

1 **Title**

2 Juvenile Barn Owl *Tyto alba alba* dispersal: roost site selection in relation to landscape features — a
3 radio tracking study

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13 **Short Title**

14 Juvenile Barn Owl Dispersal

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16 **Key words**

17 Altitude, major roads, movement, post-fledging, rivers, telemetry

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21 **Summary**

22 **Capsule:** Radio tracking 19 juvenile Barn Owls in England gives insight into their dispersal behaviour.

23 Different spatial patterns emerged for males and females, tree branches were frequent roost sites, and
24 altitudinal distribution changed after owls acquired home ranges.

25 **Aims:** To gain new understanding on the natal dispersal phase of a nocturnal raptor by identifying roosts
26 and analysing their spatial pattern, site type, altitude, and location in relation to linear features.

27 **Methods:** Day-roost sites of 19 juvenile Barn Owls were located by radio tracking over four years in
28 southwest England. We evaluated the possibility of sex-bias in natal and between-roost dispersal
29 distances and tested for change in the site types used as natal sites and day-roosts. We tested for
30 change in altitude between roosts used during dispersal and those on the acquired home range, and we
31 analysed the location of roost sites in relation to major roads, railways and rivers.

32 **Results:** Barn Owls commenced dispersal when they were between 63 and 122 days old (median = 94).
33 Roost sites used by females were more widely scattered than those used by males. Owls roosted most
34 frequently in trees, despite most natal sites being in buildings. The altitude of roost sites used by owls
35 during dispersal in elevated landscapes was higher than those on their acquired home range. We could
36 find no evidence that owls followed linear features during dispersal, nor that hills were barriers.

37 **Conclusion:** Post-fledging roosting behaviour of female and male Barn Owls differed spatially and was
38 congruent with a wider pattern of sex-bias in avian natal dispersal. Frequent roosting on tree branches
39 had implications for exposure to adverse weather. Some juveniles roosted at altitudes that were higher
40 than subsequent roosts on their acquired home range. We found no evidence to support the proposal
41 that linear landscape features constituted dispersal corridors.

42 **Introduction**

43 Studying the ecology of birds where they are sedentary is usually more straightforward than during their
44 dispersal phase. In ornithology, the general concept of dispersal as a one-way movement from one
45 home site to another (Lincoln *et al.* 1998) is usefully separated into natal dispersal (movement between
46 the natal site and the first breeding attempt) and breeding dispersal (movement between successive
47 breeding attempts: Greenwood & Harvey 1982). Importantly, there is a strong interspecific pattern of
48 greater distances in natal dispersal than in breeding dispersal (Paradis *et al.* 1998). Although natal
49 dispersal may lead to increased risk of predation, lower survival, and high energetic costs, it can also
50 reduce intraspecific and kin competition, prevent inbreeding, and allow distribution ranges to expand
51 (Liu & Zhang 2008). Despite advances in knowledge, developing theoretical frameworks for observed
52 patterns in avian dispersal has proved challenging (Clarke *et al.* 1997, Paradis *et al.* 1998, Liu & Zhang
53 2008).

54 For Barn Owls, an estimated 52% of deaths in the UK occur within six months of fledging
55 (Ramsden 2003) and 47% of juvenile mortality occurs between August and November, when most post-
56 fledging dispersal takes place (Bunn *et al.* 1982, Newton *et al.* 1991). Indeed, total population size is
57 strongly influenced by juvenile survival rate (Percival 1990), which is largely determined by food supply
58 (Hone & Sibly 2002). Despite the importance of this phase, little is known about the influence of
59 altitude, landscape features, roost site type, or weather on juvenile dispersal in Barn Owls.

60 UK ring recoveries showed that within two weeks of fledging, 37% of juveniles had moved over
61 3 km from their nest sites and three to four weeks later this had risen to 59% (Bunn *et al.* 1982). By 8 to
62 11 weeks after fledging, the median ring recovery distance becomes similar to the median natal
63 dispersal distance (8 km; Pringle *et al.* 2016) and most surviving birds have settled by late November
64 (Toms 2002). Sibling birds show no tendency to disperse or roost together (Mikkola 1983) and males
65 usually settle closer to their natal sites than females (van den Brink *et al.* 2012; Pringle *et al.* 2016), as is
66 common among bird species (Taylor 1994, Arlt & Pärt 2008). Despite relatively short average dispersal

67 distances, the UK and European maximums are 624 km and >1000 km, respectively (BTO 2017a, Poprach
68 2010).

69 Hills have been proposed as both barriers (Shawyer 1994, 1998) and conduits (Martin 2017) for
70 dispersing juveniles, albeit without compelling evidence. In conjunction with elevation constraints on
71 the distribution of UK Barn Owl nest sites, these possibilities have implications for range expansion as a
72 result of climate change (Batey 2013). A recurrent speculation is that juvenile Barn Owls disperse along
73 linear features, such as strips of grassland, river corridors or roads (Shawyer 1987, 1994, 1998, Shawyer
74 & Dixon 1999, Tomé & Valkama 2001, Bond *et al.* 2005, Regan *et al.* 2018). However, data has not been
75 available to test the idea that dispersal corridors (*sensu* Koford *et al.* 1994) provide spatial linkage that
76 facilitates the movement of juvenile Barn Owls away from their natal site. Radio-tracking provides a
77 means of testing these hypotheses.

78 The only previously published UK telemetry study on juvenile Barn Owls was carried out in
79 Anglesey, North Wales (Seel *et al.* 1983). Based on 10 juveniles, dispersal consisted of a series of
80 movements between sites 0.1 to 1 km apart. Between movements, birds roosted for periods of 1 to 28
81 days, although clusters of sites were sometimes used for up to 15 weeks (Seel *et al.* 1983). Similarly, a
82 radio-tracking study in Portugal found that 12 juveniles alternated between dispersal movements and
83 periods when individuals remained in one area (Roque *et al.* 2017). Data from both studies was probably
84 biased towards birds that had not moved far, because many tagged birds were permanently lost at a
85 very early stage (6/10 in Anglesey and 16/41 in Portugal) and this was possibly because they had moved
86 beyond the range of hand-held receivers. In both studies roost sites were mainly in trees. This is
87 surprising for the Anglesey birds, because they had all fledged from nestboxes that were mainly in
88 buildings (Seel *et al.* 1983). This suggests that tree roost selection behaviour in dispersing Barn Owls is
89 either inherent or opportunistic, in response to site availability.

90 In this study we use radio tracking data to capture the timing of life history events and provide a
91 quantitative description of the relationship between age and distance from the natal site. In our
92 analyses we aimed to assess sex-bias in distances between relocations, test if post-fledging roost site

93 type reflected natal site type, and disclose any altitudinal changes between dispersal and home range
94 phases. Finally, we evaluated the relevance of major roads, rail lines and rivers as linear features in the
95 landscapes through which juvenile Barn Owls move during their dispersal phase.

96 **Materials and methods**

97 **Study Areas**

98 The three study areas were in the counties of Cornwall, Devon and Dorset in southwest England, lying
99 between 50–51°N and 2–5°W (Figure 1). The regional annual rainfall varies from 900 mm to 2000 mm.
100 The lowest daily mean minimum temperature is in February, at 1.5 °C, and the highest is in July and
101 August, at between 19 °C and 21.5 °C (Met Office 2019). The areas comprised undulating mixed
102 arable/pastoral farmland, typical of the region and similar to the Anglesey study area cited above (Seel
103 *et al.* 1983). There were fields, hedgerows with isolated trees, and patches of dense woodland, plus
104 numerous hazards such as minor roads, electricity infrastructure, and water troughs. All three areas
105 presented modern and traditional farm buildings, some of which contained Barn Owl nestboxes, and
106 afforded many potential roost sites.

107 The general topography of all three study areas consisted of higher ground to the north and
108 lower ground to the south, with rivers flowing in a southward direction towards the coast. The mean
109 altitude of the tracked birds' natal sites was 102 m a.s.l. (n = 8), ranging from 27 m a.s.l. in Dorset to 191
110 m a.s.l. in Devon. The mean distance to the nearest coast was 12.1 km (range = 2–28 km), allowing space
111 for dispersal in any direction. All three areas contained potential dispersal corridors (Shawyer 1987,
112 1994, 1998, Shawyer & Dixon 1999).

113 **Fitting VHF radio tags**

114 In collaboration with Biotrack (www.biotrack.co.uk), a pair of captive adult Barn Owls of wild origin was
115 fitted with backpack harnesses with dummy tags. Careful monitoring using CCTV and motion detection
116 software showed increased preening activity by the male, sometimes focused on the tag. Using a slightly
117 modified harness design, two wild nestlings were then fitted with dummy tags and monitored on film.
118 Footage from five days before and after the harness showed no change in the owl's behaviour. Both

119 were recaptured after two weeks and close examination revealed no feather wear or skin abrasion from
120 the harness. Two other owls were recaptured after fledging, one at four months and another at eleven.
121 In both cases the harnesses had not caused any wear or abrasion and were not noticeably tighter or
122 looser. The older bird was female and recaptured on May 27th with no brood patch or moult. Given that
123 she was not breeding, her weight of 332 g was healthy.

124 Radio-tagging was done at well-known nest sites with suitable access. The whole brood was
125 usually tagged, except for two owlets in Cornwall that were not found at a suitable developmental
126 stage. The sample comprised 19 owlets from eight broods: five from two broods in 2004 (Dorset and
127 Cornwall), two siblings in 2005 (Dorset), nine from four broods in 2008 (Devon), and three siblings in
128 2009 (Devon). Birds were BTO ringed, aged using a wing length-age chart (Percival 1990), and sexed
129 according to plumage (Taylor 1993). Immediately prior to fledging, TW-3 transmitters were attached
130 using a soft Teflon[®] backpack harness as shown in Figure 2 (Dunstan 1972, Kenward 2001). Each radio
131 transmitter (tag) weighed 9 g (approximately 3% of the bird's body weight) and had a battery life of
132 around one year.

133 **Radio tracking**

134 We used 'Sika' receivers with 'Yagi Flex' antennas for tracking (Biotrack Ltd., Dorset, UK). Recording
135 effort was approximately 12 tracking team hours/week, with time allocated to birds according to their
136 movement. Birds that had not previously been recorded away from their natal site were checked first,
137 followed by checks for birds at their last recorded position. Locating new roost sites involved taking
138 receivers to higher ground. On detecting a signal, the owl's location was determined by triangulation to
139 avoid flushing birds from roosts. Fifty-five percent of consecutive relocations of individual birds
140 happened within four days of the previous relocation. The distribution of time intervals between
141 relocations was positively skewed, with a median of 4 and maximum value of 65 ($P_{25} = 2$ and $P_{75} = 10$).

142 We considered the dispersal phase to have begun when a bird was no longer recorded at its
143 natal site and to have ended when it had acquired a home range. The transition between dispersal and
144 home range phases was determined on a case-by-case basis by examining the timing and spatial pattern

145 of relocations. Tracking continued until the radio tag was recovered or the bird could not be relocated
146 despite extra effort. The number of times a bird was found to have moved between day-roost sites
147 during the dispersal phase was used as a measure of the number of dispersal movements. The number
148 of tree-roosts and building-roosts where a bird was found was recorded during its dispersal phase and,
149 where relevant, after settling on a home range.

150 **Overview of statistical models**

151 Where appropriate, we applied classical two-sample tests after evaluating normality of distribution and
152 homoscedasticity of variance. For other tests, Generalised Linear Mixed Models (GLMMs) provided a
153 robust alternative for analysing variables with a given error structure and non-independent data points
154 (Harrison *et al.* 2018). We used the Gamma family log link function to handle positively skewed
155 continuous data (Bates *et al.* 2015, R Core Team 2020) and report effect sizes with their standard error
156 (SE). Where tests involved relationships between numerical variables, these were rescaled to lie
157 between 0.001 and 100. Model assumptions were checked with diagnostic plots and tests on residuals
158 (Hartig 2020).

159 We consistently included individual bird identity as a random factor, because repeated
160 measurements violated the assumption of independent data points (Harrison *et al.* 2018). In models
161 including between-roost distances and altitude, bird identity was initially nested within a second
162 random factor grouping siblings to account for variation among broods in different study areas and
163 years. However, the second random factor was dropped if non-convergence or singularity compromised
164 model fitting, as were interactions between independent variables.

165 **Natal dispersal onset and distances**

166 Basic statistics were calculated for the age of dispersal onset and home range establishment (where
167 applicable) and we obtained date ranges for these events. Distances from nest sites and between day-
168 roosts were obtained from a distance matrix generated using six-figure grid references (UK Grid
169 Reference Finder 2011). To achieve a quantitative overview of change over time we plotted median,

170 interquartile and extreme distances from the natal site by fortnightly periods over the first six months
171 following the first day-roost away.

172 We used a two-sample test to compare the mean dispersal distances of male and female birds
173 that successfully established a home range. These were calculated as the distance between a natal site
174 and the centroid of the relocations recorded on the home range, after removing extreme values. We
175 refer to them as natal dispersal distances because surviving owls would probably attempt to breed on
176 the acquired home range (Greenwood & Harvey 1982). To reflect differences between sexes in ranging
177 behaviour during the dispersal phase, we used GLMMs to model non-zero distances to previous roosts
178 as a function of sex. We included a second independent variable grouping birds by year to control for
179 possible interannual variation in juvenile dispersal movements (Roulin 2002). Bird identity was nested
180 within the random effect of brood. Because relocations were a sample of the day-roosts actually used,
181 and distance should vary with time between fixes, we tested for any difference in the number of days
182 elapsed for male and female relocations.

183 **Roost sites, altitude and linear features**

184 We used the binomial proportions test to compare the proportion of birds with trees as natal sites to
185 the proportion of day-roost sites that were in trees during dispersal. Three birds that hatched in
186 nestboxes in buildings were excluded, two because they were not recorded in any subsequent day-
187 roosts and the third because it was not recorded roosting during the dispersal phase. To allow a clear
188 comparison of trees and buildings, we also excluded the one bird that had hatched in a pole-box.

189 The altitude of natal sites and all relocations at roost sites was established using an online GPS
190 Visualizer (Schneider 2003). We used a two-sample test for paired observations to compare the altitude
191 of natal sites with the mean altitude of day-roosts recorded after birds settled on the home range (after
192 removing relocations we considered to be off the home range). We used a GLMM to compare relocation
193 altitudes recorded after settling on an acquired home range with those recorded during the
194 corresponding dispersal phase. As it was reasonable to believe that change in roost site altitudes could
195 respond differently in lowland and elevated contexts, we included 'altitudinal group' as a second

196 independent variable. This divided birds into two groups based on their ranked dispersal phase means.
197 Altitude was square-root transformed to improve distribution and the random factor brood was
198 dropped due to fitting constraints.

199 To evaluate roost site locations in relation to potential dispersal corridors, we defined linear
200 features as major roads, rail lines, major rivers, and their tributary rivers. These were the A38 and A380
201 dual-carriageways, the Riviera and Dart rail lines, the Dart, Teign, Webburn, and Mardle Rivers in Devon,
202 and the Stour and Allen Rivers in Dorset. Analyses excluded birds that were unlikely to encounter these
203 during tracking and relocations from after birds settled on a home range. Because juvenile dispersal is
204 punctuated by a series of closely-spaced sites (Seel *et al.* 1983), we also excluded observations
205 associated with the 25% quartile of inter-roost site distances.

206 We treated intersecting linear features as continuous when their orientation was similar ($<90^\circ$
207 change). Using digital Ordnance Survey Mapping, we measured distances from roost sites to the closest
208 point on connecting linear features, with connecting linear features defined as those with the lowest
209 combined distance from two consecutive roost sites. Using UK Grid Reference Finder (2011), we
210 measured straight line distances between consecutive closest points on connecting linear features
211 (hereafter referred to as linear feature distances: LFDs). By using straight line distances, we assumed
212 that the flight path to the linear feature was at least as indirect as the path of the linear feature.

213 We assumed that the proximity of Barn Owl roost sites to linear features was positively related
214 to the likelihood that the owl had arrived at the site by moving along the feature. This implied that the
215 closer a roost site was to a linear feature, the closer the alignment would tend to be between the linear
216 feature's orientation and the direction to the site from the owl's previous roost. Furthermore, if linear
217 features facilitated movement, then we expected a positive tendency in the relationship between the
218 proximity of roost sites to linear features and the distance along linear features that connected the
219 closet point to the roost site to the closest point to the previous roost site (i.e. the corresponding LFD).

220 To test this hypothesis, we used a GLMM with the distance from roost sites to connecting linear
221 features as the response variable and two independent variables. Firstly, we used the R package

222 geosphere (Hijmans 2019) to obtain the absolute difference in degrees between a) bearings from roost
223 sites to previous roost sites, and b) back bearings along corresponding LFDs. Secondly, we used the
224 corresponding LFDs themselves. We implemented a rerun of this test including just major roads and rail
225 lines.

226 **Results**

227 **Radio tracking**

228 Most birds were repeatedly recorded at their natal sites before dispersal (mean = 13.53, SD = 14.29) but
229 after they had used a day-roost elsewhere, only one was ever recorded at the natal site again, and only
230 once. The mean number of relocations after dispersal had commenced was 13.42 (SD = 9.21; range: 0 to
231 30). The mean age of final relocation was 184.6 days (SD = 86.13), taking place between 9 September of
232 the first calendar year and 16 May of the second.

233 Of the 19 birds tagged, one or more dispersal movements were recorded for 17 of these birds
234 and the accumulated distance between previous roosts averaged 17.2 km. Thirteen birds were still being
235 tracked one month into dispersal, 12 after two months, 9 after three months, 8 after four months, 6
236 after five months, and 4 after six months. Twelve were considered to have been successfully tracked in
237 that they did not disappear or die within 21 days of the last recording at the natal site. Ten birds were
238 tracked throughout their entire post-fledging dispersal phase and nine of these continued to be tracked
239 afterwards. The tenth bird was found dead soon after settling (Table 1). By the end of the study, 8 of the
240 birds had been recovered dead, 10 birds were never recovered and 1 bird was re-trapped alive at 363
241 days old (Table 1).

242 **Natal dispersal onset and distances**

243 Median age of dispersal onset was 94 days (mean = 93.3, SD = 15.55; range: 63 to 122), between 2
244 August and 26 September. Median age of home range established was 139.5 days (mean = 142.1, SD =
245 30.03; range: 96 to 184), between 14 August and 20 November. Following the first day-roost away from
246 the natal site, distances from nest sites increased during the first three months, at which point median

247 values were at their highest, and by six months values were similar to those recorded at two months
248 (Figure 3).

249 Natal dispersal distances for the ten birds that established a home range presented a normal
250 distribution (Wilk's $W = 0.90$, $P = 0.23$), marginal homoscedasticity ($F = 7.10$, $P = 0.07$) and a mean of
251 5.65 km (SD = 3.21). Mean natal dispersal for males (4.43 km, SD = 4.16) was lower than for females
252 (6.88 km, SD = 1.47), but not significantly so ($t_{4.99} = 1.25$, $P = 0.27$). Non-zero distances between previous
253 roosts were greater for females (median = 1.36, 72 distances) than males (median = 1.28, 52 distances)
254 and this difference was marked (GLMM effect size for males = -0.58 ± 0.29 , $P = 0.042$). Although main
255 effects for years were important in this model (P -values < 0.05), trial models showed that the effect of
256 sex on distance was not dependent upon year, even though this interaction was dropped due to fitting
257 constraints. The number of days elapsed between relocations did not differ markedly between females
258 and males (Wilcoxon rank sum test $W = 1529.5$, $P = 0.12$).

259 **Roost sites, altitude and linear features**

260 The test on roost site type included thirteen birds hatched in nestboxes in buildings and two hatched in
261 a tree-mounted nestbox. The proportion of birds with natal sites that were in trees (0.13) was markedly
262 different to the proportion of day-roosts that were in trees during dispersal (0.84; $\chi^2_{1} = 24.87$, $P < 0.001$,
263 $n = 57$ day-roost sites). Out of the 17 birds that were recorded roosting outside their natal site, 16 used
264 a tree or hedge as their first recorded day-roost away from the nest and only nine roosted in barns (or
265 nestboxes in barns) at any time (Figure 4). Overall, 68% of roost sites were in trees or hedges and 32%
266 were in buildings ($n = 244$).

267 Distribution was non-normal for natal site altitudes (Wilk's $W = 0.83$, $P = 0.032$) and mean home
268 range altitudes (Wilk's $W = 0.77$, $P = 0.006$) and these altitudes were comparable (natal site mean =
269 105.6, SD = 67.7; mean home range altitude = 101.6, SD = 47.2; Wilcoxon signed rank test $V = 26$, $P =$
270 0.92). For birds that settled on a home range, the mean relocation altitude during the home range phase
271 was lower (96.3 m, SD = 47.3) than during the dispersal phase (106.3 m, SD = 77.7). This difference was
272 not marked for birds in the lower altitudinal group (GLMM effect size = 0.035 ± 0.050 , $P = 0.479$).

273 However, a clear interaction between dispersal phase and altitudinal group showed that birds dispersing
274 at higher altitudes settled on markedly lower home ranges (effect size for interaction = -0.290 ± 0.067 , P
275 < 0.001 ; Figure 5).

276 Twelve owls were tracked in landscapes where they were likely to encounter significant linear
277 features, four from two broods in Dorset and eight from four broods in Devon. There were 39
278 relocations with inter-roost distance above the 25% quartile of 758.5 m (Table 2). Distance from roost
279 sites to linear features bore no relation to alignment of bearings to previous roost sites with back
280 bearings along corresponding LFDs (GLMM slope effect size = 0.009 ± 0.01 , $P = 0.52$) or the length of
281 corresponding LFDs (GLMM slope effect size = -0.006 ± 0.01 , $P = 0.63$). Qualitatively similar results were
282 obtained when including 20 observations from roads and rail lines, which excluded the two broods from
283 Dorset. It should be noted that our hypothetical dispersal movements are based entirely on the
284 proximity of daytime roost sites — foraging, commuting, and exploratory flights were not recorded.

285 **Discussion**

286 We obtained a quantitative description of the onset, advance and outcome of the dispersal phase of
287 juvenile Barn Owls in the southwest of England. Telemetry enabled us to detect greater distances
288 between consecutive relocations of female Barn Owls than those of males. It revealed a marked reliance
289 on trees as day-roosts and phase-specific patterns in altitudinal distribution. The evidence we acquired
290 leads us to question the role of linear features as dispersal corridors in this context. Although sample
291 size was limited by the challenging logistics of recovering data from wide-ranging and unpredictable
292 juveniles, the empirical basis we obtained creates a valuable opportunity for research to develop.

293 **Radio tracking**

294 The maximum range at which Advanced Telemetry Systems 'SM1' tags could be detected with 'LA12'
295 receivers in Wales was 3.7 km (Seel *et al.* in 1983). The detectable distance in this study varied from 1 –
296 6 km depending on whether the signal was weakened by roost site shielding (e.g., thick walls) or line-of-
297 sight obstructions, such as hills. Movements of over 5 – 10 km are unlikely to be recorded using
298 conventional VHF radio tracking. Thus, the two natal dispersal distances recorded in Wales (2.36 km at

299 25 – 27 weeks old; Seel *et al.* 1983) and the ten reported here are biased towards owls that stayed
300 within receiver range. This may explain why these values are lower than the mean natal dispersal
301 distances obtained from UK ring recovery data (e.g., 10.56 km for live bird recoveries and 17.53 km for
302 dead recoveries: Pringle *et al.* 2016). The overall ring recovery rate in this study (1 in 2.1) was higher
303 than the recovery rate for BTO-ringed Barn Owls (1 in 7.4; BTO 2017b), partly due to findings via radio
304 tags.

305 **Natal dispersal onset and distances**

306 The mean age at which nine Barn Owls tracked in Wales commenced dispersal (73 days: Seel *et al.* 1983)
307 was younger than in this study and both were younger than the UK average obtained from ring
308 recoveries (98 days: Bunn *et al.* 1982). When calculated as days after ringing, the age of last contact in
309 the tagged owls was less (mean = 137 days) than the age of live or freshly dead ring recoveries in Devon
310 and Cornwall during the same years (Barn Owl Trust unpublished data: mean = 270 days, $n = 26$), which
311 likely reflects limitations of VHF radio tracking methods.

312 Distance plots from radio tracking (Figure 3) and ring recoveries are similar in that maximum
313 distances are at three months after fledging (Pringle *et al.* 2016). Slightly lower maximum distance for
314 tagged birds during these first six months was possibly due to the limited range of the equipment. The
315 range of dates at which birds settled on their home range agrees with the dispersal period of four to five
316 months post-fledging given in the BTO Migration Atlas (Toms 2002). The early settlement of some of the
317 birds in this study is compatible with detailed observations from southwest Scotland, where some birds
318 settled within two months of fledging (Taylor 1994).

319 Natal dispersal was 56% further for females than males, although our small sample size limited
320 scope for inference. These results agree with natal dispersal in the BTO UK dataset (Pringle *et al.* 2016:
321 males = 6.00 km and females = 8.03 km), natal dispersal in southwest Scotland (Taylor 1994: males ≤ 5
322 km and females = 6 – 10 km), and mean recovery distances from 207 sexed Barn Owls ringed in Devon
323 and east Cornwall (males = 10.66 km and females = 13.38 km: Barn Owl Trust unpublished data). Sex-
324 bias in natal dispersal distances is also characteristic of a wide range of philopatric bird species

325 (Greenwood & Harvey 1982). The markedly higher distances between consecutive roost sites for female
326 Barn Owls suggest that their trajectories were less punctuated than those of males, producing a more
327 widely scattered array of day-roosts. It is also suggestive of a greater range in exploratory flights (Ferrer
328 1993).

329 One explanation for sex-biased natal dispersal in Barn Owls is inbreeding avoidance (van den
330 Brink *et al.* 2012). Alternatively, the constrained site availability hypothesis posits that when male birds
331 search for a potential nest site they can choose from all vacant sites, whereas dispersing female birds
332 must travel further because they are constrained to settle at sites with advertising males (Arlt & Pärt
333 2008). This possibility is compatible with observations of male Barn Owls increasing vocalisation prior to
334 breeding, presumably to advertise site ownership (Taylor 1994, p 151).

335 Habitat selection may be relevant in the settling response of dispersing male Barn Owls (Davis &
336 Stamps 2004) because males settling in higher quality habitat will usually be more successful providers
337 of critical food while females are not hunting during incubation and brooding. Nonetheless, dispersing
338 males may settle where widowed females are already established. In Scotland, some juveniles replaced
339 dead adults within two months of fledging (Taylor 1994). Although we know very little about
340 interactions between tracked birds and established adults, most of the roost sites identified were not
341 known Barn Owl sites and on all ten occasions when a radio tracked bird was seen roosting, they
342 appeared to be alone.

343 Movements between day-roosts can be highly multi-directional. Seel *et al.* (1983) noted that
344 dispersing Barn Owls sometimes returned to near the natal site and we recorded this behaviour in three
345 birds, with one case involving multiple returns over distances of approximately 5 km. These observations
346 highlight the variability of day-roost use during dispersal. Given that relocations were not daily, it is
347 possible that returns to near the natal site were common and that many exploratory flights were made
348 in various directions.

349 **Roost sites, altitude and linear features**

350 Most of the radio-tagged owls hatched in buildings. Because they usually roosted at the natal site for
351 over one month after fledging, tree branches would have contributed relatively little to their imprinted
352 behaviour. The high proportion of tree roosts used during dispersal could suggest behavioural flexibility
353 in response to site availability, or that trees were positively selected because of inherent roosting
354 behaviour. Imprinting at their natal site could cause owls to subsequently select nest sites in buildings
355 (Ratcliffe 1980). Given the high proportion of Barn Owls nesting in buildings (56% in the 1990s: Toms *et*
356 *al.* 2000), the influence of natal nest site type on nest site selection has potential implications for this
357 species' capacity to colonise areas where buildings are scarce (Kleinstäuber *et al.* 2018). Alternatively,
358 nest site types may simply be selected in proportion to their availability (Ramsden 1998).

359 Environmental conditions can produce important cues for both innate and learned behavioural
360 responses in birds (Mery & Burns 2010). Between 13 and 30 November 2008, four owls switched from
361 outdoor to indoor roosts and this period coincided with deteriorating weather conditions (Met Office
362 2008). December 2009 was the coldest for 30 years and three birds were still being tracked. One
363 switched from tree-roosting to using a building and a tree-mounted nestbox, the second switched to
364 using tree cavities (rather than tree branches or Ivy), and the third continued to roost on tree branches
365 in sub-zero temperatures and was found dead two days later. These observations highlight the benefit
366 of providing sheltered roost sites for juveniles in the form of nestboxes.

367 In Wales, all the study birds hatched in nestboxes (mainly in buildings), but 70% of the 60 roost
368 sites identified during dispersal were in trees. The owls were seen perching in low branches of hedgerow
369 trees (Seel *et al.* 1983), as was observed during the present study. Interestingly, both studies were
370 carried out in the generally wetter West/SW of Britain as opposed to the East of England, where tree-
371 roosting might be more viable due to lower rainfall. Observing Barn Owls in aviaries reveals that wet
372 individuals are unable to fly silently (D. Ramsden *pers. obs.*), which must inhibit prey detection in a
373 largely auditory hunter. Indeed, wild Barn Owls do not generally hunt in heavy rain (Mikkola 1983).
374 Therefore, that 68% of roost sites in this study gave little protection against rainfall was surprising.
375 Although 6 of the 19 birds survived exposure to wet weather for five months, the possible role of this

376 exposure in the birds' demise is unknown. Research has shown that roost site selection can be
377 influenced by weather (Smith *et al.* 1974) and we note that six of the birds we tracked switched to more
378 sheltered roost sites as weather deteriorated.

379 Altitude mediates climatic variation, which appears to limit the location of Barn Owl nest sites in
380 southwest England: an estimated 98.2% were below 250 m a.s.l. compared to approximately 90% of
381 land availability below that (Batey 2013). Although nest sites are not confined to valleys (Barn Owl Trust
382 2012, p 188), analysing two altitudinal groups showed that birds occupying elevated areas during
383 dispersal shifted to lower altitude roost sites after settling on a home range. Furthermore, acquired
384 home ranges were not generally higher than natal sites. Taken together, these patterns suggest that
385 altitudinal constraints on distribution were linked to the sedentary phase of life, rather than dispersal.
386 Altitudinal ranges associated with dispersal and home range phases can be expected to increase due to
387 climate change.

388 Data in this study does not support the idea that juvenile Barn Owls avoid crossing hilly areas
389 (Shawyer 1994 p 91, 1998 p 94). Although we do not know if uplands such as Dartmoor reduce dispersal
390 rates, it is likely that some parents of the tagged birds had successfully dispersed in relatively elevated
391 landscapes. The drop in altitude among tagged birds dispersing in elevated landscapes raises the
392 possibility that they had to disperse further before encountering environmental cues that triggered a
393 settling response. Interestingly, natal dispersal was further among birds in the higher altitude group
394 than the lower (range: 1.9 – 7.7 km *versus* 3.1 – 12.9 km). However, if natal dispersal distances were
395 increased by juveniles moving through elevated landscapes, we suggest that these areas comprise sub-
396 optimum habitat with possible survival costs. In this sense, hilly areas are not corridors that facilitate
397 spatial linkage.

398 The wide range of distances we recorded from roost sites to linear features suggests that roost
399 sites were available in the vicinity of the linear features and in the wider landscape. This is compatible
400 with our finding that the owls often selected tree branches as day-roosts. In the absence of data directly
401 describing movement, we tested for pattern in the distance from Barn Owl roost sites to linear features

402 (Bond *et al.* 2004). While roost site selection must be influenced by multiple processes, we assumed
403 some degree of association between roost site location and the proximate landscape features. We also
404 assume that roost sites in the vicinity of the roads are not negatively selected.

405 Because there was no tendency for roost sites nearer linear features to be preceded by bearings
406 that were relatively aligned with the linear feature, or to be preceded by sites that were relatively
407 further back along the feature, our study implies that juvenile dispersal is not contingent on the
408 availability of dispersal corridors. In ten cases dispersal was completed and a home range established,
409 which means that the analysis reflected the full post-fledging dispersal period.

410 Our findings are inconsistent with the idea that in Britain young Barn Owls follow river courses
411 when they leave their natal areas (Shawyer 1994, p 91). Moreover, they contradict the notion that rivers
412 and their associated rough grassland corridors are critical habitat features for dispersing Barn Owls
413 (Shawyer & Dixon 1999, p 42), or that these features are followed almost exclusively (Shawyer 1998, p
414 95). Importantly, we note that the rivers in the Devon study area descend rapidly through hilly
415 landscapes and generally lack rough grass banks. However, three birds tagged 400 m from the Stour in
416 Dorset dispersed directly away from the river, despite its rough grass banks, and only one of the 15
417 roosts used subsequently was near the river. These results are incongruent with the expectation that
418 owls dispersing along river courses roost in areas the river has led them to. Regarding the proposal that
419 roadside edges constitute an important dispersal network for juvenile Barn Owls (Shawyer 1987, p 56;
420 Shawyer & Dixon 1999, pp 4, 12 and 39), we could find no evidence that juveniles encountering a major
421 road use a series of roost sites distributed along it and within easy foraging distance.

422 Previous analyses of linear features and Barn Owls used a resource selection approach to
423 characterise buffers where occupancy rates or breeding success was higher (Bond *et al.* 2005, Regan *et*
424 *al.* 2018). In particular, in the USA a positive association between occupancy rates and cumulative
425 stream length within a 1 km radii was attributed to the distribution of prey and roost sites for dispersing
426 juveniles (Regan *et al.* 2018). In contrast, we used the relocation sequences of individuals to infer
427 movements and relate these to linear features. We exploited the best available technology and using

428 batteries rather than solar power still imposes constraints; however, innovations such as downloading
429 VHF data via a beacon to GPS or GSM should facilitate future research.

430 In the UK, 50% of Barn Owl deaths recorded between 1991 and 1996 were found on roads
431 (Newton *et al.* 1997). Nonetheless, we found no evidence to suggest that Barn Owls encountering major
432 roads quickly become casualties (Ramsden 2003). Six birds definitely encountered a major road, but the
433 only known road traffic fatality happened at least 19 weeks after the bird had initially encountered the
434 hazard (Bird 209: Table 1). Eight other birds were tracked in landscapes containing major roads, but only
435 one was definitely killed: Although bird 108 was never recorded crossing a major road, it roosted <
436 900 m from the A38 in November and died on that road 16 months later. Moreover, three birds that
437 crossed the A38 repeatedly survived until the end of our study and recent research on adult Barn Owls
438 in Ireland documents them surviving many such crossings (Lusby & O’Cleary 2017). However, it seems
439 unlikely that Barn Owls can learn to completely avoid collisions on major roads or railway lines, given
440 that some Barn Owl casualties are older, and presumably more experienced, birds. It may be that
441 learning opportunities are unusual because the outcome of contact with vehicles is often lethal.

442 **Conclusions**

443 Different distances in female and male dispersal movements highlight unknown aspects of how young
444 birds acquire a home range. Selection of trees as day-roosts by juvenile Barn Owls that hatch in buildings
445 suggests inherent or flexible roosting behaviour, despite higher risk of predation, loss of heat energy,
446 and becoming wet. Contrasting behaviour of juveniles dispersing in lowland and elevated contexts
447 suggest that altitudinal constraints are more influential during the sedentary phase than during
448 dispersal. Based on the proximity and alignment of consecutive day-roosts, we conclude that major
449 roads, rail lines and rivers did not link the natal site with home ranges and are not critical dispersal
450 corridors for post-fledging Barn Owls. It is hoped that further development and use of GPS tracking
451 devices will enable a greater understanding of Barn Owl behaviour during their critical dispersal phase.

452 **Supporting Material:** A full report containing further details of the relocations in this study is available
453 from the Barn Owl Trust.

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583

584 Table 1. Fledging Barn Owls radio tracked in southwest England. Row shading indicates separate
 585 broods/sites ($n = 8$). M = male, F = female, disp. = dispersal, mov. = movements, RTA =road traffic
 586 accident. Roosts are sites used during the dispersal phase, with those after settling on the home range
 587 given in parentheses.

Bird no. (sex)	Tracking success	Age at disp. (days)	No. disp. mov.	Home Range Established	Roosts used		Outcome	Found - at km
					Tree / Building			
209 F	Yes	96	7	21 Sep	2 (6)	0	Dead - RTA	Visual - 13.5
109 M	Yes	95	16	11 Nov	5 (1)	4	Dead	Tag - 3.2
309 F	Yes	92	3	21 Sep	2 (6)	1	Dead - Fox	Tag - 7.9
208 M	Yes	109	4	30 Sep	3 (3)	0 (1)	Survived	No
108 M	Yes	107	3	15 Sep	0 (3)	0 (3)	Dead - RTA	Ring - 3.2
308 F	Yes	93	4	20 Nov	4 (1)	1 (2)	Survived	No
408 F	Yes	93	4	3 Nov	4 (2)	0 (4)	Survived	No
508 F	Only 14 days	84	2		1	0	Dead	Ring - 23.0
708 M	Yes	101	4	7 Nov	4 (2)	0	Just tag found	Tag - 1.8
608 F	Disappeared	94						No
908 F	Disappeared	78	1		1	0		No
808 M	Disappeared	79	1					No
105 M	Yes	88	2	Unknown	2	0	Dead	Ring - 4.0
205 M	Yes	86	4	14 Aug	2 (8)	0	Survived	No
404 F	Only 21 days	88	5	No	4	1	Dead - starved	Ring - 1.4
504 F	Yes	80	5	24 Aug	4 (2)	0	Survived	No
304 F	Yes ⁶⁴	78	11	No	9	0	Survived	No
1104 F	Only 14 days	65		No	2	1	Dead - Fox?	Tag - 1.8
1004 M	Only 11 days	63		No	2	1	Dead - starved	Tag - 0.1

588

589 Table 2. Relocations at day-roost sites for 12 radio tracked juvenile Barn Owls in relation to linear
590 features (l.f.) in southwest England. Observations were obtained prior to owls settling on their home
591 range and exclude relocations below the 25% quartile of inter roost-site distances. *n* = the number of
592 relocations. The distance along linear features connects points that were closest to relocations and the
593 bearings referred to in column five are between roost sites and along corresponding linear features.
594 Row shading indicates separate broods/sites.

Bird no. (<i>n</i>)	Connecting l.f.	Distance to l.f. (km)	Distance along l.f. (km)	Difference between bearings (°)
209 (3)	Road	2.69 ± 1.731	7.48 ± 3.29	25.5 ± 0.2
109 (7)	Road, River, Rail	1.49 ± 1.26	4.50 ± 2.22	25.3 ± 19.6
309 (3)	Road	1.97 ± 1.32	6.12 ± 3.04	18.4 ± 1.4
208 (2)	Road, River	2.33 ± 0.93	3.94 ± 0.20	32.9 ± 14.5
108 (1)	Road, River	1.63 ± NA	4.43 ± NA	11.9 ± NA
308 (5)	Road, River	1.38 ± 0.32	5.57 ± 2.72	16.5 ± 14.0
408 (4)	Road, River	1.41 ± 0.26	7.22 ± 1.89	15.7 ± 11.2
708 (4)	Road	1.54 ± 0.72	0.48 ± 0.65	56.8 ± 10.3
105 (2)	River	0.08 ± 0.11	1.79 ± 0.78	16.6 ± 19.0
205 (1)	River	2.13 ± NA	3.11 ± NA	21.8 ± NA
504 (3)	River	1.20 ± 1.26	1.56 ± 1.02	33.0 ± 24.6
304 (4)	River	2.33 ± 1.26	0.54 ± 1.1	109.1 ± 37.6

595

596 **Figure Legends**

597 Figure 1. Three areas of southwest England where 19 juvenile Barn Owls (*Tyto alba*) were radio-tagged.
598 Points indicate nest sites and shaded areas are minimal convex polygons (MPCs) from pooled
599 relocations of two birds in 2004 in Cornwall (A, MPC = 0.22 km²), nine birds in 2008 and 2009 in Devon
600 (B, MPC = 264.55 km²), and five birds in 2004 and 2005 in Dorset (C, MPC = 75.52 km²). The inset shows
601 the island of Britain with these counties in dark shading. MPC areas were calculated in the R package
602 adeHabitatHR (Calenge 2006, R Core Team 2020).

603 Figure 2. Soft Teflon® backpack harness attaching a TW-3 radio transmitter for radio tracking Barn Owl
604 *Tyto alba*. Ideally, owlets are tagged at approximately 40 days old. The breast band strap is close to and
605 parallel with the sternum, the body loop rests on the lower edge of the pectorals, and the neck loop
606 follows the outer edge of the clavicular pit. Once the feathers around the tag have been preened, only
607 the antenna is visible.

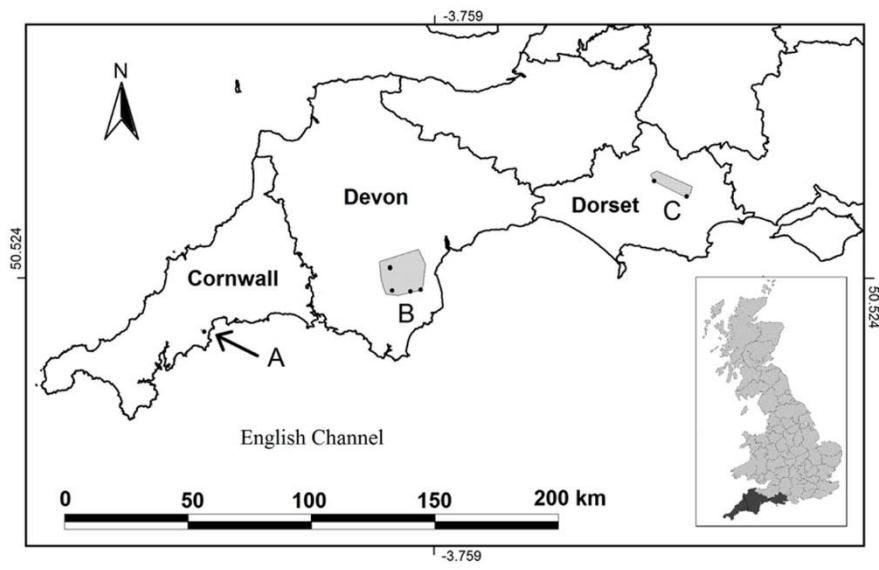
608 Figure 3. Median, interquartile and extreme distances between natal nest sites and relocations for 17
609 Barn Owls at 12 fortnightly intervals from the last fix recorded at the natal site. Distances were obtained
610 from radio tracking 18 individuals in southwest England between 2004 and 2009.

611 Figure 4. The proportion (*p*) of day-roost sites that were recorded in trees during dispersal for 16 radio-
612 tagged Barn Owls tracked in southwest England in 2004, 2005, 2008 and 2009. Natal sites (*x*-axis) were
613 all nestboxes and included one pole-mounted box. The number of sites used is given above each bar.

614 Figure 5. Modelled changes in altitude between the dispersal phase and the acquired home range phase
615 of ten radio-tagged post-fledging Barn Owls in two altitudinal groups. Adjusted means and standard
616 errors are from a GLMM and the *y*-axis is scaled to the square-root of altitude. Mean (\pm SD) relocation
617 altitudes of the lower altitudinal group (squares) were 70 ± 40 and 85 ± 30 m a.s.l. during dispersal and
618 on the home range, respectively, and the corresponding altitudes for the higher group (circles) were 162
619 ± 85 and 100 ± 52 m a.s.l.

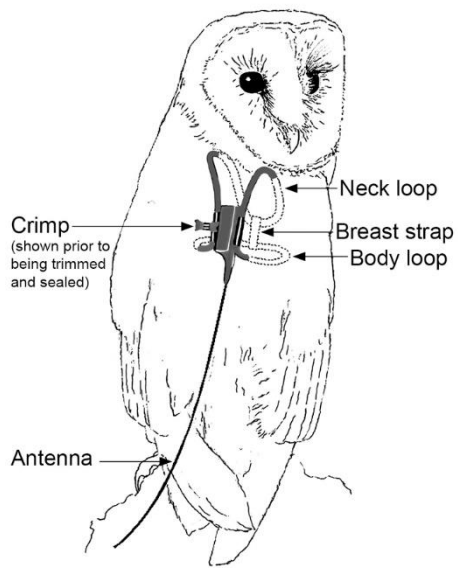
620

621 Figure 1



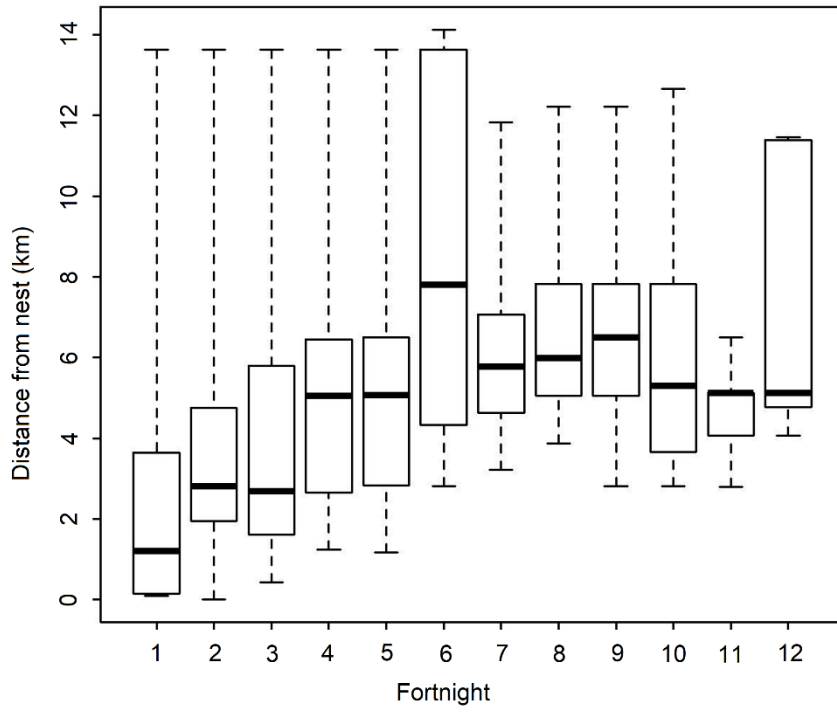
622

623 Figure 2



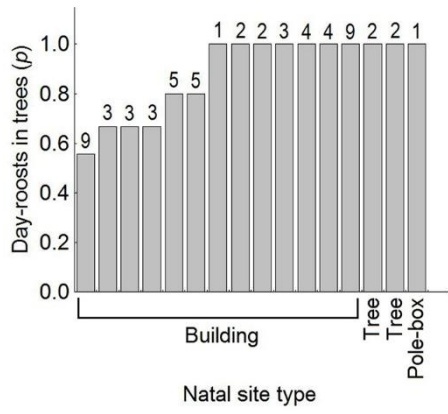
624

625 Figure 3



626

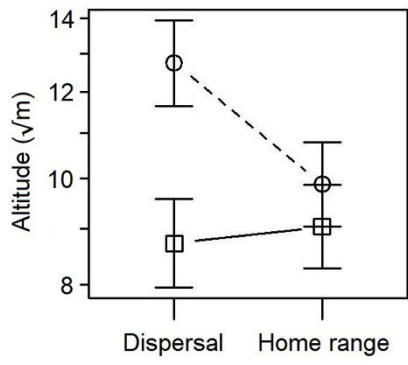
627 Figure 4



628

629

630 Figure 5



631