

1 **Movement of feeder-using songbirds: the influence**
2 **of urban features**

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10 Private gardens provide vital opportunities for people to interact with nature. The most
11 popular form of interaction is through garden bird feeding. Understanding how landscape
12 features and seasons determine patterns of movement of feeder-using songbirds is key to
13 maximising the well-being benefits they provide. To determine these patterns we established
14 three networks of automated data loggers along a gradient of greenspace fragmentation. Over
15 a 12-month period we tracked 452 tagged blue tits *Cyanistes caeruleus* and great tits *Parus*
16 *major* moving between feeder pairs 9,848 times, to address two questions: (i) Do urban
17 features within different forms, and season, influence structural (presence-absence of
18 connections between feeders by birds) and functional (frequency of these connections)
19 connectivity? (ii) Are there general patterns of structural and functional connectivity across
20 forms? Vegetation cover increased connectivity in all three networks, whereas the presence
21 of road gaps negatively affected functional but not structural connectivity. Across networks
22 structural connectivity was lowest in the summer when birds maintain breeding territories,
23 however patterns of functional connectivity appeared to vary with habitat fragmentation.
24 Using empirical data this study shows how key urban features and season influence
25 movement of feeder-using songbirds, and we provide evidence that this is related to
26 greenspace fragmentation.

27

28 **Introduction**

29 As urbanization increases globally, greenspaces in cities and towns are becoming of greater
30 importance for the provision of ecosystem services^{1,2}. Domestic gardens are a major
31 component of these green spaces³⁻⁵. They constitute easily accessible and immediate
32 locations where people can interact with nature, enabling access to the broad range of health
33 and well-being benefits that nature provides^{6,7}. Birds are a key component of garden wildlife⁸
34 and for many people their interactions with wild birds may form the main daily wildlife
35 interaction⁹. Watching birds and listening to their song have been shown positively to
36 influence human psychological well-being¹⁰⁻¹⁵. Given these benefits, it is perhaps
37 unsurprising that the provision of supplementary food is the most popular form of wildlife
38 gardening (reviewed by¹¹).

39

40 Domestic green spaces are often characterised by numerous small and densely packed
41 gardens that are utilised and managed by an equivalent number of households^{4,5}. This results
42 in individual birds typically moving between multiple gardens to forage and visit feeders,
43 where they will be seen by, and so provide benefits to, multiple people. The ability of birds to
44 move between gardens thus increases the potential benefits that any individual bird can
45 provide, with actual movement being determined by the structures of the gardens themselves,
46 including their geographical location in relation to one another, the habitat for birds within
47 the gardens, and the surrounding urban features.

48

49 Previous studies in urban areas have estimated connectivity for birds within and between
50 public green spaces¹⁶⁻²⁰. These studies suggest that vegetation between green spaces
51 preserves connectivity, while multiple barriers, such as roads and rivers, cumulatively
52 decrease landscape permeability. However, despite the clear importance of domestic gardens

53 in generating connectivity in their own right and for facilitating connectivity between larger
54 green spaces^{1,4}, fragmented land ownership and management mean that their role in shaping
55 connectivity is largely unexplored empirically^{21,22}. Indeed, how structural patterns of key
56 features that distinguish different urban forms affect the flow of birds around the landscape is
57 currently unknown. In the wider landscape there is seasonal variation in connectivity that is
58 related to habitat quality and quantity^{23,24}, therefore we might expect this also to occur across
59 domestic gardens and to vary across different urban forms. For example, birds defend smaller
60 home ranges when breeding in summer than when foraging more widely in winter.

61

62 Birds that utilize feeders provide an ideal group for exploring the relationships among urban
63 form, connectivity and cultural service delivery. Radio Frequency Identification (RFID)
64 technology provides a means of doing so. This can produce a continuous record of the time
65 and date of when an individual bird carrying a Passive Integrated Transponder (PIT) tag
66 visits a resource patch. Networks of RFID readers can thus be used to record individual
67 movement in time and space as birds visit different feeders. This allows the influence of
68 different urban features on structural and functional connectivity to be determined, structural
69 connectivity here being the presence-absence of connections made by birds moving between
70 feeders and functional connectivity the frequency of those connections. We set up three
71 networks of custom-designed low-powered RFID equipped bird feeders within domestic
72 gardens in the Cranfield triangle in Southern England, UK, with each network within a
73 different urban form that is common in Europe; these had, respectively, low, medium or high
74 green space fragmentation. We used hyperspectral and LiDAR data to characterise the
75 landscape structure through which tagged birds were likely to move between feeder pairs
76 within each network. There were 17 feeders per network, and these were operated
77 continuously over a 12-month period to explore two general questions:

78 (i) How do different features within each urban form, and season, influence general
79 patterns of structural and functional connectivity for birds?

80 (ii) Are there general patterns of structural and functional connectivity across these
81 forms?

82

83 **Results**

84 In total we tagged 452 individuals of two common species of feeder-using birds (blue tit
85 *Cyanistes caeruleus* and great tit *Parus major*) between June 2013 and August 2014 (see
86 Supplementary Table S1 and Fig. S1). We divided the year into four equal seasons: summer,
87 autumn, winter, spring. We then considered that a tagged bird visiting first one and then a
88 different feeder within each network and within each season made a connection, with data
89 collection starting on the 1st September 2013. Across the three networks, 51% (± 2 SD) of
90 tagged individuals made one or more connections between feeders ($n = 9,848$; Fig. 1).

91 Eighty-eight percent of connections occurred within two days ($n = 8,652$; See Supplementary
92 Fig. S2). We discarded from the analysis connections that took longer to make because we
93 considered there was a high probability that birds travelled to the second feeder via a non-
94 direct route. Using hyperspectral and LiDAR data we categorised the habitat in an ellipsoid
95 between feeder pairs to establish variation in urban form across the three networks of RFID
96 readers (Table 1). For each feeder pair we calculated the distance between feeders, the
97 shortest distance between feeders and a bird catching site, and finally within each ellipsoid
98 we calculated vegetation cover and the number of road gaps (Table 1; Fig. 1).

99

100 URBAN FEATURES WITHIN FORMS AND SEASON

101 The first stage of our analysis tested for the effect of different urban features and season on
102 structural connectivity (the presence or absence of a connection between feeder pairs in any

103 season) and functional connectivity (the frequency of these movements between feeder pairs
104 in any season) within each of the networks.

105

106 For structural connectivity, in each network the likelihood of a connection being present
107 between feeders (i.e. connectivity) increased with the percentage vegetation cover (Table 2a;
108 Fig. 2a), while the presence of one or more road gaps did not affect movement (Table 2a; Fig.
109 2b). In the networks of low and medium fragmentation, connectivity decreased with distance
110 between feeders. In the network of low fragmentation, connectivity was lowest in summer
111 and highest in the autumn and winter (Table 2a; Fig. 2c). In the network of medium
112 fragmentation, connectivity was higher across the year relative to summer (Table 2a; Fig. 2c).
113 In the network of high fragmentation, connectivity was highest in spring relative to the other
114 seasons (Table 2; Fig. 2c). Great tits moved between fewer feeder pairs than blue tits in the
115 medium and high fragmentation networks, while there was decreased movement with
116 increasing distance from the ringing site in the network of medium fragmentation (Table 2).

117

118 For functional connectivity, vegetation cover increased the frequency of movement across all
119 networks (Table 2b). In the network of low and medium fragmentation the frequency of
120 connections decreased with increasing distance between feeders, while decreasing in all
121 networks in the presence of road gaps (Table 2b; Fig. 2d). There was seasonal variation in
122 connectivity relative to summer that varied across networks; in the network of low
123 fragmentation connectivity was higher across the year relative to summer, while in the
124 network of medium fragmentation connectivity was lowest in autumn and winter (Table 2b;
125 Fig. 2e). In the network of low fragmentation connectivity was lowest in autumn and highest
126 in spring (Table 2b; Fig. 2e). Movement decreased with distance to ringing site in the
127 network of medium fragmentation (Table 2b).

128

129 PATTERNS OF MOVEMENT ACROSS URBAN FORMS

130 The second stage of our analysis explored general patterns of structural and functional
131 connectivity across the three networks. We found that structural connectivity decreased
132 significantly across the three networks with increasing green space fragmentation (low
133 fragmentation, 77%; medium fragmentation, 68%; high fragmentation, 55% of feeder pairs
134 had connections; ANOVA of quasi-binomial model, network $X^2 = 20.4$, $df = 2$, $P = <0.0001$;
135 $R^2 = 0.15$; Table 3a; Fig. 3a). Functional connectivity was greatest in the network of low
136 fragmentation, whilst there was no difference between the networks of medium and high
137 fragmentation (ANOVA of quasi-Poisson model, network $X^2 = 1708.0$, $df = 2$, $P = <0.0001$;
138 $R^2 = 0.39$; Table 3b; Fig. 3b). In both models connectivity decreased with distance between
139 feeder pairs (Table 3).

140

141 **Discussion**

142 Understanding how the spatial and temporal heterogeneity of urban green spaces determines
143 patterns of connectivity is critical for manipulating the flow of ecosystem services around
144 where people live and work. This is the first study that uses empirical data to model both
145 structural (a measure of the ability of birds to move through the landscape) and functional (a
146 measure of the frequency of movement of individuals) connectivity. Due to the labour and
147 time intensive nature of a study of this kind it is not possible within realistic budgets to test
148 variation in movement across large numbers of networks (e.g. replicating different urban
149 forms or across a gradient of forms). However, we show that key urban features and season
150 influenced movement within three distinct urban forms, and (recognising the limitations of a
151 three-site comparison) there is evidence that overall levels of connectivity varied across
152 forms with increased movement being associated with reduced green space fragmentation.

153

154 In the network of low fragmentation movement focused around a large central cluster with
155 birds using green corridors to move to, and between, feeders away from ringing sites, and
156 movement then decreased as green spaces became more fragmented (Fig. 1a). This was
157 supported in our models with both forms of connectivity increasing with vegetation cover,
158 and decreasing with distance between feeder pairs. Functional but not structural connectivity
159 was negatively correlated with the presence of road gaps, suggesting that birds do travel
160 between green fragments but roads cause resistance to frequent movement. Connectivity
161 varied by season, being lowest in the summer probably as a consequence of breeding season
162 territoriality. Structural connectivity was then greatest in autumn, at a time when birds are
163 engaged in natal and post-breeding dispersal, before decreasing in winter as garden songbirds
164 become more settled in their wintering territories²⁵. Relative to the summer, functional
165 connectivity increased during the year, peaking in winter when food supplies were
166 constrained and birds moved frequently between known feeders. The increased availability of
167 vegetation and green corridors in this network may allow ecological processes most closely
168 to mimic those we expect to see in more natural habitats^{25,26}.

169

170 In the network of medium fragmentation movement mostly occurred within the central
171 woodland area and along vegetation corridors that largely originated from the wooded area,
172 while there was little movement between feeders within suburban gardens (Fig. 1b).

173 Connectivity increased with vegetation cover, but decreased with distance from ringing site
174 indicating that suburban gardens reduced landscape permeability. Functional connectivity but
175 not structural connectivity decreased in the presence of road gaps supporting this conclusion.
176 Structural connectivity decreased in summer when birds remain in their breeding territories,
177 but was higher across the rest of the year possibly because birds were more likely to explore

178 into gardens. Functional connectivity decreased in autumn and winter relative to spring and
179 summer, suggesting that birds visited feeders opportunistically as they passed through a
180 garden as opposed to having established wintering territories²⁷. Great tits showed lower
181 structural connectivity relative to blue tits in the networks of medium and high fragmentation,
182 possibly because they were less abundant around these networks (see Supplementary Table
183 S1). Great tits tend to forage in mature trees and so may have been more reluctant to move to
184 feeders away from vegetated corridors possibly as a consequence of relatively high blue tit
185 populations²⁸.

186

187 In the network of high fragmentation, green space corridors between streets with terraced
188 housing appeared to funnel movement (Fig. 1c). This could in part be a consequence of the
189 ringing locations being located at the periphery of the network, however, there was very little
190 movement into the relatively vegetation-impooverished central green islands located between
191 the two ringing locations suggesting that crossing terraced streets causes resistance to
192 movement relative to moving along green spaces. In this highly fragmented urban form
193 structural and functional connectivity were positively correlated with vegetation but
194 unaffected by distance between feeder pairs (at the scale of the study). Again, functional but
195 not structural connectivity was negatively correlated with the presence of road gaps. The
196 presence and frequency of connections were greatest in spring, possibly because birds were
197 searching for breeding territories²⁹. At a time when birds are undergoing post breeding
198 dispersal connectivity was least in autumn, suggesting that tagged birds did not linger but
199 instead were passing through.

200

201 There was variation in structural connectivity across networks, with 22% more feeder pairs
202 forming connections in the network of low compared to that of high fragmentation (Fig. 3a).

203 Despite the large numbers of possible drivers behind the movement of feeder-using birds
204 (such as non-experimental bird feeding, density of cat populations or intra-specific
205 territoriality) this study shows a gradient in the ability of birds to move between different
206 feeders with green space fragmentation. Of particular concern is that over the whole 12-
207 month period tagged birds failed to visit feeders within the relatively impoverished green
208 fragments in the highly fragmented network, suggesting that residents in these areas will
209 effectively be cut off from this form of nature connection. High quality green space maintains
210 the flow of birds across a broad range of gardens, providing opportunities to a greater number
211 of households to interact with birds.

212

213 Functional connectivity was also greatest in the network of low fragmentation. However, we
214 found no difference in this regard between the networks of medium and high fragmentation,
215 and their relatively low functional connectivity suggests that the associated gardens contained
216 relatively poor quality habitat so that birds either passed through the networks, or the
217 networks were too fragmented to establish territories. The networks of medium and low
218 fragmentation both contained green corridors surrounding residential houses, mainly
219 differing in the relative absence of trees in the medium fragmented network. Large trees are
220 known to be keystone structures in urban areas for increasing connectivity³⁰. Their loss may
221 be a key factor in contributing towards the reduced movement into gardens in this network.
222 This is of concern because this urban form is representative of new developments (within the
223 last 25 years) that are common in European cities.

224

225 The phenomenon of garden bird feeding is growing in many developed regions, with bird
226 feeders now being a common component of urban areas¹¹. The provision of large quantities
227 of supplementary food drives movement patterns and abundances of feeder-using birds^{31,32}.

228 Understanding how individual birds move between gardens with bird feeders, thus provides
229 real world insights into actual movement in the urban landscape. Watching birds at garden
230 feeders provides people with a sense of increased psychological well-being, feelings of
231 relaxation¹³ and of being connected to the natural world^{12,13}. Listening to bird song and
232 watching birds in the garden have been shown to contribute towards attention restoration and
233 recovery from stress^{10,15}. Greater connectivity will increase the probability that birds will be
234 seen by and so provide pleasure to multiple households, thus multiplying the benefits
235 provided by any individual bird even though it is usually impossible for households to
236 distinguish between these individuals.

237

238 Understanding and quantifying the relationship between the movement of wildlife and urban
239 features is key for ecologically sensitive planning to aid the flow of cultural services within
240 existing cities. Given that many existing urban areas have relatively inflexible urban forms,
241 improved movement could be achieved through targeted greening at focal points of
242 connectivity (e.g. in specific parks and gardens). The applied use of high quality remote
243 sensing techniques, landscape ecology principles and theory (e.g. patch and matrix
244 frameworks) and systematic conservation planning approaches to identify and exploit these
245 focal points has the potential disproportionately to increase the movement of birds into
246 impoverished areas. Targeted greening could be achieved through a combination of
247 management by local authorities, while also raising public awareness of the importance of
248 best practise habitat management in their own gardens. Future research needs to focus on
249 producing real world tools for ease of use by public and private stakeholders for mapping
250 connectivity and identifying and exploiting these focal points. How we improve existing
251 forms and design new residential areas will have a large impact on the daily nature exposure

252 of the people that live there, and thus has the potential to mitigate many of the negative
253 impacts of urbanisation.

254 **Materials and methods**

255 STUDY NETWORKS

256 The focal geographical area for this study is what has been termed the ‘Cranfield triangle’
257 (52°07’N, 0°61’W). Located ~60km to the north of London, UK, the main urban areas
258 consisted of Milton Keynes, Luton and Bedford, having a combined population of c. 524,000.
259 Each study network occupied approximately 0.5 km², with its precise location determined by
260 the presence of suitable areas in which to mist-net feeder-using birds. Relative to each other,
261 the networks consisted of one characterized by physically well connected green spaces with
262 high levels of vegetation cover and detached houses (in Milton Keynes; Network of low
263 fragmentation; Fig. 1a), a network with intermediate levels of connected green spaces and
264 vegetation cover with semi-detached houses (in Luton; Network of medium fragmentation;
265 Fig. 1b), and a network with terraced houses consisting of fragmented green spaces with low
266 levels of vegetation cover (in Bedford; Network of high fragmentation; Fig. 1c).

267

268 EXPERIMENTAL DESIGN

269 Bird feeders with integrated RFID reader and antenna were constructed utilising custom-
270 made Arduino components (Relchron LTD, Kirkcaldy, Scotland; ³³). Rectangular antennas
271 (40 mm x 32 mm) recording at 125 kHz were fixed using cable ties and epoxy plastic to the
272 underside of a single perch on a standard medium sized seed feeder (360 mm, The Royal
273 Society for the Protection of Birds, Sandy, UK). Other perches on the feeder were removed
274 and associated feeding ports sealed closed to ensure all visitations were recorded. Data-
275 loggers were programmed to alternate 400 ms of recording with 400 ms of pause. When a
276 PIT tag was within range of the antenna the data logger recorded the time and date along with
277 the tag’s unique identification number onto a 4gb memory card (SanDisk, Milpitas, USA).

278 The readers were powered 24 hours a day by a 12v battery (Xplorer 88 amp deep cycling,
279 Alpha-batteries, Rochdale, UK), allowing continuous monitoring of feeder usage.

280

281 Each network considered of 17 RFID bird-feeding stations. Each station was set up in a
282 private garden averaging 81 m (± 20 m SD) from its nearest neighbour station. Within the
283 constraint of there being suitable locations within gardens, feeders were placed ~ 0.5 m from
284 cover for birds, although the actual position was inevitably influenced by property residents
285 who volunteered use of their gardens (Fig. 1). Feeders were installed in gardens up to six
286 weeks before the experiment began to allow birds to familiarise with them. Every feeding
287 station consisted of a bird feeder with an RFID reader, antenna and power source, a bird
288 feeder stand (Kingfisher, Paddington, UK) and a universal squirrel baffle (Gardman,
289 Peterborough, UK). The bottom of the feeder was suspended ~ 1 m above the ground. We used
290 the same seed mix in all feeders throughout the experiment (Summer Seed Mix, Haithes, Bird
291 Food specialists, UK). The feeder was maintained by the property residents to ensure that
292 birds could access seed at all times, and a researcher visited all stations every 30 days to
293 replace the battery and to download the data. All 51 feeding stations were fully operational
294 between 1st September 2013 and 31st August 2014.

295

296 TAGGING IN THE FIELD

297 Birds were caught and tagged in private green spaces at two locations in each network,
298 chosen to maximize catching rates and with the nearest RFID feeding station approximately
299 15 m from the closest net (Fig. 1). Mist-nets and tape lures were used to catch two garden
300 species that commonly visit bird feeders: blue tit *Cyanistes caeruleus* and great tit *Parus*
301 *major*. Mist netting was carried out intensively during the experimental set-up period and
302 then monthly in each network, with birds being fitted with British Trust for Ornithology

303 (BTO) metal rings and with a PIT tag, which was fully moulded into an 8mm plastic ring (IB
304 Technology, Aylesbury, U.K.). All bird ringing was carried out under BTO license A/5780
305 with a special endorsement to attach PIT tags to target species. This research was
306 conducted with approval from, and in accordance with, the University of Exeter
307 Biosciences ethical review committee, project number 2013/72.

308

309 LANDSCAPE CHARACTERIZATION

310 We characterized the spatial pattern of vegetation and non-vegetation, and canopy height in
311 the landscape for each network using airborne remote sensing, specifically with hyperspectral
312 and LiDAR data (see Supplementary Appendix S1). We described the habitat that birds are
313 likely to use when moving between any pair of feeders within a network by applying a buffer
314 around and between each pair of feeders equal to 0.25 times the distance between them.
315 Based on previous studies, such an ellipsoid, with a constant length to width ratio of three,
316 represents a reasonable area for a bird seeking to move between feeders (for example, see
317 Supplementary Fig. S3; see also ^{19,34}). Within each buffer we calculated the percentage of
318 pixels containing tall vegetation (> 0.7m; vegetation cover according to the pixel values
319 exceeding a basic threshold for a vegetation index; Table 1; see Supplementary Appendix
320 S1). Finally, we counted the number of road gaps between each feeder pair, where a road gap
321 was considered to be present when a road dissected the buffer (for example; see
322 Supplementary Fig. S3). At the spatial extent of study, three or more road gaps were rare and
323 so these were pooled with two road gaps. This was then treated as a three-level factor of 0-2
324 road gaps (Table 1). We calculated the distance in meters of the closest feeder of each pair
325 with the closest ringing site (termed here as ringing site distance; mean = 42m, SD = 46m).
326 We then divided the year into four equal seasons: autumn (1st Sep–30th Nov), winter (1st Dec–
327 28th Feb), spring (1st Mar–31st May) and summer (1st Jun–30th Aug 2014). To assess the

328 probability of whether a bird passed within the ellipsoid between feeders, we calculated the
329 time taken to make each connection.

330

331 STATISTICAL ANALYSIS

332 URBAN FEATURES WITHIN FORMS AND SEASON

333 All statistical analyses were performed in R version 3.1.2³⁵, with mixed effects models built
334 using the lme4 package³⁶. To explore how different features within the three networks
335 determined seasonal movement of feeder-using birds we used a hurdle modelling
336 framework³⁷. The hurdle model consisted of a binomial model (presence-absence of at least
337 one connection in any season by species as the response variable, with one replication per
338 species, per feeder pair, per season) and a count effect model (frequency of these connections
339 in any season as the response variable, with one replication per individual tagged bird, per
340 feeder pair where connections ≥ 1) based on a Poisson distribution truncated at 0 (i.e. no
341 stochastic absence of connection). A hurdle modelling approach differentiated the effects of
342 network on structural and on functional connectivity, and better accommodated marked
343 overdispersion in our response variable than using a Poisson model³⁷

344

345 To characterise the role of urban structures on movement in each network we then built
346 binomial and Poisson mixed effect models for each network separately. We standardized the
347 continuous variables vegetation cover, distance between feeder pair and ringing site distance
348 (i.e. each was rescaled to have a mean of zero and a standard deviation of 1). To explore
349 structural connectivity we built a generalized linear mixed model (GLMM) with a binomial
350 error distribution to test for the effect of vegetation cover, distance between feeder pair,
351 number of road gaps and season on the presence-absence of connections between feeder pairs
352 (see Table 1 for a summary of covariates by network). We also included species and the

353 distance from ringing sites as covariates. Finally, to control for replication of feeder pairs
354 across the seasons, for each feeder station we included a unique identification number
355 (FeederID) within network as two random effects. To explore functional connectivity we
356 built a GLMM with a Poisson error distribution to test the effect of the same predictor
357 variables on the frequency of connections between feeders at the individual level (i.e. where
358 connections ≥ 1). We included three random effects; FeederID for each feeder station to
359 control for replication of feeder pairs across the season and a unique tag number to control
360 for multiple individuals moving between the same feeder pair in any season.

361

362 PATTERNS OF MOVEMENT ACROSS URBAN FORMS

363 To explore general patterns of movement across the networks, we pooled connections by
364 season before again using a hurdle modelling framework. The hurdle model consisted of a
365 quasi-binomial model (presence/absence of at least one connection between feeder pairs, with
366 one replication per feeder pair) and a count effect model (frequency of connections, with one
367 replication per feeder pair where connections ≥ 1). It was assumed that general patterns of
368 movement and associated cultural service provision by feeder-using songbirds were
369 dependent on individual birds and not species, so we pooled connections by species. In each
370 case we then tested for the effect of network type (included as a three level factor: low
371 fragmentation; medium fragmentation; high fragmentation) on the response variable. We
372 included distance between feeder pairs within feeder groups (in meters) as a covariate to
373 control for slight variation between networks (Table 1).

374

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465 to the demand for durable goods. *Econometrica* **39**, 829-844 (1971).
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474

475 **Author contributions**

476 DTCC, RI, KJG conceived and designed the study. DTCC carried out the fieldwork, analysed
477 the data and wrote the paper. SH and KA processed and provided the remote sensing data.
478 All authors edited the paper.

479

480 **Additional Information**

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483

484 **Table 1.** Summary of urban features per feeder pair in each of the three networks: mean
485 distance between pairs of feeders, mean vegetation cover within the buffer and the total
486 number of road gaps crossing buffers (as a measure of overall green space fragmentation).
487 Associated standard errors are shown in brackets.

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Network	Distance between feeders (metres)	% Vegetation cover	Total number of road gaps
Low fragmentation	203 (±92)	45.8 (±8.4)	121
Medium fragmentation	218 (±98)	28.1 (±10.4)	182
High fragmentation	213 (±98)	19.3 (±7.6)	302

492 **Table 2.** The relationships between a) structural (binomial) and b) functional (Poisson)
493 connectivity and the presence of key urban features and season by network, for two feeder-
494 using songbirds. We show parameter estimates with standard errors and confidence intervals
495 (CI) for factor levels relative to a comparative base factor level (0 road gaps, summer and
496 blue tits, respectively). Significant variables and factor levels are shown as: * $P < 0.05$; ** P
497 < 0.01 ; *** $P < 0.001$. We show the marginal $R^2_{\text{GLMM}(m)}$ and conditional $R^2_{\text{GLMM}(c)}$.

	Low fragmentation		Medium fragmentation		High fragmentation	
	Estimate (±se)	CI (2.5%; 97.5%)	Estimate (±se)	CI (2.5%; 97.5%)	Estimate (±se)	CI (2.5%; 97.5%)
a) Structural connectivity						
Intercept	-1.7 (±0.4)***	-2.7; -0.7	-1.8 (±0.4)***	-2.6; -0.8	-2.4 (±0.6)***	-3.7; -1.0
Vegetation cover	0.3 (±0.1)**	0.1; 0.6	0.8 (±0.2)***	0.4; 1.1	0.5 (±0.2)**	0.1; 0.9
Distance	-1.3 (±0.1)***	-1.6; -1.0	-1.2 (±0.2)***	-1.6; -0.9	-0.2 (±0.3)	-0.7; 0.4
1 road gap	-0.1 (±0.3)	-0.6; 0.4	-0.3 (±0.3)	-0.8; 0.3	0.1 (±0.4)	-0.8; 0.9
2 road gaps	-0.2 (±0.4)	-1.0; 0.7	-0.0 (±0.4)	-0.7; 0.7	-0.7 (±0.6)	-1.8; 0.4
Autumn	1.5 (±0.2)***	1.0; 2.0	0.8 (±0.3)**	0.3; 1.4	0.3 (±0.3)	-0.4; 1.0
Winter	0.8 (±0.2)**	0.3; 1.3	0.6 (±0.3)*	0.0; 1.1	0.6 (±0.3)	-0.1; 1.2
Spring	0.1 (±0.2)	-0.4; 0.6	0.8 (±0.3)**	0.3; 1.3	0.9 (±0.3)**	0.3; 1.6
Species	0.0 (±0.2)	-0.3; 0.4	-1.1 (±0.2)***	-1.4; -0.7	-1.6 (±0.2)***	-2.1; -1.1
Ring site distance	-0.2 (±0.3)	-0.7; 0.2	-0.5 (±0.2)**	-0.8; -0.1	-0.3 (±0.3)	-0.8; 0.4
	$R^2_{\text{GLMM}(m)}$	0.29		0.4		0.28
	$R^2_{\text{GLMM}(c)}$	0.57		0.55		0.62
b) Functional connectivity						
Intercept	1.2 (±0.3)***	0.6; 1.7	1.3 (±0.2)***	1.0; 1.6	1.2 (±0.3)***	0.5; 1.7
Vegetation cover	0.1 (±0.0)*	0.0; 0.2	0.2 (±0.1)**	0.1; 0.3	-0.2 (±0.1)*	-0.5; -0.1
Distance	-0.5 (±0.0)***	-0.6; -0.5	-0.3 (±0.1)***	-0.4; -0.1	-0.2 (±0.1)	-0.5; 0.0
1 road gap	-0.4 (±0.1)***	-0.6; -0.3	-0.2 (±0.1)**	-0.4; -0.1	-0.1 (±0.2)***	-1.5; -0.9
2 road gaps	0.3 (±0.2)	-0.1; 0.7	-0.3 (±0.2)*	-0.6; -0.0	-2.4 (±0.4)***	-2.9; -1.4
Autumn	0.3 (±0.1)***	0.1; 0.4	-0.5 (±0.1)***	-0.7; -0.4	-0.3 (±0.1)**	-0.5; -0.1
Winter	0.4 (±0.1)***	0.3; 0.6	-0.5 (±0.1)***	-0.7; -0.4	-0.0 (±0.1)	-0.2; 0.2
Spring	0.2 (±0.1)**	0.1; 0.4	0.1 (±0.1)	-0.1; 0.3	0.6 (±0.1)***	0.4; 0.8
Species	0.2 (±0.2)	-0.1; 0.5	-0.1 (±0.1)	-0.3; 0.1	-0.0 (±0.2)	-0.5; 0.4
Ring site distance	-0.1 (±0.1)	-0.2; 0.0	-0.2 (±0.1)**	-0.3; -0.0	-0.1 (±0.2)	-0.4; 0.2
	$R^2_{\text{GLMM}(m)}$	0.13		0.15		0.17
	$R^2_{\text{GLMM}(c)}$	0.22		0.17		0.23

498

499 **Table 3.** Hurdle model testing for the relationships between networks on overall levels of
500 movement of feeder-using garden bird: a) Structural connectivity; b) Functional connectivity.
501 We show parameter estimates and associated standard errors, t values and confidence
502 intervals (CI) for medium and low fragmentation networks relative to the base factor level of
503 the high fragmentation network. Significant factor levels are shown as: * $P < 0.05$; ** $P < 0.01$;
504 *** $P < 0.001$. The pseudo R^2 is McFaddens.

	Estimate (\pm se)	t value	CI (2.5%; 97.5%)
<i>a) Structural connectivity</i>			$pR^2 = 0.15$
Intercept	1.7 (± 0.3)	5.6***	1.2; 2.4
Medium fragmentation	1.0 (± 0.3)	3.7***	0.5; 1.6
Low fragmentation	1.1 (± 0.3)	4.1***	0.6; 1.7
Distance	-0.008 (± 0.001)	-6.9***	-0.01; -0.006
<i>b) Functional connectivity</i>			$pR^2 = 0.39$
Intercept	5.0 (± 0.2)	20.2***	4.9; 6.0
Medium fragmentation	0.02 (± 0.3)	0.1	-0.6; 0.5
Low fragmentation	0.6 (± 0.2)	2.4*	0.2; 1.1
Distance	-0.1 (± 0.001)	-7.5***	-0.02; -0.01

505 **Figure 1.** The frequency of connections (i.e. functional connectivity) of two species of garden bird moving between bird feeders, within a) the network
506 of low fragmentation, b) the network of medium fragmentation, c) the network of high fragmentation. Connections occurred over a 12-month period.
507 The upper panel rasters were generated using hyperspectral and LiDAR data (Appendix S1), we show the location of rfid bird feeders in red. Habitat
508 classification: white; vegetation free surfaces at ground level, light grey, buildings; medium grey, grass & low lying vegetation, dark grey; vegetation
509 (at 2m resolution). The lower panels show the frequency of each connections (black line, >100; >50-100, dark grey line; >10-50, medium grey line; 1-
510 10 light grey line) and the total number of connections made by each feeder (divided into 4 categories denoted by increasing size and brightness of the
511 red circle: 0; 10; 50; 100; >200). ◆ Bird catching locations. Images were created in R version 3.1.2³⁴.

512

513 * To increase the clarity of the image only those connections that occurred between feeder pairs that were less than the mean distance between all
514 feeder pairs are shown (<213 m); this only loses 9% of the total connections made, and does not exclude any feeder pairs with =>10 connection.

515

516 **Figure 2.** The effect of urban features, and season, on structural (a-c) and functional (d-e)
517 connectivity across networks, for feeder-using birds. Structural connectivity (presence-absence of
518 connections): a) the percentage vegetation cover of feeder pairs with connections present and absent
519 by network; b) the number of feeder pairs against the number of road gaps and c) the number of
520 feeder pairs that formed connections in each season. Functional connectivity (frequency of
521 connections where ≥ 1 connection was made (log 10 on y-axis): d) frequency against the number of
522 road gaps by network, and e) frequency against season.

523 **Figure 3.** Comparison of the movements of tagged birds between feeder pairs across networks: a)
524 Structural connectivity (the numbers of feeders that each feeder is connected to), and b) Functional
525 connectivity (the total number of connections made to each feeder). Pseudo R^2 from quasi-models
526 shown.





