recognition. A similar mechanism for inbreeding
583 avoidance would be expected in long-tailed tits, although it has not yet been demonstrated.

584 We have assumed that individuals decide which flocks to join, but these decisions may also
585 depend on interactions between existing flock members and newcomers. This idea that aggressive
586 interactions between residents and dispersers play a major role in dispersal and settlement decisions is
587 supported in several cooperative breeders (e.g. Kleiber, Kyle, Rockwell & Dickinson, 2007; Mares,
588 Young, Levesque, Harrison & Clutton-Brock, 2011; Radford, 2003; Mueller & Manser, 2007), and in

589 Siberian jays, aggression by residents influences the probability of settlement by potential dispersers
590 (Griesser, Nystrand, Eggers & Ekman, 2008). In our playback experiment, despite rapid and
591 aggressive responses to the churr calls of non-group members, the flock's hostility to playback did not
592 depend on the kinship of a subset of flock members to the simulated newcomer. This result suggests
593 that aggression towards non-relatives does not cause kin-oriented flocking decisions in long-tailed tits,
594 although the small number of playback experiments we were able to perform limits our confidence in
595 concluding that such decisions are made entirely by the disperser. In western bluebirds, Kleiber et al.
596 (2007) found that aggression towards intruders was driven by sexual competition rather than by an
597 aggressor's relatedness to other group members. However, in our study, the large flock size and rapid
598 movements of birds in focal flocks precluded assessment of individual responses, so we could not test
599 whether responses were a function of individuals' relatedness to either other flock members or to the
600 bird whose call was being played.

601 The apparent absence of kin discrimination in response to playback by flocks during the non-
602 breeding season is consistent with Napper, Sharp, McGowan, Simeoni & Hatchwell (2013), who
603 found little evidence for a kinship effect on social interactions during roost formation in captive
604 wintering flocks of long-tailed tits. It also contrasts with the outcome of two previous playback
605 experiments conducted during the nestling period, each showing kin discrimination with the same
606 sample size (Hatchwell, Ross et al., 2001; Sharp et al., 2005). Why should responses be so different in
607 breeding and non-breeding contexts? Two explanations are likely. First, cooperative interactions
608 during breeding occur among a small number of related individuals (Nam et al., 2010), while in
609 flocks, groups are much larger and comprise both kin and non-kin. Second, the fluid nature of flock
610 composition, the presence of multiple families and low average relatedness, may reduce the
611 opportunity for any particular kin group to assert dominance over immigrants. This is in sharp
612 contrast to the situation in Siberian jays, where dispersers attempt to join small, stable family kin-
613 groups as subordinates (Griesser et al., 2008).

614 The dispersal decisions that we have described lead to kin-structured non-breeding
615 populations of long-tailed tits. Demographic traits also contribute to this kin structure, specifically the
616 skewed reproductive success of pairs that results in a small effective population size (Beckerman,

617 Sharp & Hatchwell, 2011). The availability of kin subsequently plays a critical role in the expression
618 of cooperative behaviour in long-tailed tits by generating the opportunity for kin selection to operate
619 (Hatchwell et al., 2014). However, the kin neighbourhoods within which cooperative breeding occurs
620 are very different to the nuclear family groups that are the key social unit of typical avian cooperative
621 breeders because most individuals with which a focal long-tailed tit associates outside breeding, and
622 most close neighbours during the breeding season are unrelated to them. Therefore, for kin-selected
623 helping to evolve it is important that failed breeders are able to recognise kin and discriminate in their
624 favour when making helping decisions. The final question that we addressed, therefore, was whether
625 interactions among individuals during the non-breeding season influence behaviour during breeding.

626 Each sex was more closely associated with birds of the same or opposite sex if they were
627 related; this was particularly true of males, even after controlling for the effect of philopatry. This
628 makes sense because dispersal in long-tailed tits is female-biased (Sharp, Baker, et al., 2008) so social
629 bonds among related females are weaker than among males. Indeed, the finding that females are more
630 closely associated with kin than non-kin is perhaps surprising because females are less likely to help
631 than males, and Sharp, Simeoni, McGowan, Nam & Hatchwell (2011) suggested that this was because
632 they are not closely associated with relatives during the non-breeding season. This is clearly not the
633 case and our results support Sharp et al.'s (2011) alternative suggestion that females are simply less
634 likely to help than males, perhaps because they are in poorer condition than males after breeding.

635 The strength of prior association was a significant factor in helper decision-making; most
636 helpers fed at the nests of associates, and association strength was a significant predictor of who was
637 helped even after controlling for the effects of relatedness and spatial factors. Thus, long-tailed tits
638 behave in a similar way to more typical cooperative breeders in which helping usually occurs between
639 familiar relatives on the same territory, but they must be more discriminating than most other species
640 to achieve this (Cornwallis et al., 2009). However, a third of non-helpers had associated relatives in
641 the population but did not assist them when the opportunity arose, so the presence of an associated
642 relative nearby does not guarantee helping. Meade and Hatchwell (2010) attributed this failure to help
643 when the opportunity arose to poor condition of these 'non-helpers'. We also found that the few
644 helpers caring for non-kin usually helped prior associates. Long-tailed tits gain no direct benefits from

645 helping (Meade & Hatchwell, 2010), and it is possible that help for non-kin results from recognition
646 errors. Kin recognition in this species is based on calls learned during development (Sharp et al.,
647 2005). If learning extends into the non-breeding season, association with non-kin could lead to
648 categorisation of non-kin as kin. Our finding that instances of apparently misdirected care occurred
649 among birds that were associated during the non-breeding season is consistent with this idea.

650 In conclusion, long-tailed tits tend to flock with their relatives, even after dispersal,
651 suggesting either that there are benefits of flocking with kin, or costs of flocking with non-kin.
652 Differential interactions between kin and non-kin could occur in several contexts, including anti-
653 predator behaviours (e.g. Griesser & Ekman, 2004; Maklakov, 2002), food-sharing (e.g. Dickinson et
654 al., 2009), and access to communal roosts (e.g. McGowan, Sharp, Simeoni & Hatchwell, 2006),
655 although Napper et al. (2013) found little effect of kinship on dominance status that might influence
656 these social interactions. We think it is more likely that the inclusive fitness benefits of kin-directed
657 helping behaviour in long-tailed tits (Hatchwell et al., 2014) selects for prolonged association with kin
658 outside the breeding season to maximise individuals' ability to recognise and discriminate in favour of
659 relatives during breeding. Our finding that non-breeding social interactions influence cooperative
660 breeding behaviour indicates that prior association is an important factor in helpers' investment
661 decisions. Further studies are needed to determine whether this is common among species where
662 helping occurs within kin neighbourhoods, or indeed in any other cooperative species where helpers
663 have a choice of broods that they may care for.

664

665 **Acknowledgments**

666 We are grateful to all those who have contributed to the long-term data that has contributed to this
667 study, especially Douglas Ross and Martin Fowlie who collected data on winter flocks in 1996-1999,
668 and Ben Ellison-Smith, Angela Chira and Thomas Mondain-Monval who assisted with the playback
669 experiment. Thanks also to landowners in the Rivelin Valley who gave us access to their land. Andy
670 Radford and Terry Burke provided helpful feedback on the study. This work was funded by a Natural
671 Environment Research Council PhD studentship (CJN) and grant NE/1027118/1 (BJH).

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854 **Table 1** Results of GLMM analyses investigating the effects of kinship (proportion of the flock that
855 were relatives at $r = 0.5$, $r \geq 0.25$ and $r \geq 0.125$) and distance (measured from a failed breeder's last
856 breeding attempt to the centre of a flock's range) on failed breeders' flocking decisions

	Model parameter	Relative importance	Estimate	Unconditional SE	Lower CI	Upper CI
$r = 0.5$	(Intercept)		-1.932	0.236	-2.394	-1.470
	Proportion of relatives	1.00	2.508	0.596	1.339	3.677
	Distance	1.00	-3.061	0.478	-3.999	-2.123
	Proportion of relatives*Distance	1.00	2.525	0.895	0.771	4.279
$r \geq 0.25$	(Intercept)		-1.912	0.219	-2.342	-1.482
	Proportion of relatives	1.00	0.809	0.485	-0.144	1.761
	Distance	0.71	-3.089	0.452	-3.978	-2.200
	Proportion of relatives*Distance	0.49	1.304	0.625	0.073	2.534
$r \geq 0.125$	(Intercept)		-1.986	0.235	-2.446	-1.527
	Proportion of relatives	1.00	1.267	0.360	0.562	1.973
	Distance	1.00	-3.295	0.484	-4.244	-2.346
	Proportion of relatives*Distance	1.00	1.884	0.601	0.705	3.062

857

858 Standardised parameter estimates, unconditional standard errors and relative importance of
859 explanatory variables were obtained by averaging across three models within two AICc of the top
860 model when relatedness was defined as $r \geq 0.25$. There were no models within two AICc of the top
861 model when relatedness was $r = 0.5$ and $r \geq 0.125$ so estimates were calculated from the top model
862 alone.

863 **Table 2** The relatedness of long-tailed tits to other members of the flock of origin and the destination
 864 flock from birds that switched permanently between flocks

865

Dataset	Relatedness	Status in previous season	Proportion of flock of origin that were relatives (mean \pm SD)	Proportion of destination flock that were relatives (mean \pm SD)	<i>N</i>	<i>V</i>	<i>P</i>
All	0.5	All	0.083 \pm 0.174	0.052 \pm 0.185	69	273.5	0.043
Males		All	0.138 \pm 0.227	0.076 \pm 0.245	32	131.0	0.049
All	≥ 0.25	Chick	0.216 \pm 0.286	0.100 \pm 0.267	26	169.5	0.065

866

867 *P*-values were determined using Wilcoxon signed-rank tests and *V* is the sum of ranks assigned to
 868 differences with a positive sign. Analyses were conducted at three levels of relatedness ($r = 0.5$, $r \geq$
 869 0.25 , $r \geq 0.125$), for all birds combined and separately for each sex, age class and for adults of each
 870 breeding status at the end of the last breeding season. Only results where $P < 0.10$ are presented.

871 **Table 3** The effect of kinship on a flock's vocal response to playback, closest approach to the speaker
 872 or time spent within 20m of the speaker

Response	Kin (mean \pm SD)	Non-kin (mean \pm SD)	<i>V</i>	<i>P</i>
Net churr rate	1.16 \pm 1.71	1.23 \pm 1.45	15	0.74
Net triple rate	-0.62 \pm 1.17	-0.74 \pm 0.55	20	0.84
Closest approach (m)	8.25 \pm 4.89	8.38 \pm 4.81	18	1.00
Time within 20 m (s)	198 \pm 116	190 \pm 121	11	1.00

873

874 *P*-values were determined using Wilcoxon signed-rank tests and *V* is the sum of ranks assigned to
 875 differences with a positive sign.

876 **Table 4** Results of permutation tests for preferred and avoided associations

Year	Real			Random			<i>P</i>		
	SD	CV	Non-zero edges	SD	CV	Non-zero edges	SD	CV	Non-zero edges
1996-1997	0.247	1.937	0.248	0.149	1.104	0.523	0.999	0.999	0.001
1997-1998	0.235	1.818	0.310	0.120	0.891	0.676	1.000	1.000	0.001
1998-1999	0.216	2.167	0.220	0.102	1.080	0.553	0.999	1.000	0.000
2011-2012	0.135	2.574	0.171	0.094	1.742	0.280	0.999	0.999	0.001
2012-2013	0.213	2.318	0.196	0.113	1.264	0.444	1.000	0.999	0.000

877

878 *P*-values are based on the proportion of permuted CV or SD values that are lower than the observed
879 values. If the real value fell within the top or bottom 2.5% of the random distribution ($P > 0.975$ or P
880 < 0.025 , two-tailed test), we rejected the null hypothesis that the real value could have arisen by
881 chance.

882 **Table 5** Results of Mantel tests on the correlation between pedigree relatedness and half weight
 883 association matrices both alone and when controlled for nest location in the previous breeding season

Year	Number of individuals	Alone		Controlled for nest location	
		Matrix correlation	<i>P</i>	Matrix correlation	<i>P</i>
1996-1997	15	0.353	0.003	0.267	0.018
males	9	0.198	0.154	0.145	0.233
females	6	-	-	-	-
males-females		0.490	0.003	0.360	0.013
1997-1998	34	0.407	<0.001	0.305	<0.001
males	18	0.415	<0.001	0.316	0.001
females	16	0.435	<0.001	0.314	0.002
males-females		0.396	<0.001	0.298	0.001
1998-1999	44	0.578	<0.001	0.474	<0.001
males	31	0.711	<0.001	0.648	<0.001
females	13	0.493	0.006	0.269	0.033
males-females		0.452	<0.001	0.304	0.002
2011-2012	53	0.494	<0.001	0.427	<0.001
males	32	0.661	<0.001	0.612	<0.001
females	21	0.079	0.121	0.030	0.285
males-females		0.464	<0.001	0.408	<0.001
2012-2013	18	0.691	<0.001	0.609	<0.001
males	11	0.670	0.001	0.634	<0.001
females	7	0.610	0.046	0.381	0.144
males-females		0.732	<0.001	0.640	<0.001

884

885

886 **Table 6** Results of GLMM analyses investigating the effects of association strength, kinship and
887 distance from the helper's last breeding attempt on helping decisions

888

Model Parameter	Estimate	Standard Error	Lower Confidence Interval	Upper Confidence Interval
Intercept	-3.710	0.574	-4.835	-2.585
Association strength	1.557	0.533	0.512	2.602
Kinship	-1.819	0.823	-3.432	-0.206
Distance	1.746	0.449	0.866	2.626

889

890 There were no models within two AICc of the top model so standardised parameter estimates and
891 standard errors were calculated from the top model alone.

892

893

894 **Table A1** Number of opposite sex relatives in flocks of origin and destination flocks for birds that
895 switched permanently between flocks
896

Dataset	No. of opposite sex relatives in flock of origin (mean \pm SD)	No. of opposite sex relatives in destination flock (mean \pm SD)	<i>V</i>	<i>P</i>
<i>r</i> = 0.5				
All	0.449 \pm 1.165	0.261 \pm 1.093	121.5	0.115
Males	0.656 \pm 1.153	0.188 \pm 0.738	74.5	0.041
Females	0.270 \pm 0.962	0.324 \pm 1.334	7.0	1.000
Adults	0.209 \pm 0.833	0.279 \pm 1.241	13.5	1.000
Chicks	0.846 \pm 1.287	0.231 \pm 0.815	56.0	0.041
Male chicks	1.125 \pm 1.408	0.313 \pm 1.014	46.0	0.060
Female chicks	0.400 \pm 0.966	0.100 \pm 0.316	1.0	1.000
<i>r</i> \geq 0.25				
All	0.609 \pm 1.140	0.522 \pm 1.313	259.5	0.574
Males	0.688 \pm 1.230	0.656 \pm 1.285	95.8	0.900
Females	0.541 \pm 1.538	0.405 \pm 1.343	41.5	0.469
Adults	0.419 \pm 1.348	0.605 \pm 1.530	41.5	0.501
Chicks	0.923 \pm 1.383	0.385 \pm 0.852	97.5	0.119
Male chicks	1.188 \pm 1.515	0.563 \pm 1.031	70.5	0.251
Female chicks	0.500 \pm 1.080	0.100 \pm 0.316	3.0	0.371
<i>r</i> \geq 0.125				
All	0.768 \pm 1.673	0.956 \pm 1.859	292.0	0.519
Males	0.688 \pm 1.230	1.031 \pm 1.823	79.0	0.525
Females	0.838 \pm 1.993	0.946 \pm 1.914	71.5	0.830
Adults	0.581 \pm 1.776	0.721 \pm 1.623	45.5	0.418
Chicks	1.077 \pm 1.468	1.423 \pm 2.157	101.5	0.635
Male chicks	1.188 \pm 1.515	1.313 \pm 2.089	52.5	1.000
Female chicks	0.900 \pm 1.449	1.600 \pm 2.366	10.0	0.550

897
898 Analysis using Wilcoxon signed rank tests.

899

900 **Table A2** The sex ratio (proportion male among ringed birds) of flocks of origin and destination
 901 flocks for birds that switched permanently between flocks

902

Dataset	Sex ratio in flock of origin (mean \pm SD)	Sex ratio in destination flock (mean \pm SD)	<i>V</i>	<i>P</i>
All	0.594 \pm 0.178	0.522 \pm 0.130	904.5	0.261
Males	0.577 \pm 0.201	0.541 \pm 0.119	167.0	0.637
Females	0.590 \pm 0.157	0.508 \pm 0.139	303.5	0.281
Adults	0.573 \pm 0.185	0.504 \pm 0.126	375.5	0.185
Chicks	0.602 \pm 0.169	0.554 \pm 0.135	115.0	1.000
Male chicks	0.653 \pm 0.148	0.573 \pm 0.148	43.0	0.397
Female chicks	0.520 \pm 0.175	0.532 \pm 0.120	19.0	0.410

903

904 Analysis using Wilcoxon signed rank tests. Note that actual sex ratio is close to parity, and the
 905 apparent male bias is because unringed birds are more likely to be female.

906

907 Figure Legends

908 **Figure 1.** The non-breeding ranges of four flocks in 1996-1997 (a), five flocks in 1997-1998 (b), ten
909 flocks in 1998-1999 (c), thirteen flocks in 2011-2012 (d), and ten flocks in 2012-2013 (e). Colours are
910 not used consistently between years. Ranges are presented as minimum convex polygons.

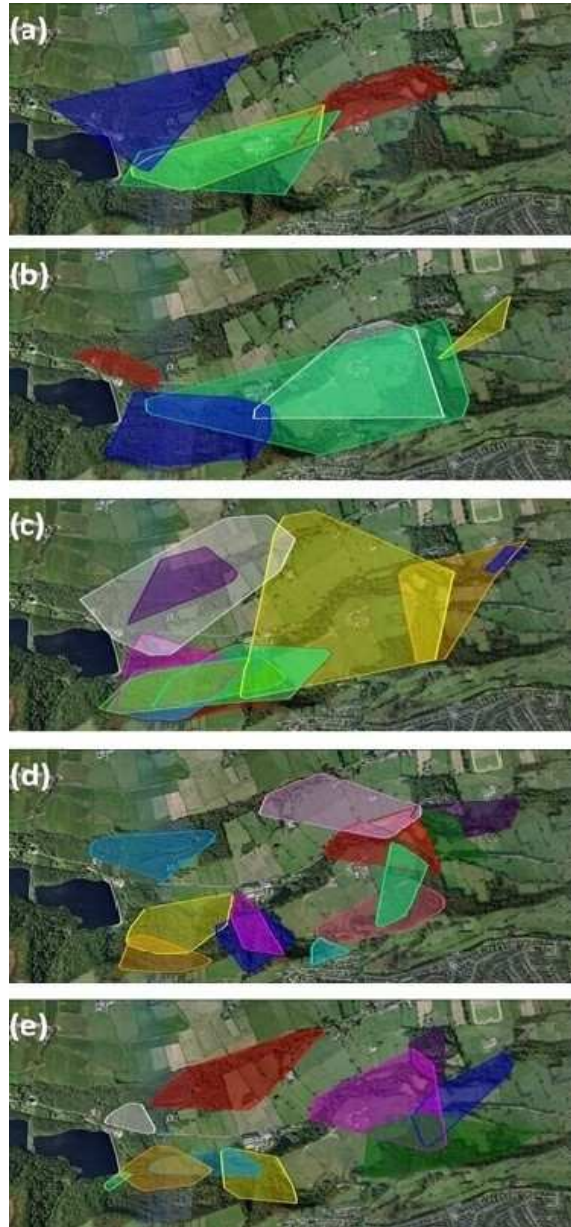
911 **Figure 2.** The distance from failed breeders' last breeding attempts (a), and first-order relatedness (b)
912 of failed breeders to the flocks that they chose to join and those that they did not join. Boxes represent
913 the upper and lower quartiles, bold lines represent the median and whiskers extend to the most
914 extreme data point that is within 1.5 interquartile ranges of the box. Circles represent any data points
915 that fell outside 1.5 interquartile ranges of the box.

916 **Figure 3.** Time in the non-breeding season of flock switches within the study site (a), and
917 disappearances of ringed individuals from the study site due to death or dispersal (b).

918 **Figure 4.** The number of churr calls (a) and triple calls (b) produced by each flock member in the five
919 minutes before (control) and during playback (playback). Boxes represent the upper and lower
920 quartiles, bold lines represent the median and whiskers extend to the most extreme data point that is
921 within 1.5 interquartile ranges of the box. Circles represent any data points that fell outside 1.5
922 interquartile ranges of the box.

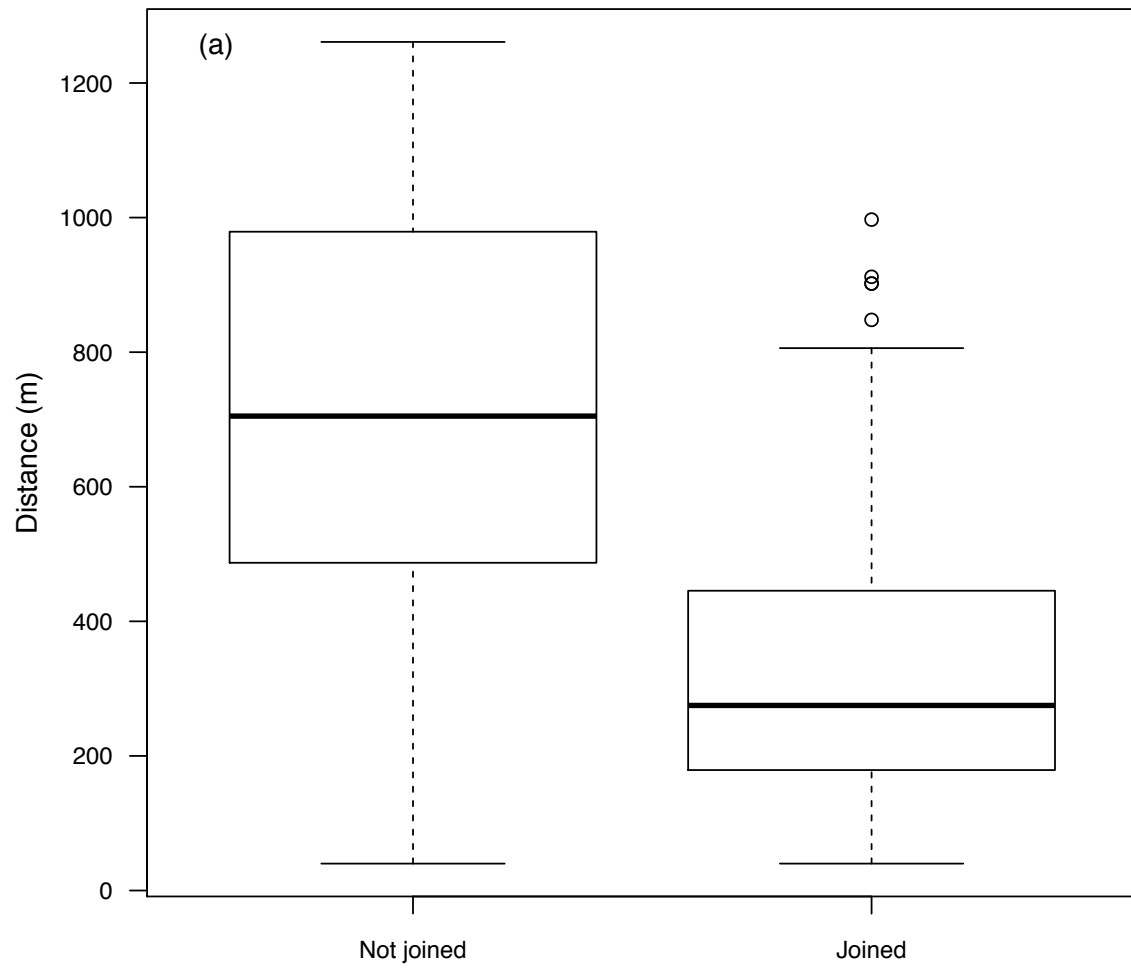
923 **Figure 5.** Weighted network of individual long-tailed tits in 1997-1998, illustrating typical pattern of
924 associations. Dots represent individuals, black lines represent ties between non-relatives, green lines
925 represent ties between associated relatives and red lines represent individuals that are linked by
926 kinship but were not associated in the network. Line thickness represents the strength of association
927 between two individuals. See Table 5 for statistical analysis of all years.

928 **Figure 6.** The association strength between helpers and the most closely associated member of the
929 breeding pair at nests they chose to help and those they did not in all years. Boxes represent the upper
930 and lower quartiles, bold lines represent the median and whiskers extend to the most extreme data
931 point that is within 1.5 interquartile ranges of the box. Circles represent any data points that fell
932 outside 1.5 interquartile ranges of the box.



933

934 Figure 1



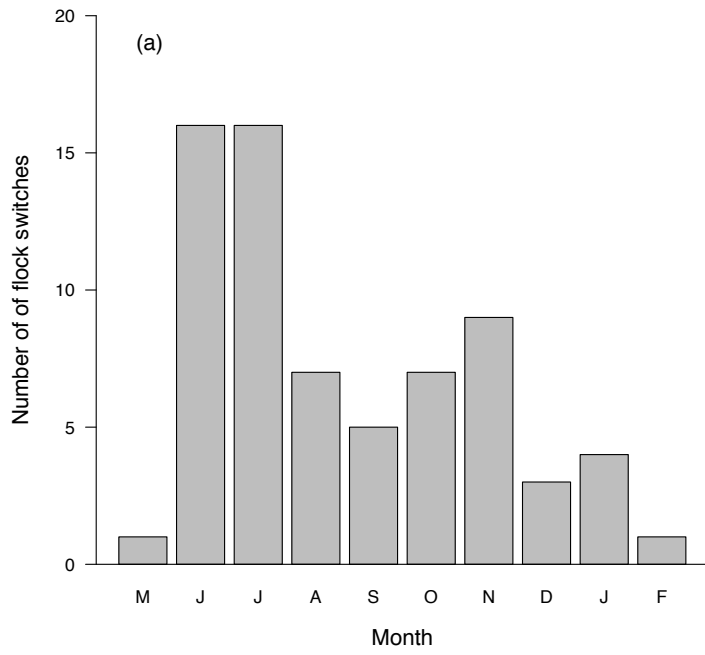
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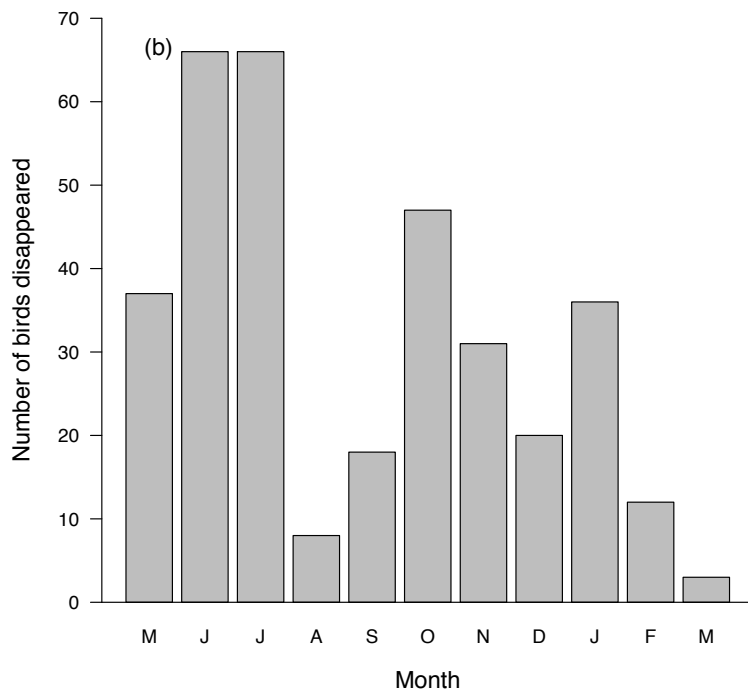
937 Figure 2

938

939



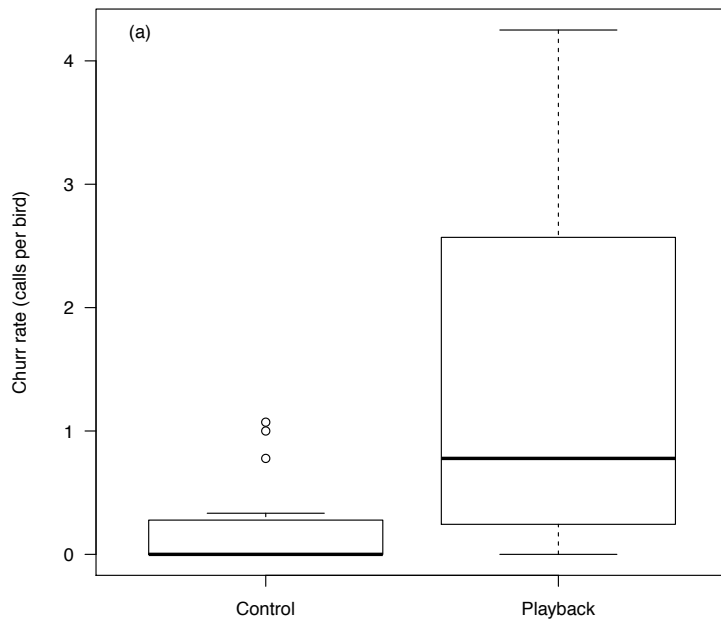
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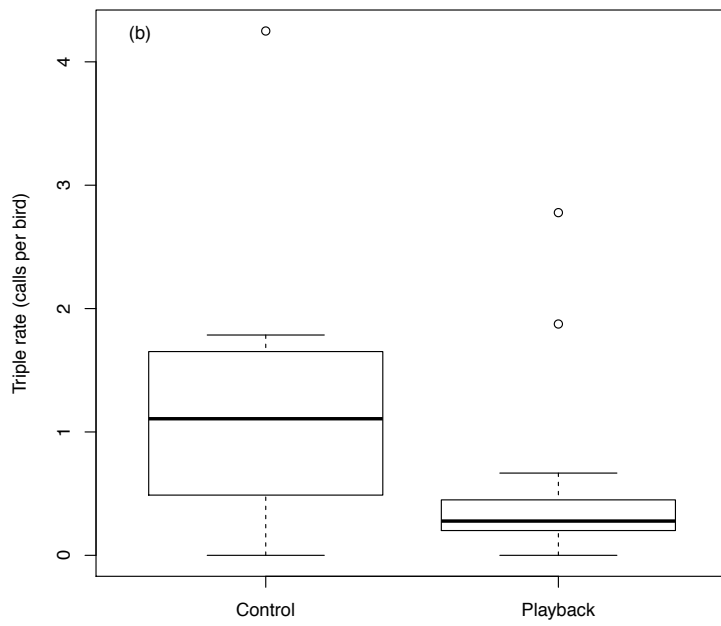
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942 Figure 3

943



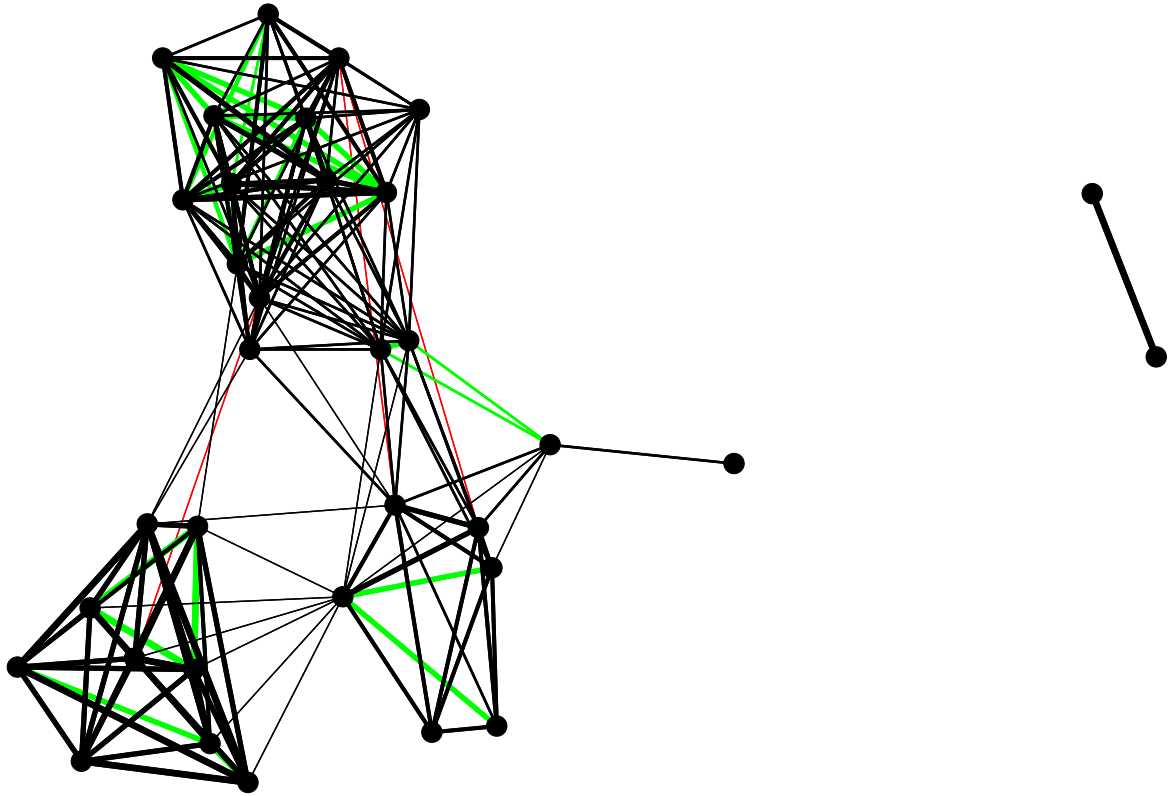
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945

946 Figure 4

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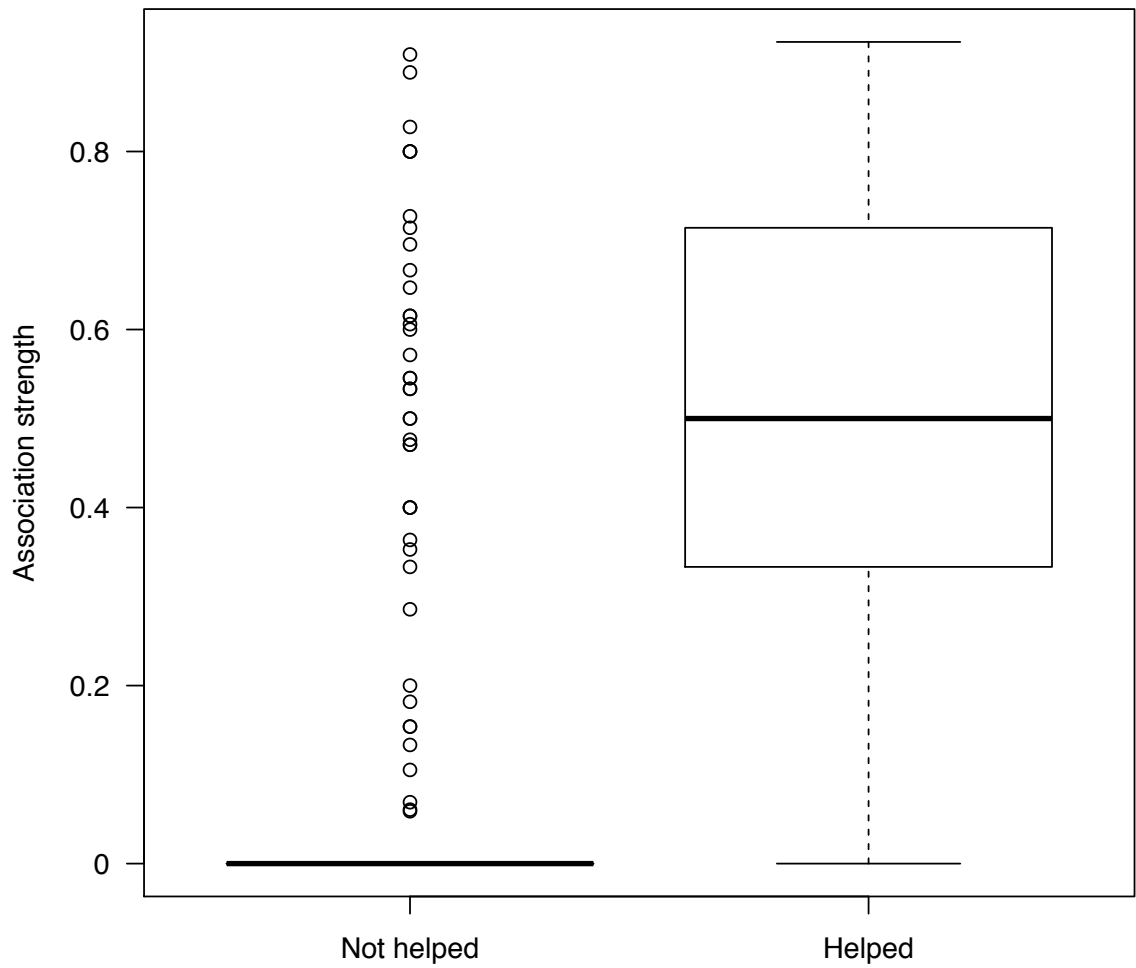


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950 Figure 5

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954 Figure 6