

1 **Wild birds respond to flockmate loss by increasing their social network**
2 **associations to others**

3

4 Josh A. Firth^{1*}, Bernhard Voelkl^{1,2}, Ross A. Crates^{1,3}, Lucy M. Aplin¹, Dora Biro⁴,
5 Darren P. Croft⁵, Ben C. Sheldon¹

6 ¹*Edward Grey Institute, Department of Zoology, University of Oxford, Oxford, OX1*
7 *3PS, UK*

8 ²*Animal Welfare Division, Vetsuisse Faculty, University Bern, Laenggassstrasse 120,*
9 *3012 Bern, CH*

10 ³*Fenner school, Australian National University, Canberra, Australia 2601.*

11 ⁴*Department of Zoology, University of Oxford, Oxford, OX1 3PS, UK*

12 ⁵*Centre for Research in Animal Behaviour, College of Life and Environmental Sciences,*
13 *University of Exeter, Exeter EX4 4QG, UK*

14 *Correspondence: Joshua.firth@zoo.ox.ac.uk

15

16 **ABSTRACT**

17

18 Understanding the consequences of losing individuals from wild populations is a
19 current and pressing issue, yet how such loss influences the social behaviour of the
20 remaining animals is largely unexplored. Through combining the automated tracking of
21 winter flocks of over 500 wild great tits (*Parus major*) with removal experiments, we
22 assessed how individuals' social network positions responded to the loss of their social
23 associates. We found that the extent of flockmate loss that individuals experienced
24 correlated positively with subsequent increases in the number of their social
25 associations, the average strength of their bonds, and their overall connectedness within
26 the social network (defined as summed edge weights). Increased social connectivity was
27 not driven by general disturbance or changes in foraging behavior, but by modifications
28 to fine-scale social network connections in response to losing their associates.

29 Therefore, the reduction in social connectedness expected by individual loss may be
30 mitigated by increases in social associations between remaining individuals. Given that
31 these findings demonstrate rapid adjustment of social network associations in response
32 to the loss of previous social ties, future research should examine the generality of the

33 compensatory adjustment of social relations in ways that maintain the structure of social
34 organization.

35 **INTRODUCTION**

36

37 The loss of individuals from wild populations can have many consequences for the
38 remaining animals. For example, the remaining individuals may benefit from increased
39 survival or reproduction due to reduced competition [1-3]. Alternatively, individual
40 fitness could be reduced if such loss increased predation risk or decreased the potential
41 for beneficial interactions, such as mating opportunities or cooperation with others [4-
42 6]. The immediate consequences of losing members of a population are likely to depend
43 on how the remaining individuals interact with one another, i.e. the resulting social
44 structure. However, the consequences of the loss of individuals for social structure
45 remain largely unknown.

46

47 Recent developments in animal tracking technologies and analytical methods now allow
48 the fine-scale assessment of individuals' social associations to one another [7, 8]. In this
49 way, social structure can be quantified as a social network [9-12], and this approach has
50 now been applied to a wide variety of wild animal societies [13]. Such networks are
51 known to relate to various biological processes, such as transmission of disease and
52 information [14-18], various measures of fitness [19-21] and how selection operates
53 [22, 23]. The individuals that are central in a network (i.e. with high social
54 connectedness) differ from peripheral individuals both in terms of their extent of
55 influence on the social system, as well as their social experience and the pressures
56 exerted upon them [11].

57

58 Previous studies of vertebrate populations have demonstrated that individuals are
59 repeatable and consistent across time in the social positions they hold within the
60 network [20, 24, 25]. Whilst an individual's network position may rely upon its own
61 attributes and behaviour, it also intrinsically depends upon which other individuals it
62 interacts with [26]. How changes in the composition of social groups influence
63 individuals' social associations is therefore a fundamental question of group living. Yet,
64 an empirical assessment of the direct consequences of one of the most significant of
65 such changes – the loss of individuals – is currently lacking.

66

67 Research into general network theory has typically assessed the effects of the loss of
68 certain ‘nodes’ (individuals) by simulating node removal, and assessing the resulting
69 network structure [27, 28]. Applying these simulation approaches to wild mammalian
70 populations has shown that the removal of socially-central individuals can fragment
71 social networks or increase the social distance between individuals [29-32]. Whilst such
72 approaches are potentially very informative, their validity is currently limited due to the
73 lack of knowledge regarding how the loss of individuals may affect the behavior of the
74 remaining members within natural populations [33-35].

75

76 Previous experiments have been mainly limited to captive, rather than wild, animal
77 groups. These experiments have indicated actual individual loss may indeed have
78 different consequences than those expected from simulations. For instance, within
79 captive pigtailed macaques (*Macaca nemestrina*), the removal of high-ranking group
80 members caused more extensive social dissolution than that predicted by simulations, as
81 these individuals promote social cohesion [36]. In contrast, in captive Indian queenless
82 ants (*Diacamma indicum*), the removal of central individuals had less impact than
83 simulations predicted [37], as remaining individuals up-regulated their activity [37].
84 Similarly, analyses tracing the changes in path length and connectivity in experimental
85 colonies of social wasps (*Ropalidia marginata*) following removal of individuals
86 demonstrated that the redundancy within the original network provided substantial
87 resilience to losses [38].

88

89 In this study, we experimentally test the social consequences of the loss of individuals
90 from a wild population of great tits (*Parus major*). Through tracking the flocking
91 patterns of over 500 individuals using the large-scale deployment of Radio-Frequency
92 Identification (RFID) technology, we monitored individuals’ positions within the social
93 network whilst temporarily removing birds from the population. In this way, we directly
94 assess how birds that lost their flockmates subsequently altered their social associations,
95 and examine the extent to which the social consequences of the removals depended on
96 the individual’s prior social connection to the removed birds. Finally, we show that
97 removed birds largely regained their previous social associations upon return to the
98 wild. We discuss the significance of these findings for understanding how natural

99 populations respond to the loss of individuals, the mechanisms driving these responses,
100 and their potential applied implications.

101

102 **METHODS**

103

104 *Study System*

105 This study was conducted on a long-term study population of great tits in Wytham
106 Woods, Oxford, UK (51°46'N, 1°20'W), where breeding adults and their chicks have
107 been marked with unique BTO (British Trust for Ornithology) metal leg rings since the
108 1960s [39]. Since 2007, all captured great tits have also been fitted with plastic leg
109 bands containing RFID microchips. From September to February (non-breeding
110 season), great tits aggregate in winter foraging flocks [40] and extensive mist netting is
111 carried out to also mark immigrant birds with RFID tags. These tags allowed the
112 detection of the time, date and location of each individual's presence at sunflower seed
113 feeding stations equipped with RFID antennae attached to two opposing access holes
114 (Dorset ID, Aalten, Netherlands). These were placed in a stratified grid at 65 fixed
115 locations, ~250m apart throughout Wytham Woods, and opened automatically every
116 weekend over the winter, scanning for RFID tags from pre-dawn until after dusk.

117

118 *Inferring Social Networks*

119 Detections of RFID tags at the feeding stations provide a fine-scale temporal datastream
120 made up of bursts of activity as flocks arrive and feed [41, 42]. These 'flocks' (or
121 'flocking events') can be identified using a machine learning algorithm which employs
122 a Gaussian mixture model (GMM) to assign each individual detection to the event it
123 most likely occurred in [41]. This provides an objective way of identifying flocks, and
124 is preferable to applying techniques requiring the specification of arbitrary parameters,
125 such as set time windows, to define co-occurrences [42].

126

127 By calculating the flock co-memberships amongst all individuals, we created a 'group-
128 by-individual' matrix [9], specifying co-occurrences between all birds. We used R 3.2.2
129 [43] for all analyses, and applied the Simple Ratio Index (SRI) [44] to calculate
130 weighted social associations among individuals to create social networks. In this way,
131 the network 'nodes' represent the individual birds, whilst the 'edges' linking them
132 represent the dyadic social associations. Social networks within this system are known

133 to be non-random after accounting for spatial structure, carry over across contexts, and
134 be important to various social processes [16-18, 25, 45-49]. We created social networks
135 for each weekend separately. Further, previous work has indicated that pooling data
136 over longer time periods can provide a more accurate depiction of individuals' social
137 phenotypes than single sample periods [25]. Therefore, for each weekend, we also
138 calculated cumulative networks by considering all flocking events recorded from the
139 beginning of the season and up to the end of the focal weekend, creating a social
140 network from all possible data available at that time.

141

142 ***Experimental Procedure***

143 The experiment began in September 2013, four weeks into standard winter data
144 collection. Four replicates were carried out, with one week between each replicate. All
145 experiments followed the same standard protocol. In each replicate (i.e. each week), two
146 neighbouring feeding stations (hereafter referred to as an 'area') were chosen for the
147 removals (Figure 1). To ensure that removals were feasible, we used previous logging
148 data to choose an area with relatively high numbers of birds. Removals were carried out
149 using standard mid-week winter mist-netting, which was carried out at the chosen
150 feeding stations. In each replicate, we aimed to capture and remove 6 RFID-tagged
151 great tits. On one occasion, twelve birds were caught so 6 were randomly selected,
152 whilst in another replicate only 5 were caught and removed. Removed birds were then
153 held in captivity over the weekend logging period, and released the following Monday.
154 The experimental period spanned four weeks and took place over four areas (two
155 neighbouring feeding sites in each) and consisted of temporarily removing 23 RFID-
156 tagged great tits in total.

157

158 During the experimental period, we also carried out controls (Figure 1). This consisted
159 of carrying out standard mid-week catching sessions of similar intensity (~3.5hrs) at
160 areas (each also consisting of paired feeding stations) that had similar number of birds
161 to the concurrent removal sites but minimal exchange of individuals between them.
162 During the control catching sessions, all birds were released within 30 minutes after
163 capture. Over the experiment, we alternated whether catching took place first at the
164 removal or the standard capture areas. Entirely standardized effort and matching under
165 the field conditions was impossible due to variation in weather conditions and
166 environmental surroundings changing the number and ease of catching individuals.

167 However, from the onset of data collection to the end of the experiment (but excluding
168 the experimental weekends at each site), a similar number of birds were recorded each
169 weekend in the removal (mean \pm standard error: 24.00 \pm 2.2), and control (21.0 \pm 1.3)
170 areas, with no significant difference based on treatment assignment (linear model
171 controlling for time and replicate: $t = 1.01$, $p = 0.32$). Further, the turnover of birds (i.e.
172 number of birds remaining in an area divided by the total number of birds recorded over
173 both weekends) was also not significantly related to treatment assignment (removal =
174 0.54 \pm 0.03, control = 0.52 \pm 0.04, linear model: $t = 0.02$, $p = 0.98$). Carrying out the
175 standard capture sessions (without removal) in matched areas ensured we were
176 subsequently able to compare the effects of experimentally-imposed loss of individuals
177 to any underlying effects produced simply by the mist-netting procedure.

178

179 *Ethical Note*

180 All work (mist netting, ringing, and captivity), was carried out under BTO (A5435,
181 C6030) and Natural England licences (20131205 & 20123075), and adhered to U.K.
182 standard requirements. Removed birds were transported to John Krebs Field Station
183 (Oxford University) within 1.5h of capture, and monitored throughout the first day.
184 They were housed indoors at ambient temperature under a natural light regime in separate,
185 but neighbouring, wire-mesh cages (45x45x68cm) equipped with roost boxes, and were
186 provided with food and water daily. Before release at their initial capture site, all
187 individuals' body mass changes (-2.1g to 0g) were within the natural fluctuation range
188 [50].

189

190 *Assessing the experimental effects*

191 For each trial, the focal individuals were defined as those recorded in the weekend
192 directly before and after the trial. We refer to birds recorded in the same flock before the
193 trial as 'flockmates'. Across the woodland, focal individuals whose flockmates were not
194 captured or removed were categorised as 'non-affected'. The flockmates of birds who
195 were removed were categorised as having their 'flockmate removed', whilst the
196 flockmates of birds captured at the control sites were categorised as having their
197 'flockmate captured'. No birds fell into multiple categories during a trial. Birds who
198 were actually captured/removed during the trial were not considered as focal
199 individuals. Further, when assessing changes in social associations in response to the

200 experiment (see below) captured/removed birds' associations to others were excluded to
201 allow us to compare the control and removal treatment in a relevant way.

202

203 The effects of the removals may be related to individuals' number and strength of social
204 associations towards the removed birds. For example, birds experiencing the removal of
205 a single, weakly associated, flockmate should be affected less than those who lost six
206 flock members with which they held strong social associations. Therefore, we
207 calculated the proportion of each focal individual's total social associations (i.e. total
208 'strength' – the sum of their edge weights) in the week before the trial that was directed
209 towards subsequently removed individuals (or directed towards captured and released
210 individuals in the controls). We refer to this measure as the extent of the 'social impact'
211 experienced. We then examined how this social impact predicted changes in
212 individuals' associations.

213

214 *Assessing changes in behaviour and social associations*

215 As changes to individuals' general foraging behaviour could potentially indirectly
216 influence their social associations, we first considered three basic measures of foraging
217 behaviour. These were individuals' average (i) raw activity (i.e. second-by-second
218 detections) at the feeders, (ii) number of flocking events (i.e. output of the GMM), and
219 (iii) number of feeding sites visited. We then assessed four social metrics that are
220 known to be repeatable within individual great tits over weeks and years, even when
221 accounting for space use [25]. We calculated each individuals' (i) average flock size,
222 (ii) number of unique flockmates (i.e. '*unweighted degree*'), which represents their
223 general gregariousness, (iii) the sum of all their social associations (i.e. '*strength*'),
224 which measures their general network centrality, and (iv) '*betweenness*' i.e. the number
225 of shortest paths between other individuals in the network that pass through the
226 individual, which represents how an individual might act as a bridge for transmission of
227 information and disease [10]. Betweenness was log transformed to reduce skew [25].
228 Finally, we assessed (v) the average score of their dyadic social associations to each of
229 their flockmates (i.e. '*average edge weight*'), which indicates the tightness of their
230 social bonds [51].

231

232 We assessed how each focal individual's social metrics changed following the trial (i.e.
233 immediately 'post-trial') in relation to their pre-trial metrics. Pre-trial networks were

234 calculated from all of the weekend network data recorded before the trial took place
235 (but see *Supplementary Information* for alternative analysis). However, as unweighted
236 degree is intuitively expected to be larger in cumulative networks than any stand-alone
237 sampling period, we calculated pre-trial unweighted degree as birds' average degree
238 score over the previous weekends. As network parameters are likely to change even
239 over short periods due to the dynamic and variable nature of the fission-fusion system
240 [45], we expressed each individual's change as relative to the average change over all
241 individuals over this time-frame.

242

243 *Assessing the relationship between social loss and change in metrics*

244 We primarily aimed to assess whether the social impact of the removals caused changes
245 in individuals' social associations over and above that expected. Thus, for all
246 individuals that had a flockmate removed/captured in a trial, we assessed how
247 subsequent changes in behaviour were predicted by (i) treatment category i.e. whether
248 their flockmates were subjected to just standard capture (control) or removal (ii) the
249 proportion of their social associations to these removed/captured flockmates (i.e. 'social
250 impact', and, importantly, (iii) the interaction of these two predictors. The interaction
251 term allows the separation of whether behaviour changes are due to the extent of social
252 loss they experience or simply due to exposure to the procedure whereby flockmates are
253 captured. Therefore, we ran linear mixed models (LMM) for each social metric
254 (response variable). The predictor variables were set as the treatment category, the
255 social impact, and the interaction between these. We included trial week as a fixed
256 effect to account for temporal changes, and set individual identity as a random effect.

257

258 Due to the implicit non-independence of network data, we also used simple network
259 permutations to derive p-values by comparing the *t*-value of each model's coefficients
260 to those generated from 10000 node randomisations [9, 52]. For each trial, the
261 permutations randomly reassigned each individual to another individual's pre- and post-
262 trial network position. This maintained the same network structure and distribution of
263 changes in metrics, but randomised the treatment category that each within-individual
264 change was assigned to within each trial.

265

266 *Re-introductions*

267 Whilst our main goal was to determine how individuals respond to the loss of social
268 associates, we were also able to examine whether individuals changed their behaviour
269 upon the re-introductions of removed birds (as removed birds were re-introduced after
270 one weekend). Therefore, we used the same structure models described above, but
271 instead of setting the response variables as individuals' change in social metrics
272 immediately following the trial, we considered their change in social metrics following
273 the reintroductions. In this way, we tested whether prior social associations towards
274 removed birds related to changes in individuals' social metrics upon the reintroduction
275 of their flockmates.

276

277 Further, we also examined whether reintroduced birds regained their social associations
278 to their previous flockmates. Firstly, we tested if removed birds' previous social
279 associations towards other birds co-occurring at the same feeders as them (prior to their
280 removal) predicted whether they would be flockmates following reintroduction using a
281 GLMM with binomial error structure and logit-link function. We included replicate
282 number, removed individuals' time until resighting, and distance from initial capture
283 site upon resighting, as fixed effects, and set individuals' identities as random effects.
284 We then used the same structure GLMM to assess whether removed individuals' pre-
285 removal dyadic association strength to their flockmates (i.e. only considering those
286 observed in a pre-trial flocking event with them) predicted their dyadic association
287 strength following reintroduction. In this case, dyadic association strength was modeled
288 as the number of flocks the dyad co-occurred in ('successes') in relation to the total
289 number of flocks the dyad did not co-occur in ('fails') as a binomial equivalent of
290 the SRI.

291

292 **RESULTS**

293

294 Over the woodland during the main 8-week study period, 395,113 records of 542
295 unique great tits making up 18,388 flocks were recorded. The flock size experienced by
296 the average individual, i.e. 'typical' group size [53], was 4.86 ± 0.02 (mean \pm SE). The
297 number of focal individuals in each trial (i.e. those observed in sampling periods
298 directly before and after the trial but not captured themselves) ranged from 15–49 for
299 those having a flockmate removed, 7–46 for those having a flockmate captured and
300 immediately release (i.e. control treatment), and 152–192 for those whose flockmates

301 were unaffected. The average network each weekend contained 307 individuals (range:
302 287–352) with an edge (social connection) density of 3.86% (range: 3.5–4.2%). On a
303 weekend-to-weekend basis, the social network remained highly consistent as
304 individuals largely maintained their dyadic associations to others (weekend-to-weekend
305 mantel tests range: $r = 0.65-0.78$, $p < 0.0001$).

306

307 *Effect of removals on foraging behaviour of flockmates*

308 We found no differences between birds whose flockmates were captured (control), birds
309 that experienced flockmate removal, and birds whose flockmates were unaffected
310 (LMMs, all category factor t values < 1.8 , $p > 0.06$, Figure S1) in their change in the
311 number of flocks they occurred in and number of sites they visited. Birds that
312 experienced flockmate removal showed increased activity at the feeding stations (LMM,
313 removal category factor $t = 2.5$, $p < 0.05$). However, the interaction between treatment
314 category (i.e. whether an individual experienced flockmate loss, or flockmate capture)
315 and social impact (proportional association strength to removed/captured flockmates)
316 did not predict changes in any measures of foraging behaviour (LMM, $t < 0.76$, $p > 0.45$,
317 Table 1a-c). Therefore, while birds which fell into the ‘flockmate removed’ category
318 showed a small increase in activity at feeding stations, the extent of loss of social
319 associates had no influence on any of these behaviours above that expected by the
320 capture procedure alone.

321

322 *Effect of removals on social behaviour of flockmates*

323 Amongst the treatment categories (i.e. (i) no treatment, (ii) flockmate capture and
324 immediate release, and (iii) flockmate removal), the only difference found in social
325 metrics was that those who experienced flockmate removal had, on average, a slightly
326 higher increase in network strength compared to birds whose flockmates were either
327 just captured or not affected at all (permutation test, $p < 0.01$, Figure 2a-e). Thus,
328 treatment group alone had little influence on the change in individuals’ social network
329 metrics (Figure 2a-e).

330

331 Importantly, by assessing the interaction between treatment category and the social
332 impact experienced, we determined how the extent of the social loss an individual
333 experienced affected individuals’ social metrics. We found that relative changes in
334 average flock size were not significantly predicted by this interaction (Figure 2f; Table

335 1d). Therefore, the extent of social loss did not affect this relatively simple measure of
336 sociality more than expected from any disturbance caused by the capture procedure
337 alone. However, when considering individuals' social network metrics, we found that
338 the interaction between treatment class and social impact significantly predicted
339 changes in average unweighted degree and strength (Figure 2g-h; Table 1e;1f).
340 Flockmates of birds that were just captured showed no change in their social
341 associations with increased social impact, but those birds that lost flockmates showed
342 increases in degree and strength with increasing levels of previous social association to
343 the removed birds (Figure 2g-h).

344

345 Therefore, those experiencing the most social impact in terms of removing their
346 previous flockmates showed the greatest increases in their degree and strength to
347 remaining individuals. For instance, around one third of birds that experienced
348 flockmate removal only lost a small proportion (>10%) of their network connection
349 strength (i.e. summed edge weights), and these generally showed very little change in
350 number of flockmates (Figure 2g). Yet, around one fifth of birds experiencing
351 flockmate removal lost >50% of all their previous network connection strength and
352 generally increased their number of connections to the remaining individuals by five
353 (Figure 2g). Those suffering this large social impact also increased their overall network
354 strength metric by ~1 (Figure 2h). This increase, for example, roughly equates to
355 spending an additional 20% of their time with five social associates who also occur 20%
356 of the time with them. Indeed, the general increase in network strength was not entirely
357 due to increasing their number of new social associates, as individuals experiencing the
358 most social loss from removals also showed an additional increase in the tightness of
359 their social connections (average edge weight) (Figure 2j). This is demonstrated by the
360 interaction between treatment category and social impact having a significant effect on
361 relative change in average edge weight (Table 1h - but note marginally non-significant
362 when using permutations).

363

364 We also assessed 'betweenness' which is more complex than the other social network
365 metrics as it considers associations amongst all individuals, even between those not
366 directly associated with the focal individual and therefore might depend less on the
367 focal individual themselves [12]. We found that the social loss an individual

368 experienced did not cause changes in betweenness, as there was no significant
369 interaction between treatment category and social impact (Figure 2i; Table 1g).

370

371 ***Construct validity***

372 As social network metrics can be inferred/derived in various ways, we assessed whether
373 our findings that individuals increased their social connectivity in response to
374 experiencing social loss were validated under alternative analysis (see *Supplementary*
375 *information* for details). We found the same patterns of effects of social loss on social
376 association metrics when using a more basic measure of social impact (proportion of
377 flockmates removed/captured) (Figure S2a-e) and when using averaged scores of social
378 association metrics (Figure S2f-j). The estimated statistical significance of the model
379 parameters differed slightly amongst the three approaches (Table 1; Table S1), but the
380 primary approach is expected to be the most reliable due to the higher resolution of both
381 the estimate of social impact (i.e. using strength rather than degree) and of the response
382 variables (i.e. using cumulative data rather than averaged networks). We also found that
383 before the experiments took place, individuals' weekly change in their social network
384 metrics (i.e. the response variables of interest) was unrelated to whether or not they
385 subsequently experienced removal or capture of their flockmates and the subsequent
386 'social impact' they would experience (Figure S3a-e). Therefore, individuals' increases
387 in degree, strength, and average edge weight in response to experimentally-imposed
388 flockmate loss do not appear to be driven by any pre-existing differences between
389 individuals or sites, but instead caused by the removals.

390

391 ***Reintroductions***

392 As 20 out of 23 removed individuals were resighted after reintroduction, we were
393 additionally able to examine the effect of the reintroductions. Upon release, 85% of
394 resighted reintroduced birds were first detected on the same, or neighbouring, feeding
395 station that they were removed from. In 80% of occasions, this was on the first weekend
396 following their release. We firstly considered how birds that had experienced flockmate
397 removal responded upon the reintroduction of their flockmates. We found that pre-trial
398 social associations towards removed birds did not relate to changes in social
399 associations metrics upon the reintroduction of the removed birds (Figure S3f-j).

400

401 We then considered the reintroduced birds themselves, and found these generally
402 regained the same social associates upon reintroduction. Removed birds' social
403 associations towards other birds co-occurring at the same feeders as them prior to their
404 removal strongly predicted whether they would be flockmates following reintroduction
405 (GLMM: Estimate = 8.4 ± 2.1 , $z = 3.926$, $p < 0.001$ - Figure 3a; Table S2a). Further, the
406 pre-removal social association strength of reintroduced birds to their previous
407 flockmates strongly related to the post-reintroduction association strength to the same
408 flockmates (GLMM: Estimate = 3.8 ± 0.4 , $z = 8.659$, $p < 0.001$ - Figure 3b; Table S2b).

409

410 **DISCUSSION**

411

412 By temporarily removing individuals from a social network of wild great tits, we
413 demonstrate experimentally that the loss of conspecifics has significant social
414 ramifications for the remaining individuals. Experiencing the loss of social associates
415 caused birds to form new associations with others, increase their general connectedness
416 within the social network, and form tighter social ties to their remaining flockmates
417 (Figure 2; Table 1). The changes were particularly striking as they appear to be driven
418 by fine-scale modifications of social association patterns in response to loss of their
419 flockmates, rather than by changes to individuals' general foraging behaviour (Table 1a-
420 c; Figure S1).

421

422 These findings represent an important contribution to understanding the social
423 consequences of losing individuals from wild animal societies, as previous knowledge
424 has been largely based on computer simulations [29-31, 35, 54]. Although simulations
425 could potentially be applied to a variety of systems, any such findings are currently
426 difficult to interpret given the lack of understanding regarding biological systems'
427 responses to perturbations [33-35]. In particular, studies on captive animals have
428 demonstrated how individuals might react to social loss in ways that would be difficult
429 to account for using simulations alone [36, 37]. Through demonstrating that individuals
430 experiencing loss of their associates showed increased social associations to the
431 remaining individuals, we illustrate the importance of considering behavioural
432 responses to social loss in wild populations.

433

434 In natural settings, gain and loss of individuals (due to birth/deaths, or
435 migration/immigration) may be expected to continually alter individuals' interaction
436 partners. Even with such turnover, remaining individuals may maintain consistent social
437 network positions. For example, great tits express repeatable social phenotypes over
438 years despite ~50% annual turnover [25]. Our findings, indicating an up-regulation of
439 other social associations in response to loss, potentially illustrate the means by which
440 individuals demonstrate repeatable social phenotypes despite a continually changing
441 pool of interaction partners. As great tits naturally experience reasonably high levels of
442 social turnover, the evolution of strategies to buffer their own patterns of social
443 associations against perturbation may be expected in comparison to species
444 experiencing less social mixing. Indeed, if social network connections influence fitness
445 [19-21], repeatable differences between individuals create the potential for selection to
446 shape the social network structure [55].

447

448 The biological mechanisms underpinning individuals' responses to social perturbations
449 have been relatively unexplored. In this study, the fact that birds appear to increase their
450 general sociability upon losing their associates may represent a rapid behavioural
451 response to compensate for the loss of connectedness. Social associations are known to
452 be valuable to individuals [56]. For instance, within our study population, the most
453 central individuals benefit from increased access to information regarding new food
454 sources [16]. Thus, whilst the loss of flockmates may reduce an individual's access to
455 information, rapidly acting to increase their centrality may mitigate this. In the same
456 sense, previous experiments that separated flockmates from foraging together [47]
457 indicated that birds can increase their usage of social information from heterospecifics
458 in response to social segregation [18].

459

460 Maintaining high numbers of flock members can also help protect against predation
461 [56], and, within this study system, simulated predation risk has been shown to increase
462 flock turnover, potentially causing individuals to form more social associations [57].
463 Therefore, it could be hypothesized that increases in social centrality with increasing
464 amounts of flockmate removal (but not simply with increasing exposure to the capture
465 procedure), is due to birds recognizing the actual loss of their associates, and
466 interpreting this as a cue of high predation conditions (thus causing them to favour
467 central network positions). In this case however, changes to other foraging behaviours

468 linked to anti-predator responses, such as activity and movements, would also be
469 expected. Yet, none of these foraging behaviours were strongly related to the extent of
470 flockmate loss. Indeed, along with short-term benefits (such as predation avoidance),
471 the future benefits of sustaining associations may be as, or more, important. For
472 instance, pair members remain strongly associated through the winter and base their
473 behaviour around one another [49]. Birds also appear to shape their breeding positions
474 and territories around their close winter associates, potentially to reduce competition
475 and increase cooperation during breeding [46].

476

477 Rather than a compensatory response to losing social associations, an alternative
478 hypothesis for the increase in centrality measures may be competitive replacement.
479 Early, seminal, studies of great tits found that breeding territories and locations were
480 limited, and removing individuals from their territory resulted in rapid replacement by
481 close neighbours from non-optimal territories [1]. Similarly, for various tit species,
482 removed winter groups appear to be quickly replaced by new groups [58]. Although
483 attaining and maintaining certain network positions might require considerable input
484 from individuals [55], it is unclear whether winter social network positions are
485 ‘limited’. Such limitations could occur if, for example, social centrality was a desired
486 attribute, and individuals generally aimed to associate with the most ‘attractive’
487 individuals. In this way, ‘attractive’ individuals would be able to hold the most social
488 connections (as others are attracted to associating with them), and therefore the removal
489 of individuals may ‘free up’ connections to be adopted by those socially closest to them,
490 and result in the pattern of increased centrality with increased social loss (Figure 2).

491

492 Ultimately, developing a better understanding of individuals’ responses to loss will
493 improve the ability to predict the consequences. For example, a recent observational
494 study indicated that wild African elephant (*Loxodonta africana*) populations maintain
495 their social network structure despite ivory poaching eliminating the highly connected
496 nodes (i.e. older female elephants) [59]. Whilst no active response to such loss was
497 exhibited, the robustness instead stemmed from daughters replicating their mothers’
498 social positions. This generated social redundancy, and allowed structural maintenance
499 upon the removal of the mother [59], resulting in resilient connected groups. Therefore,
500 while one might expect that poaching of elephant matriarchs would reduce the

501 availability of important information to the rest of the group [60], the expected loss in
502 social network connectivity was mitigated through this underlying resilience.

503

504 The resulting social structure following individual loss also has important implications
505 for predicting infectious disease spread [61]. For instance, culling Tasmanian devils
506 (*Sarcophilus harrisi*) known to be carriers of an infective facial tumour disease did not
507 reduce its spread, as the highly connected social system lead to rapid transmission
508 regardless of relatively small-scale losses. Similarly, attempts to control rabies within
509 vampire bats (*Desmodus rotundus*) through removing adults was found to be ineffective
510 as younger individuals were the primary transmitters [62]. Thus, although procedures
511 that actively identify and remove highly connected individuals may aid in reducing
512 disease spread, our findings caution that this too may be less effective than predicted if
513 the remaining individuals increase their social connections in response to the removals.

514

515 Various ecological studies also rely on procedures that (temporarily) remove individuals
516 from wild populations (such as for marking, behavioural assaying, or short-term captive
517 experiments). The consequences of this disturbance for study systems are generally
518 unknown. We demonstrate that removals can have social impacts that would otherwise
519 go unnoticed, particularly as individual-level activity patterns remain mostly unchanged
520 (Figure S1). The effect of re-introducing individuals into populations is also rarely
521 considered, but can also influence social behaviour [63]. Here, we show that individuals
522 experienced little interference upon the re-introduction of their flock mates (Figure S3f-
523 j). Interestingly, reintroduced individuals generally regained their prior social network
524 connections (Figure 3 – Table S2). This indicates that social associations between great
525 tits may be resilient to short-term separations and perturbations. Similarly, the social
526 structure of captive guppy shoals exhibited resilience to the reintroduction of
527 individuals following their removal during a cooperative task [64], which also suggests
528 maintenance of associations despite such disturbance. On the other hand, consequences
529 of introductions for captive catsharks (*Scyliorhinus canicula*) appears to depend both on
530 the type of individual introduced, and the characteristics of the social group [65]. Thus,
531 further examination of the social consequences of the addition of individuals within
532 wild populations appears to be a useful avenue of future research [63].

533

534

535 **Conclusion**

536 We provide experimental evidence that the removal of individuals from wild
537 populations has social implications that expand beyond the direct effects of social
538 associate loss. Individual great tits responded to increasing amounts of externally
539 imposed flockmate loss by increasing their social connectivity to others. This
540 demonstrates that reductions of connectedness within the social network itself due to
541 individual loss may be ameliorated by increases in associations between remaining
542 animals. Therefore, along with increasing our knowledge of the stability of social
543 organisation, these findings may have implications for predicting how individual loss
544 can alter social structure and social processes important to conservation efforts, such as
545 the spread of disease or information between individuals. Future work examining the
546 generality and untangling the mechanisms of this compensatory response to social loss,
547 along with experiments varying both the quantity and type of experimentally removed
548 individuals across a range of social systems, would be particularly valuable.

549

550 **Acknowledgements.** We thank all Social Network Group of the Edward Grey Institute,
551 Oxford University, for assistance with fieldwork, and Julian Howe for help with captive
552 birds, and two anonymous reviewers for their helpful feedback.

553 **Author Contributions.** J.A.F., B.V., R.A.C. & B.C.S. designed the experiments.
554 J.A.F., B.V. & R.A.C. carried out the fieldwork, J.A.F. analysed the data and wrote the
555 first draft, all authors contributed to interpreting the data and revising the manuscript.

556 **Funding statement.** The work was funded by a NERC studentship and EGI Research
557 Fellowship to J.A.F. and grants from the ERC and BBSRC (AdG 250164;
558 BB/L006081/1) to B.C.S.

559 **Data accessibility.** Supporting data is freely available at:

560 <http://dx.doi.org/10.5061/dryad.q8987>

561 **Competing interest.** We have no competing interests

562

563 **REFERENCES**

- 564 1. Krebs J.R. 1970 Territory and Breeding Density in Great-Tit, *Parus-Major* L.
565 *Ecology* **52**(1), 2-22. (doi:10.2307/1934734).
566 2. Manuwal D.A. 1974 Effects of Territoriality on Breeding in a Population of
567 Cassins Auklet. *Ecology* **55**(6), 1399-1406. (doi:10.2307/1935468).
568 3. Ekman J., Cederholm G., Askenmo C. 1981 Spacing and Survival in Winter
569 Groups of Willow Tit *Parus-Montanus* and Crested Tit *P Cristatus* - a Removal
570 Study. *J Anim Ecol* **50**(1), 1-9. (doi:10.2307/4027).

- 571 4. Allee W.C. 1949 *Principles of Animal Ecology*. Philadelphia, Saunders Co.
- 572 5. Stephens P.A., Sutherland W.J. 1999 Consequences of the Allee effect for
- 573 behaviour, ecology and conservation. *Trends Ecol Evol* **14**(10), 401-405.
- 574 (doi:10.1016/S0169-5347(99)01684-5).
- 575 6. Courchamp F., Berec L., Gascoigne J. 2008 *Allee Effects in Ecology and*
- 576 *Conservation*, Oxford University Press.
- 577 7. Krause J., Croft D.P., James R. 2007 Social network theory in the behavioural
- 578 sciences: potential applications. *Behav Ecol Sociobiol* **62**(1), 15-27.
- 579 (doi:10.1007/S00265-007-0445-8).
- 580 8. Krause J., Krause S., Arlinghaus R., Psorakis I., Roberts S., Rutz C. 2013
- 581 Reality mining of animal social systems. *Trends Ecol Evol* **28**(9), 541-551.
- 582 (doi:10.1016/J.Tree.2013.06.002).
- 583 9. Whitehead H. 2008 *Analyzing animal societies*. Chicago, University of
- 584 Chicago Press.
- 585 10. Croft D.P., James R., Krause J. 2008 *Exploring animal social networks*.
- 586 Princeton, Princeton University Press.
- 587 11. Sih A., Hanser S.F., McHugh K.A. 2009 Social network theory: new insights
- 588 and issues for behavioral ecologists. *Behav Ecol Sociobiol* **63**(7), 975-988.
- 589 (doi:10.1007/s00265-009-0725-6).
- 590 12. Brent L.J.N. 2015 Friends of friends: are indirect connections in social
- 591 networks important to animal behaviour? *Anim Behav* **103**, 211-222.
- 592 (doi:10.1016/j.anbehav.2015.01.020).
- 593 13. Krause J., James R., Franks D.W., Croft D.P. 2015 *Animal Social Networks*.
- 594 Oxford, UK, Oxford University Press.
- 595 14. Godfrey S.S., Bull C.M., James R., Murray K. 2009 Network structure and
- 596 parasite transmission in a group living lizard, the gidgee skink, *Egernia stokesii*.
- 597 *Behav Ecol Sociobiol* **63**(7), 1045-1056. (doi:10.1007/S00265-009-0730-9).
- 598 15. VanderWaal K.L., Atwill E.R., Isbell L.A., McCowan B. 2014 Linking social
- 599 and pathogen transmission networks using microbial genetics in giraffe (*Giraffa*
- 600 *camelopardalis*). *J Anim Ecol* **83**(2), 406-414. (doi:10.1111/1365-2656.12137).
- 601 16. Aplin L.M., Farine D.R., Morand-Ferron J., Sheldon B.C. 2012 Social networks
- 602 predict patch discovery in a wild population of songbirds. *P Roy Soc B-Biol Sci*
- 603 **279**(1745), 4199-4205. (doi:10.1098/rspb.2012.1591).
- 604 17. Aplin L.M., Farine D.R., Morand-Ferron J., Cockburn A., Thornton A., Sheldon
- 605 B.C. 2015 Experimentally induced innovations lead to persistent culture via
- 606 conformity in wild birds. *Nature* **518**(7540), 538-541.
- 607 (doi:10.1038/Nature13998).
- 608 18. Firth J.A., Sheldon B.C., Farine D.R. 2016 Pathways of information
- 609 transmission among wild songbirds follow experimentally imposed changes in
- 610 social foraging structure. *Biol Lett* **12**(6), 20160144.
- 611 (doi:10.1098/rsbl.2016.0144).
- 612 19. McDonald D.B. 2007 Predicting fate from early connectivity in a social
- 613 network. *Proc Natl Acad Sci USA* **104**(26), 10910-10914.
- 614 (doi:10.1073/pnas.0701159104).
- 615 20. Brent L.J.N., Heilbronner S.R., Horvath J.E., Gonzalez-Martinez J., Ruiz-
- 616 Lambides A., Robinson A.G., Skene J.H.P., Platt M.L. 2013 Genetic origins of social
- 617 networks in rhesus macaques. *Sci Rep* **3**. (doi:10.1038/srep01042).

- 618 21. Lehmann J., Majolo B., McFarland R. 2016 The effects of social network
619 position on the survival of wild Barbary macaques, *Macaca sylvanus*. *Behav Ecol*
620 **27**(1), 20-28. (doi:10.1093/beheco/arv169).
- 621 22. Oh K.P., Badyaev A.V. 2010 Structure of Social Networks in a Passerine Bird:
622 Consequences for Sexual Selection and the Evolution of Mating Strategies. *Am Nat*
623 **176**(3), E80-E89. (doi:10.1086/655216).
- 624 23. Farine D.R., Sheldon B.C. 2015 Selection for territory acquisition is
625 modulated by social network structure in a wild songbird. *J Evol Biol* **28**(3), 547-
626 556. (doi:10.1111/Jeb.12587).
- 627 24. Blumstein D.T., Petelle M.B., Wey T.W. 2013 Defensive and social
628 aggression: repeatable but independent. *Behav Ecol* **24**(2), 457-461.
629 (doi:10.1093/beheco/ars183).
- 630 25. Aplin L.M., Firth J.A., Farine D.R., Voelkl B., Crates R.A., Culina A., Garroway
631 C.J., Hinde C.A., Kidd L.R., Psorakis I., et al. 2015 Consistent individual differences in
632 the social phenotypes of wild great tits, *Parus major*. *Anim Behav* **108**, 117-127.
633 (doi:10.1016/j.anbehav.2015.07.016).
- 634 26. Wey T., Blumstein D.T., Shen W., Jordan F. 2008 Social network analysis of
635 animal behaviour: a promising tool for the study of sociality. *Anim Behav* **75**, 333-
636 344. (doi:10.1016/j.anbehav.2007.06.020).
- 637 27. Albert R., Jeong H., Barabasi A.L. 2000 Error and attack tolerance of complex
638 networks. *Nature* **406**(6794), 378-382. (doi:10.1038/35019019).
- 639 28. Albert R., Barabasi A.L. 2002 Statistical mechanics of complex networks. *Rev*
640 *Mod Phys* **74**(1), 47-97. (doi:10.1103/RevModPhys.74.47).
- 641 29. Lusseau D. 2003 The emergent properties of a dolphin social network. *P*
642 *Roy Soc B-Biol Sci* **270**, S186-S188.
- 643 30. Williams R., Lusseau D. 2006 A killer whale social network is vulnerable to
644 targeted removals. *Biol Lett* **2**(4), 497-500. (doi:10.1098/rsbl.2006.0510).
- 645 31. Manno T.G. 2008 Social networking in the Columbian ground squirrel,
646 *Spermophilus columbianus*. *Anim Behav* **75**, 1221-1228.
647 (doi:10.1016/j.anbehav.2007.09.025).
- 648 32. Lehmann J., Andrews K., Dunbar R.I.M. 2010 Social networks and social
649 complexity in female-bonded primates. In *Social brain, distributed mind* (eds.
650 Dunbar R.I.M., Gamble C., Gowlett J.A.), pp. 57-83. Oxford, U.K, Oxford University
651 Press.
- 652 33. Formica V.A., Wood C., Phoebe C.s., Brodie III E. 2016 Consistency of animal
653 social networks after disturbance. *Behav Ecol*. (doi:10.1093/beheco/arw128).
- 654 34. Mersch D.P. 2016 The social mirror for division of labor: what network
655 topology and dynamics can teach us about organization of work in insect societies.
656 *Behav Ecol Sociobiol* **70**(7), 1087-1099. (doi:10.1007/s00265-016-2104-4).
- 657 35. Mourier J., Brown C., Planes S. 2017 Learning and robustness to catch-and
658 release fishing in a shark social network. *Biol Lett* **13**, 20160824.
659 (doi:10.1098/rsbl.2016.0824).
- 660 36. Flack J.C., Girvan M., de Waal F.B.M., Krakauer D.C. 2006 Policing stabilizes
661 construction of social niches in primates. *Nature* **439**(7075), 426-429.
662 (doi:10.1038/nature04326).
- 663 37. Annagiri S., Kolay S., Paul B., Sona C. 2016 Network approach to
664 understanding the organization of and the consequence of targeted leader removal
665 on an end-oriented task. *Current Zoology*. (doi:10.1093/cz/zow058).

- 666 38. Naug D. 2009 Structure and resilience of the social network in an insect
667 colony as a function of colony size. *Behav Ecol Sociobiol* **63**(7), 1023-1028.
668 (doi:10.1007/s00265-009-0721-x).
- 669 39. Perrins C.M. 1965 Population Fluctuations and Clutch-Size in the Great Tit,
670 Parus-Major L. *J Anim Ecol* **34**(3), 601-647. (doi:10.2307/2453).
- 671 40. Hinde R.A. 1952 The behavior of the Great Tit (*Parus major*) and some
672 other related species. *Behaviour* **2**, 1-201.
- 673 41. Psorakis I., Roberts S.J., Rezek I., Sheldon B.C. 2012 Inferring social network
674 structure in ecological systems from spatio-temporal data streams. *J R Soc*
675 *Interface* **9**, 3055-3066. (doi:10.1098/rsif.2012.0223).
- 676 42. Psorakis I., Voelkl B., Garroway C.J., Radersma R., Aplin L.M., Crates R.A.,
677 Culina A., Farine D.R., Firth J.A., Hinde C.A., et al. 2015 Inferring social structure
678 from temporal data. *Behav Ecol Sociobiol* **69**(5), 857-866. (doi:10.1007/S00265-
679 015-1906-0).
- 680 43. R Core Team. 2015 R: A Language and Environment for Statistical
681 Computing. (eds. R, Computing F.f.S.). Vienna, Austria.
- 682 44. Cairns S.J., Schwager S.J. 1987 A Comparison of Association Indexes. *Anim*
683 *Behav* **35**, 1454-1469. (doi:10.1016/S0003-3472(87)80018-0).
- 684 45. Farine D.R., Firth J.A., Aplin L.M., Crates R.A., Culina A., Garroway C.J., Hinde
685 C.A., Kidd L.R., Milligan N.D., Psorakis I., et al. 2015 The role of social and ecological
686 processes in structuring animal populations: a case study from automated tracking
687 of wild birds. *Royal Society Open Science* **2**(4), 150057. (doi:10.1098/rsos.150057).
- 688 46. Firth J.A., Sheldon B.C. 2016 Social carry-over effects underpin trans-
689 seasonally linked structure in a wild bird population. *Ecol Lett*.
690 (doi:10.1111/ele.12669).
- 691 47. Firth J.A., Sheldon B.C. 2015 Experimental manipulation of avian social
692 structure reveals segregation is carried over across contexts. *P Roy Soc B-Biol Sci*
693 **282**(1802), 20142350. (doi:10.1098/Rspb.2014.2350).
- 694 48. Culina A., Hinde C.A., Sheldon B.C. 2015 Carry-over effects of the social
695 environment on future divorce probability in a wild bird population. *P Roy Soc B-
696 Biol Sci* **282**(1817). (doi:10.1098/rspb.2015.0920).
- 697 49. Firth J.A., Voelkl B., Farine D.R., Sheldon B.C. 2015 Experimental Evidence
698 that Social Relationships Determine Individual Foraging Behavior. *Curr Biol*
699 **25**(23), 3138-3143. (doi:10.1016/j.cub.2015.09.075).
- 700 50. Haftorn S. 1992 Effects of a Sudden, Transient Fall in Air-Temperature on
701 the Winter Body-Mass of 5 Species of Tits (*Parus*). *Journal Fur Ornithologie* **133**(2),
702 147-154. (doi:10.1007/Bf01639907).
- 703 51. Aplin L.M., Farine D.R., Morand-Ferron J., Cole E.F., Cockburn A., Sheldon
704 B.C. 2013 Individual personalities predict social behaviour in wild networks of
705 great tits (*Parus major*). *Ecol Lett* **16**(11), 1365-1372. (doi:10.1111/ele.12181).
- 706 52. Croft D.P., Madden J.R., Franks D.W., James R. 2011 Hypothesis testing in
707 animal social networks. *Trends Ecol Evol* **26**(10), 502-507.
708 (doi:10.1016/J.Tree.2011.05.012).
- 709 53. Jarman P.J. 1974 Social-Organization of Antelope in Relation to Their
710 Ecology. *Behaviour* **48**, 215. (doi:10.1163/156853974x00345).
- 711 54. Ilany A., Akcay E. 2016 Social inheritance can explain the structure of
712 animal social networks. *Nat Commun* **7**. (doi:ARTN 12084
713 10.1038/ncomms12084).

- 714 55. Wilson A.D.M., Krause S., Dingemanse N.J., Krause J. 2013 Network position:
715 a key component in the characterization of social personality types. *Behav Ecol*
716 *Sociobiol* **67**(1), 163-173. (doi:10.1007/S00265-012-1428-Y).
- 717 56. Krause J., Ruxton G.D. 2002 *Living in groups*. Oxford, Oxford University
718 Press.
- 719 57. Voelkl B., Firth J.A., Sheldon B.C. 2016 Nonlethal predator effects on the
720 turn-over of wild bird flocks. *Sci Rep* **6**. (doi:10.1038/srep33476).
- 721 58. Ekman J. 1989 Ecology of Non-Breeding Social-Systems of Parus. *Wilson*
722 *Bull* **101**(2), 263-288.
- 723 59. Goldenberg S.Z., Douglas-Hamilton L., Wittemyer G. 2016 Vertical
724 Transmission of Social Roles Drives Resilience to Poaching in Elephant Networks.
725 *Curr Biol* **26**(1), 75-79. (doi:10.1016/j.cub.2015.11.005).
- 726 60. McComb K., Moss C., Durant S.M., Baker L., Sayialel S. 2001 Matriarchs as
727 repositories of social knowledge in African elephants. *Science* **292**(5516), 491-494.
728 (doi:10.1126/science.1057895).
- 729 61. Weber N., Carter S.P., Dall S.R.X., Delahay R.J., McDonald J.L., Bearhop S.,
730 McDonald R.A. 2013 Badger social networks correlate with tuberculosis infection.
731 *Curr Biol* **23**(20), R915-R916. (doi:10.1016/J.Cub.2013.09.011).
- 732 62. Streicker D.G., Recuenco S., Valderrama W., Benavides J.G., Vargas I.,
733 Pacheco V., Condori E.C., Montgomery J., Rupprecht C.E., Rohani P., et al. 2012
734 Ecological and anthropogenic drivers of rabies exposure in vampire bats:
735 implications for transmission and control. *P Roy Soc B-Biol Sci* **279**(1742), 3384-
736 3392. (doi:10.1098/rspb.2012.0538).
- 737 63. Croft D.P., Edenbrow M., Darden S.K., Ramnarine I.W., van Oosterhout C.,
738 Cable J. 2011 Effect of gyrodactylid ectoparasites on host behaviour and social
739 network structure in guppies *Poecilia reticulata*. *Behav Ecol Sociobiol* **65**(12),
740 2219-2227. (doi:10.1007/s00265-011-1230-2).
- 741 64. Thomas P.O.R., Croft D.P., Morrell L.J., Davis A., Faria J.J., Dyer J.R.G.,
742 Piyapong C., Ramnarine I., Ruxton G.D., Krause J. 2008 Does defection during
743 predator inspection affect social structure in wild shoals of guppies? *Anim Behav*
744 **75**, 43-53. (doi:10.1016/j.anbehav.2007.06.004).
- 745 65. Jacoby D.M.P., Busawon D.S., Sims D.W. 2010 Sex and social networking: the
746 influence of male presence on social structure of female shark groups. *Behav Ecol*
747 **21**(4), 808-818. (doi:10.1093/beheco/arq061).
- 748
- 749
- 750

751

752

753 **Figure 1.** Wytham Woods, Oxford, UK, with RFID feeding stations shown as grey circles.
754 Rectangles show areas where the removal treatment/catching control was carried out, where
755 same colours represent the same replicate. These took place in order of red, black, blue, purple.
756 Areas where birds were captured and immediately released (control areas) are boxed in dotted
757 lines and areas where birds were subjected to removal (removal areas) are in solid.

758

759 **Figure 2.** Change in great tit social network metrics under the different treatment conditions of
760 (i) not affected (purple), (ii) flockmate/s captured and immediately released (blue), and (iii)
761 flockmate/s removed (red). Parts a-e summarise the raw data with boxplots showing the change
762 in the social metrics for individuals in each category. Thick vertical lines show mean \pm SE, mid
763 horizontal lines show median, box shows interquartile range (IQR), whiskers shows range (with
764 values outside 1.5 times IQR excluded). Parts f-j show how subsequent changes in social
765 network metrics (y axes) are related to the proportion of an individual's previous social
766 association strength that was directed towards removed individuals (the red lines show those
767 who experienced the experimental treatment of flockmate removal) and towards birds that were
768 captured and immediately released (the blue lines those who experienced the control treatment
769 of flockmate capture). Lines and surrounding shaded area show LMM fit and standard error
770 over all replicates (see Table 1d-h for full model details).

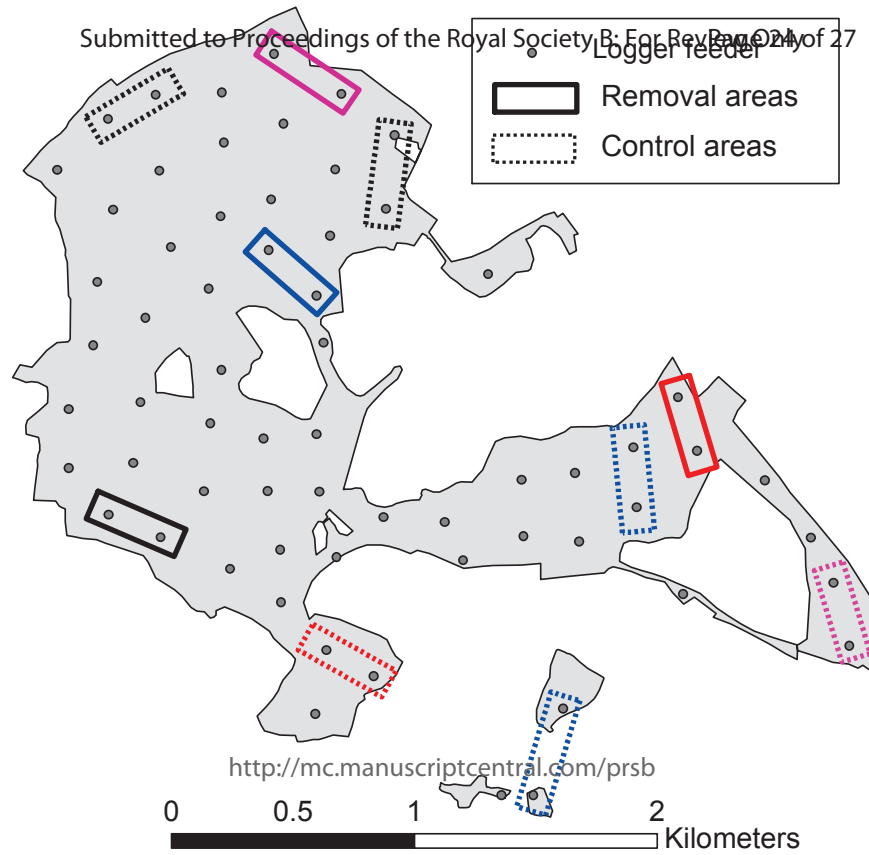
771

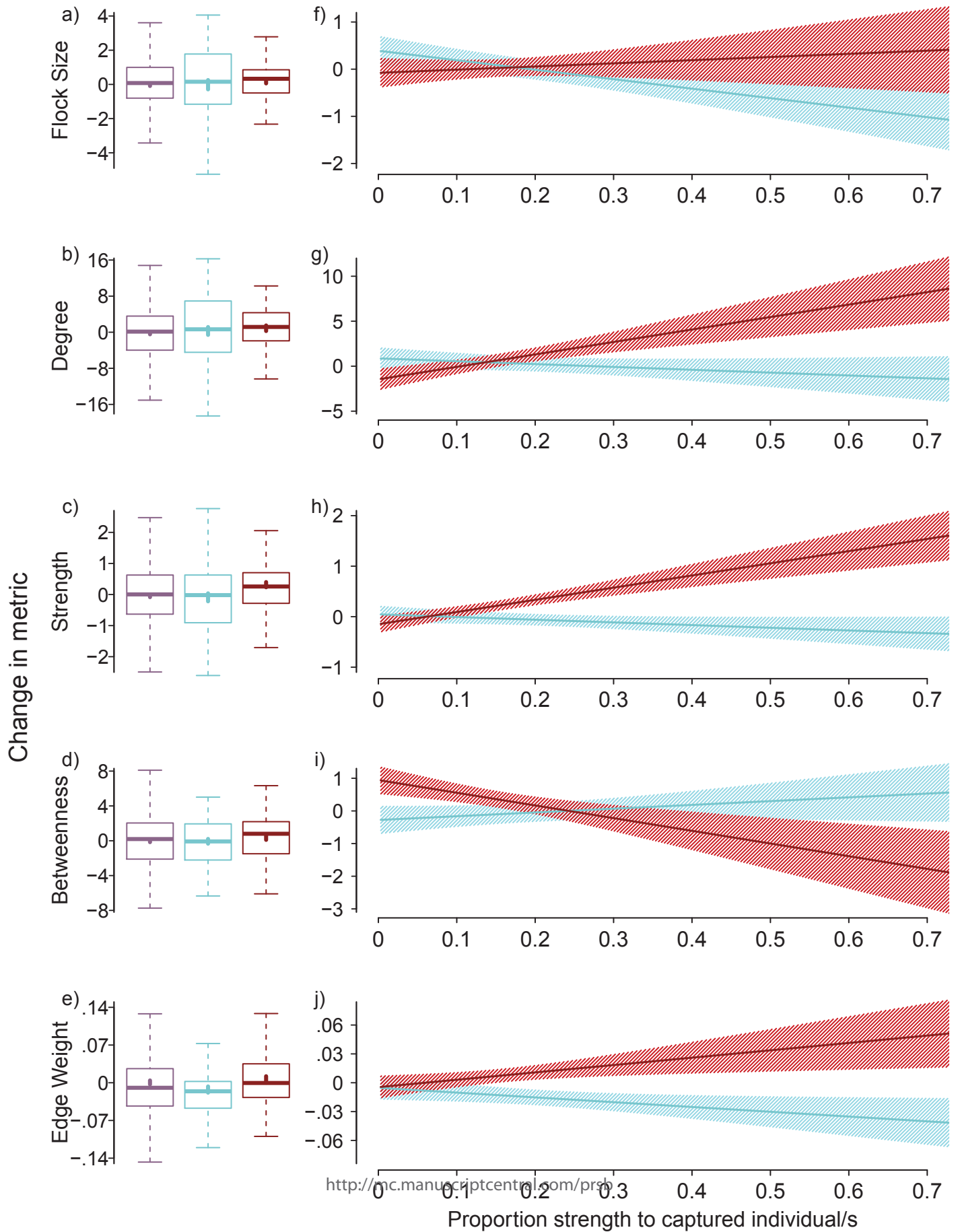
772 **Figure 3.** The recovery of previous social associations upon the reintroduction of removed
773 birds. (a) Removed birds' previous dyadic social associations with other birds occurring at the
774 same feeders as them (x axis) predicted whether they were flockmates following reintroduction
775 (y axis), and (b) Removed birds' previous dyadic social associations with their previous
776 flockmates (x axis) predicted their dyadic association strength with them following
777 reintroduction (y axis). In both panels, solid lines and surrounding hashed area show fit and
778 standard error respectively of GLMMs including individuals' identities as a random effect (see
779 Table S2 for full model results). Boxes in (a) show the raw data interquartile range (IQR), with
780 mid-lines denoting median and whiskers indicating the range (excluding values 1.5times outside
781 of IQR). Points in (b) show raw dyadic social association strengths between removed birds and
782 their flockmates.

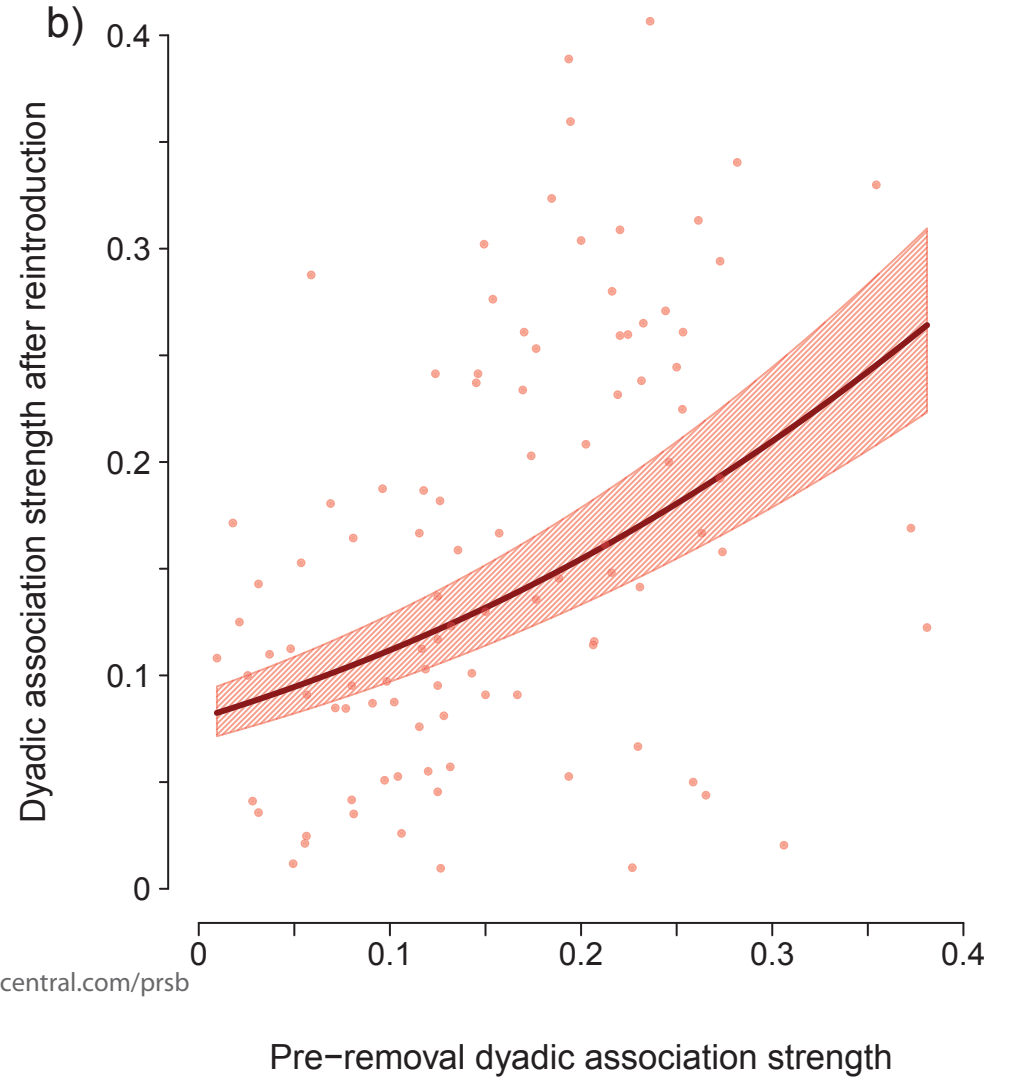
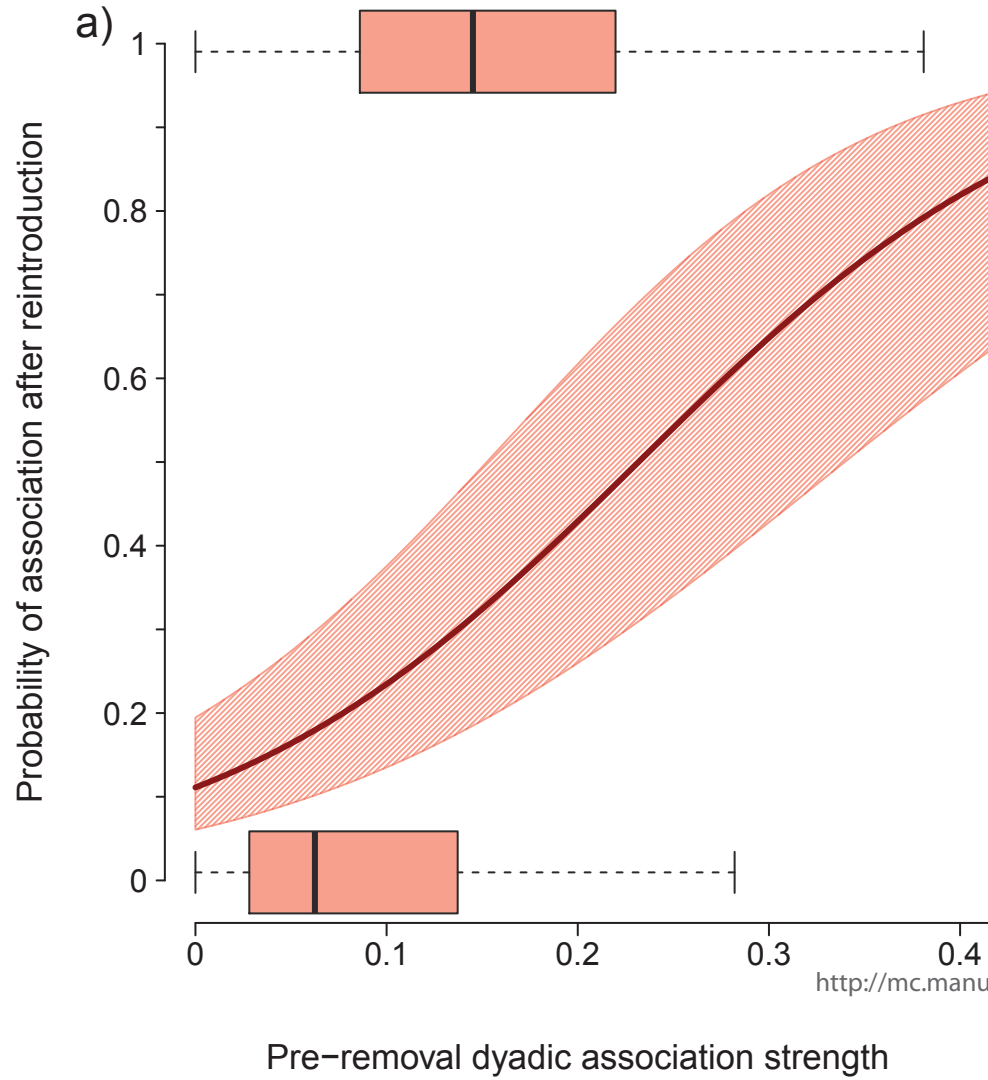
783

784 **Table 1.** Results of full models corresponding to Figure 2f-j. Linear Mixed Models (LMM) all
785 included individual identity as random effects and assessed the effect on the response variable
786 (change in the social metric) by the fixed effects of (i) 'Prop. assoc', which is the proportion of
787 an individuals association held to removed/captured individuals (ii) 'Treatment' i.e. whether the

788 individuals flockmates were just captured or actually removed, (iii) the week which the replica
789 took place and (iv) the interaction between 'Prop. assoc' and 'Treatment'. The coefficient,
790 standard error, t value and the standard p value are provided, along with the p value calculated
791 from the randomisations (P_{rand}).
792







		Coeff.	SE	t value	P	P _{rand}
a) Change in N. Records	Intercept	-11.496	22.234	-0.517	0.606	0.584
	Prop. assoc	55.479	63.729	0.871	0.39	0.411
	Treatment	6.363	23.915	0.266	0.792	0.806
	Week	3.162	6.673	0.474	0.639	0.576
	Interaction	65.683	111.49	0.589	0.559	0.535
b) Change in N. Flocks	Intercept	-2.304	2.686	-0.858	0.392	0.352
	Prop. assoc	8.084	7.797	1.037	0.307	0.283
	Treatment	0.808	2.819	0.287	0.776	0.787
	Week	0.497	0.801	0.621	0.539	0.462
	Interaction	5.544	12.922	0.429	0.67	0.652
c) Change in N. Sites visited	Intercept	-0.03	0.096	-0.31	0.757	0.751
	Prop. assoc	-0.224	0.279	-0.803	0.427	0.493
	Treatment	-0.148	0.1	-1.485	0.146	0.141
	Week	0.042	0.029	1.48	0.148	0.121
	Interaction	0.339	0.453	0.75	0.458	0.467
d) Change in Flock size	Intercept	-0.108	0.421	-0.257	0.798	0.794
	Prop. assoc	-1.497	1.224	-1.223	0.229	0.226
	Treatment	-0.591	0.445	-1.326	0.193	0.187
	Week	0.22	0.126	1.748	0.089	0.036
	Interaction	2.771	2.053	1.35	0.185	0.171
e) Change in Degree	Intercept	-1.479	1.603	-0.923	0.357	0.326
	Prop. assoc	-0.14	4.675	-0.03	0.976	0.953
	Treatment	-2.785	1.678	-1.66	0.106	0.097
	Week	1.006	0.48	2.096	0.043	0.014
	Interaction	15.233	7.652	1.991	0.054	0.051
f) Change in Strength	Intercept	-0.169	0.222	-0.762	0.447	0.411
	Prop. assoc	-0.339	0.643	-0.527	0.602	0.56
	Treatment	-0.244	0.237	-1.029	0.31	0.318
	Week	0.094	0.067	1.411	0.167	0.099
	Interaction	2.999	1.098	2.732	0.01	0.009
g) Change in Between-ness	Intercept	-0.596	0.572	-1.043	0.298	0.284
	Prop. assoc	1.539	1.659	0.927	0.36	0.402
	Treatment	1.156	0.607	1.903	0.065	0.059
	Week	0.141	0.171	0.822	0.417	0.34
	Interaction	-5.412	2.808	-1.928	0.062	0.062
h) Change in Average Strength	Intercept	0.014	0.013	1.06	0.291	0.267
	Prop. assoc	-0.061	0.039	-1.589	0.121	0.08
	Treatment	0.005	0.014	0.355	0.725	0.716
	Week	-0.008	0.004	-2.063	0.046	0.036
	Interaction	0.123	0.063	1.968	0.057	0.043