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Stable multi-level social structure is maintained by habitat geometry in a wild bird population — [Source link](#)

Damien R. Farine, Ben C. Sheldon

Institutions: Max Planck Society, Edward Grey Institute of Field Ornithology

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3 **Stable multi-level social structure is maintained by habitat**

4 **geometry in a wild bird population**

5

6 Damien R. Farine^{*a,b,c,d}, Ben C. Sheldon^a

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9 ^a Edward Grey Institute of Field Ornithology, Department of Zoology, University of Oxford,

10 South Parks Road, Oxford OX1 3PS, United Kingdom.

11 ^b Department of Collective Behaviour, Max Planck Institute for Ornithology,

12 Universitätsstrasse 10, 78457 Konstanz, Germany.

13 ^c Chair of Biodiversity and Collective Behaviour, Department of Biology, University of

14 Konstanz, Universitätsstrasse 10, 78457 Konstanz, Germany.

15 ^d Center for the Advanced Study of Collective Behaviour, University of Konstanz,

16 Universitätsstrasse 10, 78457 Konstanz, Germany.

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20 * Corresponding author:

21 dfarine@orn.mpg.de

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23

24 ABSTRACT

25

26 Social structure can have profound evolutionary and ecological implications for
27 animal populations. Structure can arise and be maintained via social preferences or
28 be indirectly shaped by habitat structure. Understanding how social structure
29 emerges is important for understanding the potential links between social structure
30 and evolutionary and ecological processes. Here, we study a large community of
31 wild birds fitted with uniquely-coded passive integrated transponder (PIT) tags and
32 recorded on a grid of automated feeders fitted with radio frequency identification
33 (RFID) antennae. We show that both large-scale and fine-scale network
34 communities are consistent across years in this population, despite high
35 generational turn-over. Studying the process that generates community structure,
36 here the movement of individual birds across the woodland, suggests an important
37 role of habitat geometry in shaping population-level social community structure.
38 Our study highlights how relatively simple factors can produce apparent emergent
39 social structure at the population scale, which has widespread implications for
40 understanding eco-evolutionary dynamics.

41

42 INTRODUCTION

43 The social environment can profoundly shape the life histories of animals. Who
44 individuals associate with can determine the information they have access to (Dall
45 *et al.* 2005; Seppanen *et al.* 2007; Valone 2007), affect how well they can exploit
46 resources (Pruitt & Riechert 2011; Aplin *et al.* 2014; Pruitt & Keiser 2014), and
47 impact their ability to successfully reproduce (Formica *et al.* 2011; Formica *et al.*
48 2012; Wey *et al.* 2013; Farine & Sheldon 2015). Social structure can also influence
49 population processes, such as the spread of information within (Aplin *et al.* 2012;
50 Allen *et al.* 2013; Aplin *et al.* 2015a) and between (Farine *et al.* 2015a) species, and
51 the spread of disease among individuals (VanderWaal *et al.* 2013; Adelman *et al.*
52 2015). Finally, individuals can experience selection arising from properties of their
53 social groups (Formica *et al.* 2011; Farine & Sheldon 2015) or their communities
54 (Pruitt & Goodnight 2014). Quantifying the factors that shape individuals' social

55 environments is a key step in identifying the evolutionary drivers of sociality
56 (Goodale *et al.* 2010; Farine, Montiglio & Spiegel 2015), as the mechanisms that
57 determine where, and with whom, individuals live their lives are what selection
58 arising from population processes (e.g. via disease burden or information use) can
59 act upon.

60

61 Social structure (the pattern of connections that emerges from interactions among
62 individuals, often represented using social networks) is generally considered to
63 arise from individuals making decisions about with whom to associate (Hinde 1976;
64 Whitehead 2008; Kurvers *et al.* 2014). The overall structural properties of a
65 population are likely to be emergent outcomes of the combined behaviours and
66 social decisions of all individuals in the population, which for most animals includes
67 heterospecifics. A number of recent studies have highlighted potential multi-level
68 social structure in animal populations (Wittemyer, Douglas-Hamilton & Getz 2005;
69 Archie, Moss & Alberts 2006; Schreier & Swedell 2009), with smaller 'groups' or
70 'communities' of individuals being embedded in larger communities containing
71 multiple groups. The implications of such population structure are profound, for
72 example individuals within a community would experience more similar modulating
73 effects of the social environment on selection relative to individuals from different
74 communities (Montiglio, McGlothlin & Farine 2018). However, we still know
75 relatively little about how multi-level societies emerge.

76

77 Because spatial proximity is a necessary requirement for associations or
78 interactions (i.e. connections) among individuals in many species of animals (Farine
79 2015), patterns of connections among individuals are bound to be shaped by a
80 number of extrinsic factors, such as geometry and structure of habitat features that
81 promote or restrict individual movements (Wiens 1976; O'Brien *et al.* 2006; Cox *et al.*
82 2016; He, Maldonado-Chaparro & Farine 2019). At a local scale, habitat structure,
83 such as the presence of understorey density, can channel individual movements,
84 thus increasing the propensity for contact among individuals. At a broader scale,
85 movement 'highways' can significantly reduce the social distance among individuals

86 despite a large spatial separation, and therefore facilitate the flow of information or
87 disease (Brockmann & Helbing 2013). For example, sleepy lizards (*Tiliqua rugosa*)
88 living in open habitats had fewer contacts with conspecifics than those living in
89 more structured habitats (Leu *et al.* 2016). Whilst habitat features can promote
90 movements, the geometry of habitat (such as the boundary of fragmented habitat)
91 can also introduce barriers that constrain individual movements. Such barriers can
92 result in a structure where the social distance between two individuals (i.e. their
93 degrees of separation in a social network) on either side of this barrier could be
94 much greater than their actual spatial distance. Habitat geometry and features can
95 therefore impose structure in a social network that could easily be interpreted as
96 arising socially. Given that local heterogeneity in gene flow can lead to rapid
97 evolutionary differentiation (Garant *et al.* 2005), integrating knowledge about fine-
98 scale environmental heterogeneity into studies of social structure could
99 fundamentally alter our understanding of adaptation and the ability for animals to
100 respond to selective pressures.

101

102 A major challenge in identifying extrinsic factors that drive population social
103 structure is the need to track the movement of individuals in space, patterns of
104 social connections among the majority of individuals in a population, together with
105 information about the habitat in which they live (Strandburg-Peshkin *et al.* 2017).
106 Recent technological advances have eased the logistical constraints of sampling
107 many individuals moving across large areas (Tomkiewicz *et al.* 2010; Rutz *et al.*
108 2012; Ryder *et al.* 2012; Krause *et al.* 2013; Finn *et al.* 2014; Kays *et al.* 2015; Levin
109 *et al.* 2015; Strandburg-Peshkin *et al.* 2015; Jacoby & Freeman 2016). In particular,
110 passive integrated transponder (PIT) tags are cheap electromagnetic tags that can
111 be fitted to many individuals at once (Bönter & Bridge 2011), thus overcoming the
112 challenges associated with studying entire animal communities. Because PIT tags do
113 not rely on battery power to emit a signal, but instead are detected by affecting the
114 magnetic field in radio frequency identification (RFID) antennas, they provide the
115 capability to track individuals across years and life stages. Further, advances in the
116 analytical tools, such as social network analysis (Farine & Whitehead 2015) and

117 community detection algorithms (Fortunato 2010), are facilitating greater insight
118 into patterns of social structure. These technological advances have underpinned a
119 boom in the study of animals' social networks (Krause *et al.* 2015), and in networks
120 formed by the movement of individuals across space (Finn *et al.* 2014; Jacoby &
121 Freeman 2016). However, much less effort has focused on identifying the key
122 mechanisms that shape overall social structure at the scale of populations.

123

124 In this paper, we investigate whether habitat structure affects patterns of
125 movement, and in turn drive social structure, in a large population comprising 5
126 species of wild songbird. A number of previous studies in our population have
127 investigated how genetic traits (Radersma *et al.* 2017), phenotypic traits such as
128 age, personality, sex, and immigration status (Quinn *et al.* 2011; Aplin *et al.* 2013;
129 Aplin *et al.* 2014; Farine 2014; Aplin *et al.* 2015b; Farine *et al.* 2015b), species
130 identity (Farine, Garroway & Sheldon 2012; Farine *et al.* 2014), and diel cycles
131 (Farine & Lang 2013; Hilleman *et al.* in press) affect individual-level movement and
132 social behaviour, and that who individuals associate with can impact their fitness
133 (Farine & Sheldon 2015). Using data from this population collected over 4
134 consecutive winters, we first quantify overall patterns of movements across the
135 landscape each winter to determine whether individuals move evenly through
136 space, or if there are consistent movement corridors. Based on studies showing that
137 birds are sensitive to open habitat (Quinn *et al.* 2012) (which heighten the risk of
138 predation), we predict that birds should show a preference for moving along
139 corridors comprising denser understory habitat. Second, we use patterns of
140 associations among individuals in each winter to construct social networks, and use
141 these social networks to determine whether social structure is consistent across
142 winters. Given that approximately 50% of individuals in the population each winter
143 are first-year birds, and approximately 50% of first-year birds are immigrants into
144 the population (born outside the study area), we predict that there would be no
145 consistent social structure at local scales. However, because the study area
146 remained identical across winters, we predict that any effects of the habitat on the
147 social structure of the population would be repeated each winter.

148

149 METHODS

150

151 *Study location, study species, and population dynamics*

152 The study was undertaken in Wytham Woods, Oxfordshire, UK (51° 46' N, 01° 20'
153 W), a 385ha area of broadleaf deciduous woodland 'island' surrounded by intensive
154 agriculture. Pairs of birds hold territories during the breeding season (April – June),
155 but form loose fission-fusion groups during the winter, flocking with unrelated
156 individuals that forage for ephemeral food sources. Flocks often contain multiple
157 species (Farine, Garroway & Sheldon 2012), and our study also includes data on the
158 five most common flocking species: great tits (*Parus major*), blue tits (*Cyanistes*
159 *caeruleus*), marsh tits (*Poecile palustris*), coal tits (*Periparus ater*), and nuthatches
160 (*Sitta europaea*). Tits are generally short-lived—great tits have a mean life span of
161 1.9 years. This short generation time results in high annual population turn-over
162 and inter-annual variation in population sizes. Good breeding conditions lead to
163 large population sizes, whereas poor breeding conditions result in fewer juveniles
164 and a much reduced population size.

165

166 *PIT-tagging birds*

167 All birds in the study were caught in either a nest box (as parents and as chicks) or a
168 mist-net (approximately half the population are birds that immigrate). Each bird
169 was fitted with uniquely numbered British Trust for Ornithology metal leg ring, and
170 a uniquely-coded passive integrated transponder (PIT) tag (IB Technologies, UK)
171 that was fully enclosed in a moulded plastic ring fitted to the other leg. Each PIT tag
172 contains a unique code that can be recorded by antennae (see next section), and
173 these were then matched to the bird's ring number. We ceased fitting PIT tags to
174 coal tits from October 2012 as the tags were aggravating pox lesions on birds legs
175 during a naturally-occurring epidemic. For each bird that was caught and tagged, we
176 recorded the age and sex (where possible following Svensson 1992).

177

178 *Data collection*

179 We placed 65 automated feeding stations in a evenly-spaced grid covering the
180 entirety of Wytham Woods and small isolated patches of woodland nearby.
181 Commercial bird feeders (Jacobi Jayne, UK) were fitted with a radio frequency
182 identification (RFID) antenna on each of the lower two access holes and other access
183 holes were blocked. The antennae recorded the unique PIT tag code, time and date
184 for each visit by a marked bird. For the duration of the study, the feeding stations
185 were scheduled to open and begin logging at 6am on Saturday mornings, and shut
186 after dusk on Sunday evening. Feeders were in place December to February in the
187 winter 2011-12 (13 weeks), from December to early March of winters 2012-13 and
188 2013-14 (14 weeks each), and for January and February in the winter of 2014-15 (8
189 weeks). This data collection resulted in 49 unique weekends and 98 complete data
190 logging days over the 4 winters. In later winters, 6 feeders covering two external
191 sites were replaced for a separate experiment, and thus the data were not included
192 in these analyses.

193

194 *Constructing movement networks*

195 From the logging data, we recorded every case of movement by a bird from one
196 feeding station to another within the same day (a total of 83071 movements over 4
197 winters), and used these to create movement networks that quantify the
198 connectedness between each pair of feeding stations in the study. We used daily
199 sequential detections to maximize our chances of correctly inferring direct
200 movement pathway (e.g. moving between locations A and D via locations B and C)
201 and minimizing our chances of incorrectly inferring movement pathways (e.g.
202 estimating only a direct movement between A and D). Because the number of
203 movements are inherently linked to the number of individuals present at a specific
204 pair of feeders, we also created a network describing the rate of movement between
205 feeders, where the rate was defined as the probability that an individual at one focal
206 feeder would be observed moving to the other focal feeder within a day.

207

208 *Understory habitat density*

209 We used data from Kirby *et al.* (Kirby *et al.* 2014) to quantify the habitat structure
210 between each feeding site. In that study, the authors recorded, among other
211 measures, the shrub cover density (0.5m to 2.5m above ground) along the diagonal
212 of 164 different 10m x 10m quadrats equally spaced throughout Wytham Woods.
213 Here we use data from the 2012 census, which falls roughly in the middle of our
214 study period, but note that there were no major changes to the habitat across years.
215 To extrapolate from the 164 sites, we generated a surface plot where we
216 extrapolated the data to a 10 x 10m grid of points using the *vgm* function in the R
217 package *gstat* (Gräler, Pebesma & Heuvelink 2016) with a spherical model, omitting
218 fitting the nugget component. The resulting figure accurately captures variation in
219 habitat density based on our knowledge of the study site. To calculate habitat
220 density between each pair of feeding sites, we calculated the mean habitat density
221 (as estimated by the surface) along a 20m-wide transect connecting the two sites.

222

223 *Inferring flocks and flock membership*

224 The data logged from the PIT tag detections produces bursts of detections in the
225 temporal data stream. These vary in length depending on the size of the flocks
226 present (which increases during the course of the day, Farine & Lang 2013;
227 Hilleman *et al.* in press). We used a recently-developed statistical tool for analyzing
228 such data involving Gaussian Mixture Models (Psorakis *et al.* 2012) to extract the
229 start and end times for each distinct flock. This machine-learning method
230 statistically fits Gaussian curves of varying sizes to each burst in the data and
231 allocates each record to the distribution, or ‘gathering event’, into which it falls. We
232 have shown that the Gaussian Mixture Model approach provides a more robust
233 estimation of the social network structure than alternative methods (Psorakis *et al.*
234 2015).

235

236 *Constructing social networks*

237 We defined edges in the social network using the simple ratio index (Hoppitt &
238 Farine 2018): $E_{AB} = \frac{x}{x+y_{AB}+y_A+y_B}$, where E_{AB} is the edge weight between individuals

239 A and B , x is the number of times they were detected in the same flock, y_{AB} is the
240 number of occasions they were both detected at the same time but not in the same
241 flock, y_A is the number of detections of A where B was not seen, and y_B is the
242 number of detections of B where A was not seen. The networks for each winter
243 were constructed using R package *asnipe* (Farine 2013).

244

245 *Detecting consistent social structure across winters*

246 For each winter's social network, inferred structural communities in each social
247 network using the edge betweenness community detection algorithm in the R
248 package *igraph* (Csardi & Nepusz 2006). We specified the algorithm to detect $k = 2$
249 to 65 communities, and recorded the identities of individuals in each community. If
250 communities are structured exclusively by extrinsic factors, we expected a drop in
251 the stability of co-membership by individuals as we created finer grained
252 communities. For example, if a population is spread across three isolated patches of
253 woodland, and birds do not move between woodlands, then we expect that birds
254 will always occur within the same three communities (one for each woodland patch)
255 each winter. By contrast, if communities are structured socially, then we expected
256 smaller communities (local cliques) to be more stable, but little stability in global
257 structure. For example, for a territorial pair-living species living in a lattice-like
258 uniform environment, an algorithm will be able to isolate each pair when identifying
259 $k=N/2$ communities, whereas the communities detected for smaller k values will be
260 essentially random.

261

262 *Linking movements to community structure*

263 To test for a link between community structure and movement networks, we
264 allocated individuals to their most common feeder, and for each of the feeding
265 stations, selected the community of which the majority of individuals present were
266 members. This enabled us to create a community label for each feeding station (and
267 for each value of k), and link these to the network formed by the movement of
268 individuals (Figure 1). To test whether the movement network shaped the
269 community structure in the network for a given value of k , we quantified the

270 assortativity coefficient of the network using communities as discrete trait values
271 (Farine 2014; Shizuka & Farine 2016). Assortativity is the measure of how well
272 connected alike nodes are compared to how well connected dislike nodes are,
273 ranging from 1 (all edges connect nodes with the same traits) to -1 (all edges
274 connect nodes with different traits).

275

276

277 RESULTS

278

279 *Movement networks*

280 We first quantified the daily movement rates between different feeding stations. Our
281 population consisted of a total of 6299 unique PIT-tagged individuals, of which 2230
282 were great tits, 3304 were blue tits, 237 were marsh tits, 169 were coal tits, and 78
283 were nuthatches. We detected 83701 movements, detections at two feeders on the
284 same day, across all winters (Figure 1). Overall, birds moved very little—our
285 analysis was based on 9612 ‘bird winters’, meaning that each bird moved (on
286 average) fewer than 10 times over a whole winter. We found that most movements
287 occurred between feeding stations where more birds were present.

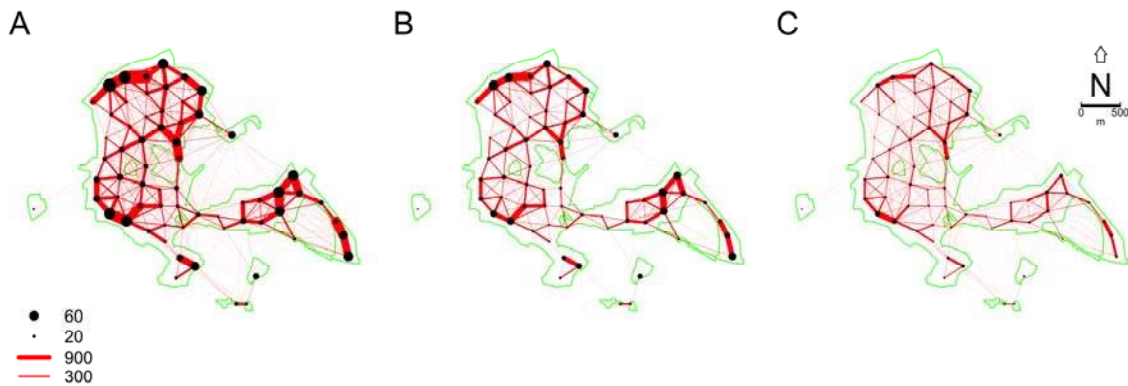
288

289 Not all birds followed the same pattern. Birds in their first winter moved more often
290 than older birds: first-year birds accounted for 61% of all movements, despite
291 making up only made up 38% of the population on average. Of the juveniles that
292 moved, each made on average 20.8 moves, which was significantly more than the
293 average 12.9 moves made by adults detected moving at least once (GLM:
294 $\beta \pm SE = 0.477 \pm 0.007$, $z = 67.08$, $P < 0.001$, family=Poisson). Further, their movement
295 networks included more long-distance movements than those of adults, resulting in
296 a significantly higher average movement distance ($\beta \pm SE = 29.5 \pm 1.35$,
297 $t = 21.77$, $P < 0.001$, see also Figures 1 and S1).

298

299 We also found species-level differences. Great and blue tits, which comprise the
300 large majority of individuals in the population, exhibited similar movement patterns

301 (difference=0.5m, $P=0.520$, see Figures S2-3). By contrast, marsh tit movements
302 were typically much more localized (difference blue tit – marsh tit: 48.8m, $P<0.001$;
303 difference great tit – marsh tit: 29.3m, $P<0.001$; see Figures S2-3). Overall, age had
304 the greatest effect on the distribution of movements, with some differences among
305 species.
306



307
308 **Figure 1:** Total movements of (A) all birds, (B) adults, and (C) juveniles (first
309 winters) from all species over 4 winters of data. The thickness of each line
310 represents the number of observations of a bird detected at two feeding stations
311 (black points) in the same day. The size of the points represents the average number
312 of individuals observed at each feeding station. The green outline represents the
313 outline of the wooded areas, which are surrounded by open agricultural land. Note
314 that there is very little movement of birds between Wytham Woods and the four
315 external woodlots, highlighting how closed this population is during the winter. See
316 Figure S1 for statistical evidence that juveniles make significantly more long-
317 distance movements.

318

319 *Do understory density or habitat geometry predict movement propensity?*

320 We compared the patterns of movement observed across winters, and related these
321 to spatial distance and habitat features. We first re-defined edges in the movement
322 network as the probability that an individual detected at either site moves between
323 them on a given day. Edge weights ranged from 0 representing no movement
324 between adjacent sites to 0.83 representing that each individual detected had an

325 83% chance of moving between the two sites on a given day (see Figure S4).
326 Weighted multiple regression quadratic assignment procedure (MRQAP)(Dekker,
327 Krackhardt & Snijders 2007) revealed that the movements by birds between feeding
328 stations were significantly more similar from winter-to-winter than expected by
329 chance, even when accounting for distance through the forest and habitat structure
330 (see Table 1, Figure 2). In all winters, birds were significantly more likely to move
331 between 'close' feeding stations than distant ones. However, contrary to our
332 predictions, we found no effect of understory habitat density on the propensity for
333 birds to move between feeders.

334

335 **Table 1:** Results of multiple regression quadratic assignment procedure used to test
336 whether previously observed patterns of movement (probability of moving between
337 sites per capita), distance between sites (through the forest), and habitat density
338 (percentage cover) between sites explain the observed patterns of movement. Bold
339 values represent significant coefficients, * represents significance at $P < 0.01$, **
340 represents significance at $P < 0.001$, based on a two-tailed test. All variables are
341 scaled to 0 mean and unit variance to enable comparison between effect sizes.

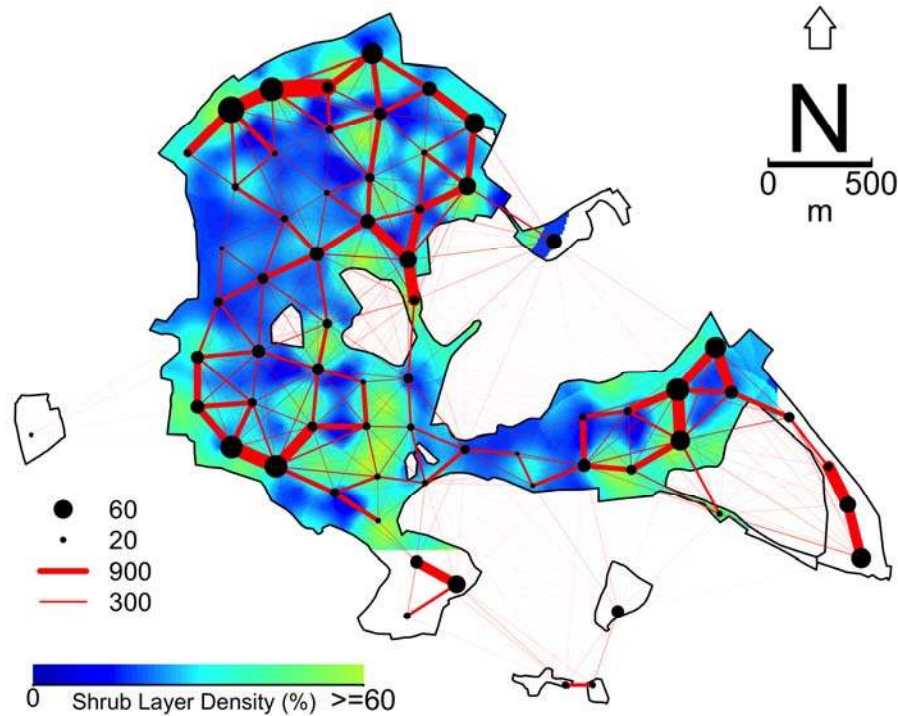
342

Winter	Previous Winter	Forest Distance	Habitat Density
2013	0.903**	-0.028*	-0.010
2014	0.877**	-0.060**	-0.010
2015	0.787**	-0.091**	-0.019

343

344

345



346

347 **Figure 2:** Total movement of all birds (from Figure 1A) overlaid on the understory
348 habitat density (0.5m to 2.5m above ground) calculated at 164 equally-spaced
349 quadrats (see Methods). Areas within the polygon with a white background have no
350 habitat data available, and any links that included such areas were excluded from
351 the analyses. Areas outside of the black polygons are open agricultural land. Blue
352 areas have a largely open understory, whereas green areas have very thick
353 understory. The vast majority of Wytham Woods is closed canopy.

354

355

356 Because for many pairs of feeding stations the geometric distance and forest
357 distance are very similar (see Figure 2), we used this information to also test
358 whether birds were less likely to move between feeding sites that were separated
359 by non-forest. We did this by calculating the difference between forest distance and
360 Euclidian distance. We found that birds moved less between feeders with a larger
361 difference in distance (i.e. the path through the forest was much longer than the
362 straight-line path), suggesting that birds are avoiding crossing open habitats (Table
363 2). However, the propensity to move between feeders observed in previous winters

364 was consistently the strongest predictor of future movements. The coefficient values
365 for movements predicted by the previous winter were typically an order of
366 magnitude larger than those of other predictor variables, suggesting that additional
367 undetected factors—potentially social—are driving patterns of movements by birds
368 across this woodland.

369

370 **Table 2:** Results of multiple regression quadratic assignment procedure used to test
371 whether birds moved less between feeding sites separated by open space. For each
372 pair of sites, we calculated the difference between the forest distance and the
373 Euclidian distance. Bold values represent significant coefficients, * represents
374 significance at $P < 0.01$, ** represents significance at $P < 0.001$, based on a two-tailed
375 test. All variables are scaled to 0 mean and unit variance to enable comparison
376 between effect sizes.

377

Winter	Previous Winter	Relative Distance
2013	0.919**	-0.001
2014	0.906**	-0.019*
2015	0.828**	-0.029*

378

379

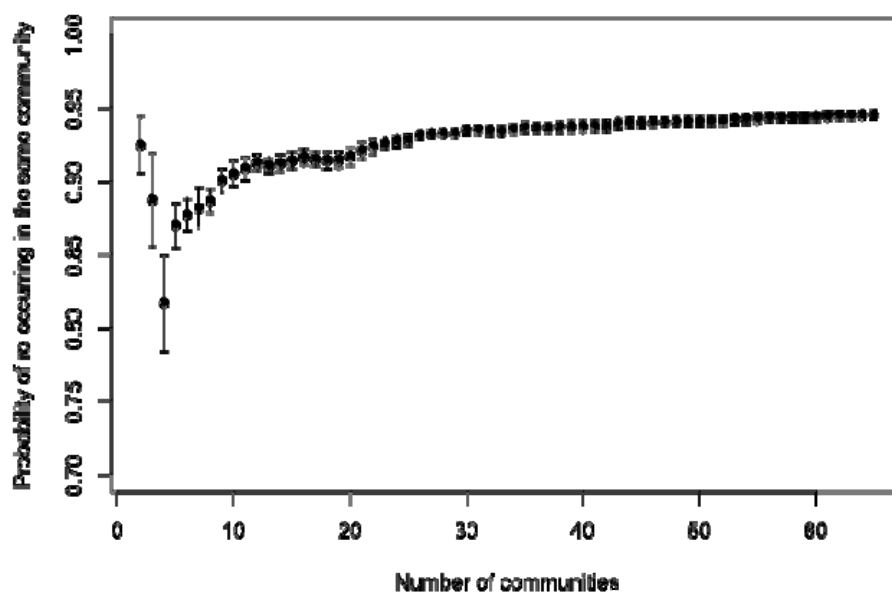
380 *Does the population have consistent social structure?*

381 Population-level social structure can have significant implications for population
382 processes. For example, high levels of clustering can reduce the spread of disease
383 within populations (Eames 2008). Thus far, we have shown that habitat geometry,
384 as well as additional unknown factors, contribute to consistent patterns of animal
385 movements. We next investigated how these patterns contribute to the emergent
386 structure of the mixed-species population.

387

388 We uncovered two scales that maximized the propensity for pairs of individuals
389 observed in the same community in winter t to be observed in the same community
390 in winter $t + 1$. When social networks were partitioned into 2 or 3 communities
391 (Figure 3), individuals observed in successive winters were seen in the same

392 community each winter approximately 90% of the time. These macro communities
393 largely reflect the geometry of the study site, with two core habitats (north-west and
394 the east), and a smaller patch of forest to the south, that is only attached by a narrow
395 neck of vegetation, representing a third community (Figure 4). Specifying the
396 algorithm to detect 4 communities significantly decreased the probability of
397 individuals being re-observed in the same community (no overlap in the ranges in
398 Figure 3), suggesting that there is no stable 4th community. Partitioning the network
399 further by specifying the algorithm to detect more than 4 communities then
400 increased the probability that two individuals observed in successive winters were
401 observed in the same community. Thus, the patterns of social organization at both
402 the population scale (2-3 communities) and at a local scale (>30 communities) were
403 the most stable winter-to-winter. This result suggest that multiple levels of
404 community structure exist in this population, with micro communities nested within
405 macro communities.
406



407
408 **Figure 3:** The probability that two birds observed in the same community in one
409 winter remain in the same community in the following winter, given that both are
410 observed. Points represent the mean, and lines represent the range from the 3 pairs

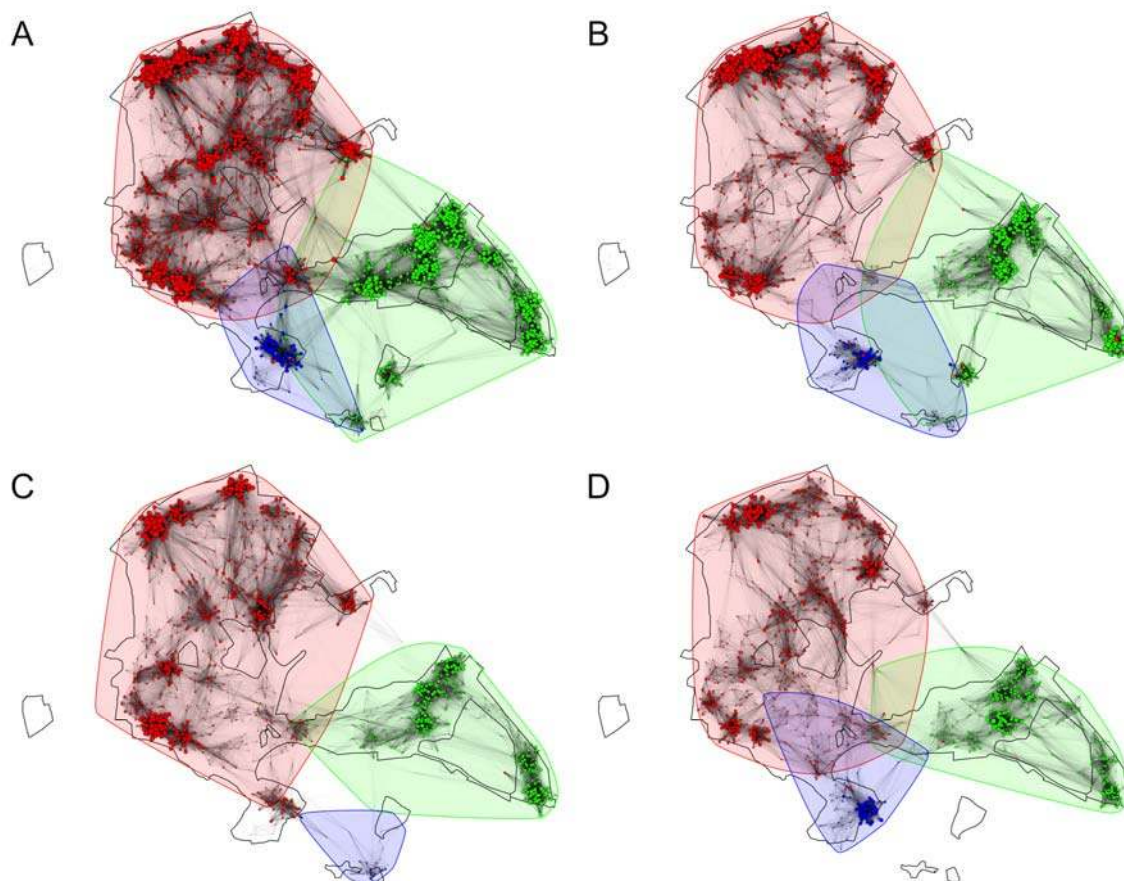
411 of winters. The probability is calculated with the social network partitioned into the
412 same specified number of communities (2 to 65) in all winters.

413

414 Partitioning the network into a larger number of communities did not result in one
415 community per feeding station, instead several large communities were maintained
416 and many small, spatially-overlapping, ones were created (Figure 5). Finally, we
417 found no evidence that the composition of species in communities changed based on
418 how many communities were created (Figure S5). Thus, the partitioning of the
419 network into more (micro) communities did not segregate individuals into species-
420 specific clusters, and so stable community structure at a local scale was not
421 explained by simple species-level processes. We note here that there is extensive
422 evidence of social processes driving community structure at these local scales
423 (Krause *et al.* 2015). Such studies of animal social networks are increasingly
424 accounting for effects such as individual home-ranges using null model (Farine
425 2017). However, fewer studies have explored links between home ranges and
426 community structure (but see Shizuka *et al.* 2014). Our study highlights the
427 importance of exploring this link.

428

429

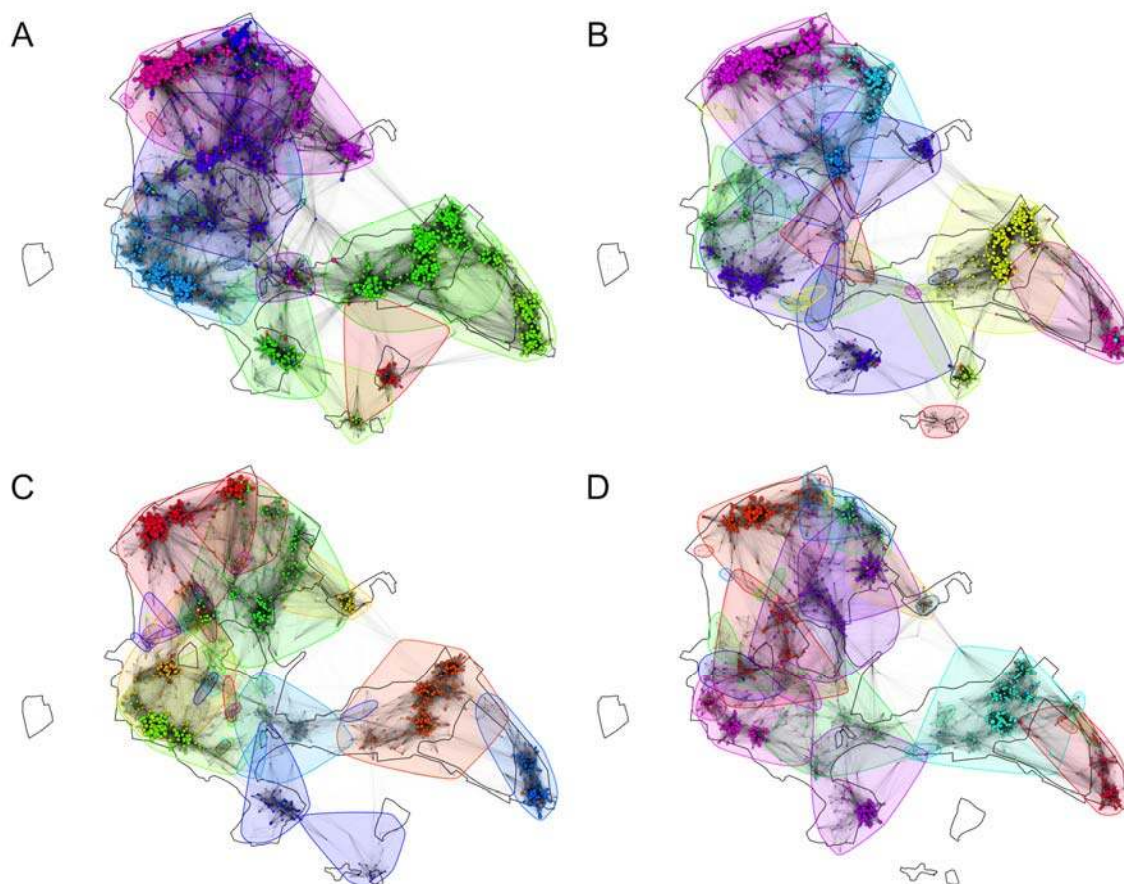


430

431 **Figure 4:** The social network for each winter of the study when partitioned into 3
432 communities. Each point represents one individual (N=3019, 2598, 2294, 1701
433 respectively), and the colours represents the community each node is assigned to.
434 The size of each point represents its weighted degree (larger points have more
435 and/or stronger connections to other individuals). Points are drawn at the average
436 location that the individual was observed, with a small amount of jittering added to
437 reduce the overlap between individuals observed in the same location. Community
438 memberships were inferred using the edge betweenness algorithm applied to each
439 winter independently with the number of communities set to 3.

440

441



442

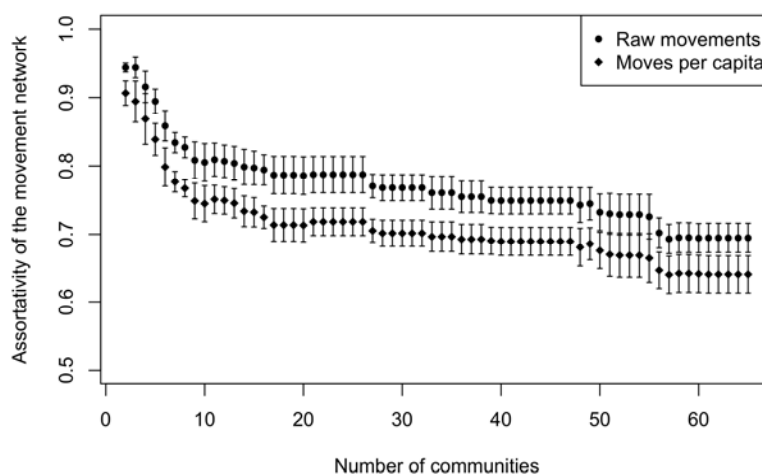
443 **Figure 5:** The social network for each winter of the study partitioned into 65
444 communities. Each point represents one individual, and colours represents the
445 community each node is assigned into (per Figure 4). The size of each point
446 represents its weighted degree (larger points have more and/or stronger
447 connections to other individuals). Points are drawn at the average location that the
448 individual was observed, with a small amount of jittering added to reduce the
449 overlap between individuals observed in the same location. Community
450 memberships were inferred using the edge betweenness algorithm applied to each
451 winter independently with the number of communities set to 65.

452

453 *Linking movement patterns to community structure*

454 We investigated whether the regular movements of individuals between particular
455 feeding stations were responsible for global community structure. Individuals living
456 at two locations with frequent movements of individuals between them will be more

457 likely to be connected in the social network, and therefore more likely to be in the
458 same community and share similar social environments. We found that when we
459 partitioned the network into few communities, almost all of the movements were
460 between feeders in the same community (Figure 6). This supports our hypothesis
461 that extrinsic large-scale habitat features shape the broad patterning of the
462 community (i.e. the presence of 2-3 distinct clusters of individuals, see Figure 4) via
463 individual movement (i.e. by disconnecting feeders not directly connected by
464 forest). However, at more local scale, we found that the assortativity coefficient
465 decreased (Figure 6). Thus, as the social network is partitioned into more
466 communities, movements between sites explained less of the community structure,
467 despite the fact that individuals become more likely to re-occur in the same
468 communities across winters (see Figure 3).
469



470
471 **Figure 6:** The correlation of movements between feeding stations and community
472 structure decreases with increasing numbers of communities. Each feeding station
473 is allocated to the community in which the majority of individuals are members and
474 used as a trait value to calculate assortment using the raw movement networks
475 (Figure 1A) and the per capita movement network (Figure S2A). High values
476 represent stronger connections between feeding stations in the same community.
477 Points represent the mean, and lines represent the range across the 4 winters.
478

479

480 DISCUSSION

481

482 Our study revealed two levels of social structure, maintained across winters, in a
483 large population of wild birds containing thousands of individuals of five species. At
484 a broad scale, the social network contained two or three communities that were
485 predicted by the regular movement paths used by birds. The movement of birds
486 through the woodland were repeatable each winter, but the similarity in
487 movements across winters was only partly explained by the geometry of the study
488 area. Our analyses suggest, in fact, that some other processes, potentially social
489 processes such as the persistence of local traditions (Mueller *et al.* 2013; Aplin *et al.*
490 2015a; Jesmer *et al.* 2018), may also be involved. If that is the case, then broad-scale
491 social structure could be, in part, the result of a socially-transmitted inter-
492 generational effect. At a more local scale, we found highly stable social structure,
493 with micro communities of individuals comprising all five species re-associating
494 each winter to maintain consistent communities. Our study thus highlights how
495 factors operating at different scales can shape the social ecology in a wild bird
496 population.

497

498 The link between extrinsic habitat factors and community structure in animal
499 populations has been investigated before. For example, community and sub-
500 community structure in Galapagos sealions *Zalophus wollebaeki* are largely driven
501 by the structure of male territories (Wolf *et al.* 2007). However, territorial
502 behaviours are unlikely to play a major role in structuring the winter population of
503 birds in Wytham Woods because the majority of individuals were great tits and blue
504 tits, which are both non-territorial during the winter, although there is some
505 evidence of linkages between summer and winter social structure (Farine & Sheldon
506 2015; Firth & Sheldon 2016). What is more likely is that individuals have relatively
507 small homeranges that overlap with many other individuals, and that these are not
508 uniformly distributed across the habitat. In non-territorial wintering golden-
509 crowned sparrows (*Zonotrichia atricapilla*), social network communities were also

510 found to be consistent across winters at very small spatial scales (Shizuka *et al.*
511 2014). The surprising aspect from that study was that golden-crowned sparrows
512 exhibit such stability despite having migrated a long distance from their breeding
513 areas. This aspect is partly replicated in our tit population as approximately 50% of
514 the individuals in any given winter are first-year birds and most birds leave the
515 study area during the summer (Matechou *et al.* 2015). The phenomenon observed in
516 both tits and sparrows suggests that winter sociality is likely to play an important
517 role that goes beyond simple group size effects, and thus could have carry-over
518 effects into the territory structure (Firth & Sheldon 2016) and breeding
519 performance in the following spring (e.g. Farine & Sheldon 2015).

520

521 The unexplained consistent structural patterns in both our study and in the golden-
522 crowned sparrow study (Shizuka *et al.* 2014) could represent local traditions that
523 are passed on through social learning. In this scenario, juvenile and immigrant birds
524 copy the movement behaviours of older, resident, birds. This could explain why
525 patterns remained consistent over 4 winters, well beyond the generation time of tits
526 (typically <2 years). Such findings would not be unprecedented. For example, one
527 study in whooping cranes found that juveniles socially learn the migration routes
528 from older individuals (Mueller *et al.* 2013). A previous study in our population
529 showed that social learning can easily lead to persistent local cultures, and that the
530 presence of experienced individuals facilitates the rapid adoption of new behaviours
531 by the next generation (Aplin *et al.* 2015a). The role of such traditions in shaping
532 animal movements and subsequent community structure warrant much further
533 investigation.

534

535 Another potentially important feature that we extracted in our study was
536 differential movement patterns between classes of individuals. We found that
537 juveniles typically made more long-distance movements than adults (Figures 1 &
538 S1). This pattern, which is likely to be linked to juvenile dispersal behaviour, has a
539 number of implications for social processes. To overcome strong seasonal changes
540 in the environment, juvenile tits rely on learning from adults in their local

541 environment (Slagsvold & Wiebe 2007). These juveniles therefore play an important
542 role in shaping the overall structure of the social network, and could play a major
543 role as transmission vectors. By coming into contact with a greater number of
544 individuals, they could facilitate the spread diseases or pathogens across
545 communities (as suggested in humans, Del Valle *et al.* 2007), or even introduce
546 novel behaviours into populations.

547

548 By investigating the stability of community structure at different scales, we found
549 evidence that tits in Wytham Woods live in a multi-level community structure.
550 Multi-level community structure occurs when animals form small groups, or
551 clusters, of individuals with whom they associate most strongly, and larger groups
552 in which these clusters are embedded. There is increasing interest in multi-level
553 community structure as it can have major implications for how social processes
554 occur (Bell & Ford 1986; de Silva & Wittemyer 2012; Grueter *et al.* 2012; Whitehead
555 *et al.* 2012). Multiple factors can shape the movement (or not) of individuals among
556 social units. These factors can be broadly split into two categories: social factors
557 [such as relatedness (Archie, Moss & Alberts 2006; Croft *et al.* 2012; Godfrey *et al.*
558 2014), cultural similarity (Cantor *et al.* 2015), or species identity (Bell & Ford
559 1986)] and habitat factors [features of the environment that modulate where in the
560 environment individuals are found (Croft *et al.* 2003), how they move, and thus
561 whom they encounter (He, Maldonado-Chaparro & Farine 2019)]. Although recent
562 studies have begun to tease apart social versus habitat factors that determine the
563 patterns of contact among individuals with different phenotypic characteristics
564 (Farine *et al.* 2015b), little is known what drives the emergence of global
565 population-level structure. Cantor *et al.* (2015) used simulations to suggest that
566 multi-level communities can emerge when individual segregate into clans formed
567 around similar cultural behaviours. In our study, we found evidence that both
568 environmental and social factors contribute to producing a hierarchical community
569 structure. The general geometry of Wytham Woods is likely to have introduced a
570 repeatable set of large-scale communities (Figure 3). Thus, the shape of the forest is
571 plays a major role in how the population is broadly structured (Figure 4). By

572 studying birds that form mixed-species communities, our study highlights that
573 hierarchical community structure can be the by-product of external processes.
574 Further, the majority of individuals in our study were great tits and blue tits. These
575 birds moved in similar ways, and we could not decompose our networks into groups
576 of one versus the other. Thus, while social mechanisms, such as social preference
577 (Farine *et al.* 2015b) and phenotypic drivers (Croft *et al.* 2003; Croft *et al.* 2009;
578 Aplin *et al.* 2013), can play a large role in determining who individuals affiliate with,
579 the woodland geometry and the resulting behaviour of all individuals combined can
580 generate large-scale static population structures.

581

582 The presence of multi-level community structure can have implications for
583 evolutionary dynamics of populations. First, restricted movement can reduce gene
584 flow and lead to divergence in the evolutionary trajectories of sub-parts of each
585 population. Garant *et al.* (2005) demonstrated that differential dispersal reinforces
586 local variation in selection for nestling body mass. In their study, they found that
587 trends in phenotypic variance for body mass in nestlings were very different in the
588 eastern sectors of Wytham Woods and the northern sectors. These two areas
589 represent the two largest population-level communities we found in our study.
590 Second, individuals in the same community will have more similar social
591 environments than individuals occurring in different communities. Thus, any social
592 effects arising via the social environment, such as indirect genetic effects (Moore,
593 Brodie & Wolf 1997), could accelerate patterns of divergence within single
594 populations. Finally, the social environment itself can act as an agent of selection
595 (Wolf & Moore 2010; Farine, Montiglio & Spiegel 2015), and therefore processes
596 that shape social structure are likely to impact the overall strength and direction of
597 selection experienced by populations (Montiglio, McGlothlin & Farine 2018).

598

599 One potential limitation of our study is that we employed bird feeders to detect the
600 presence of birds. This approach is what enabled us to collect information on so
601 many individuals simultaneously, but in doing so, we could have also influenced the
602 behaviour of birds. There are three reasons why we do not think that the presence

603 of bird feeders impacted our results. First, the feeders were all identical and open at
604 the same time, meaning that there would be little reason for a bird to choose to
605 relocate to another feeder (and as noted, most birds did not move, and birds moved
606 on average only once every two study days). Second, feeders were evenly spaced out
607 on a grid, meaning that, in the absence of habitat or behavioural heterogeneity,
608 movements between any pair of adjacent feeders should be equally likely. Finally,
609 feeders were open only two days per week, and remained shut for 5 consecutive
610 days. This means that birds would have had to maintain their natural foraging
611 behaviour rather than adapting to a new regime (noting that tits can lose up to 10%
612 of their body weight in a single winters' night, Owen 1954).

613

614 Together the findings from our study highlight several ways in which stable social
615 structure can be maintained in populations. The combination of strong clustering
616 together with some random movements in networks can facilitate the spread of
617 disease or information through the network (Eames 2008). This prediction is
618 supported by the rapid spread and establishment of novel traditions (Aplin *et al.*
619 2015a) in this population. At the same time, consistent population social structure
620 can lead to phenotypic and genotypic divergence (Garant *et al.* 2005), with potential
621 implications for how animals can adapt to changing environmental conditions.
622 Integrating information about animal social structure with data on both short-term
623 and long-term selective events could yield novel insights into the evolution of social
624 behaviour. As our study highlights, determining the capacity for populations to
625 respond to selective pressures will require an understanding of a range of different
626 drivers that could shape their social structure.

627

628

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630

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634

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