Post-fledging family space use in blue and great tit: similarities and species-specific behaviours

Post-fledging family space use in blue and great tit: similarities and species-specific behaviours

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Content:
Words: 4449 (text + references) total document 4845
1 table
2 figures

Abstract

In birds, parental escorting of dependent young to feeding areas outside the breeding territory is a commonly observed, yet poorly documented phenomenon. Using radio-tracking, we provide a detailed description of the post-fledging movements of 12 blue tit families (*Cyanistes caeruleus*) and compare these observations with a much larger dataset of the closely related great tit (*Parus major*) collected over several years in the same study area. The proportion of families making excursions outside woodlots was similar in both species (± 50%), but the spatial extent of these movements tended to be larger in blue tits (mean ± SE: 1100m ± 265, range: 643-2374, n = 6) as compared to great tits (mean ± SE: 666 m ± 42, range: 245-1898, n = 64). Blue tit families foraged significantly more in oak habitat within woodlots, independently of excursion behaviour, whereas great tits undertaking excursions shifted their range use towards more variable habitat outside woodlots. The observed excursions of blue tits appeared multiple-day or permanent shifts of the family range, and not daily excursions as most frequently observed in great tits. Although family movements in both species may be largely driven by common underlying factors, our results also points toward species-specific difference in spatial behaviour which may be linked with foraging specializations and post-fledging territory fidelity.

Introduction

Studies on parental care in birds have traditionally focused on the nestling stage with generally much less attention to the care provided after fledging. Yet, in many bird species, the duration of post-fledging care often exceeds that of the nestling stage, thus comprising a significant portion of the overall investment made in reproduction. During this critical stage of transition to independence, fledglings have to learn important skills in flight, foraging and anti-predator behaviour, while still being provisioned and protected by their parents. Since mortality rates of newly fledged young are notoriously high, particularly in small songbirds (up to 87% during the first three weeks post-fledging, e.g. Cox et al. 2014, Naef-Daenzer et al. 2001), this extended care may substantially improve juvenile survival chances, and hence, parental fitness (e.g. Grüebler and Naef-Daenzer 2010, Styrsky et al. 2005, Tarwater and Brawn 2010). However, despite its importance, the post-fledging dependency period has long been neglected in field studies, primarily because following family groups is often very difficult, particularly in closed habitats such as forests.

Due to advancements in tracking technologies over the past decade, the post-fledging dependency period has recently received considerable renewed interest. In particular, much attention has been directed lately to the spatial ecology of family movements. As opposed to the nestling period, in which parents face a central-place task with immobile chicks, the foraging conditions after fledging are often much less space-restricted, allowing parents and their dependent young to move to feeding areas far beyond their breeding territory. Variation in the spatial and temporal dynamics of these foraging movements have recently been linked to a variety of factors, including parental and environmental characteristics (van Overveld et al. 2011), reproductive stage (Vega Rivera et al. 2000), offspring condition (Naef-Daenzer and Grüebler 2008) and various aspects of habitat selection (e.g. Ausprey and Rodewald

65   2011, White and Faaborg 2008, Berkeley et al. 2007, Carneiro et al. 2012, Slagsvold et al.

66   2013). Furthermore, the spatial information that fledglings may receive during these family

67   movements may affect their subsequent dispersal decisions (Drent 1984), as shown by a link

68   between the areas visited by families and offspring dispersal direction (Matthysen et al. 2010)

69   and actual dispersal destinations (Vardakis et al. in prep). This may lead to similarity in

70   dispersal and closer proximity among siblings, with consequences for fine-scale genetic

71   structure and relatedness (Matthysen et al. 2005, Matthysen et al. 2010, Van de Casteele and

72   Matthysen 2006). However, although family movements are a widespread phenomenon

73   across a range of different bird species, they still remain poorly described and understood for

74   most species.

75

76   Here, we used radio-tracking data to provide a detailed description of the post-fledging

77   movements of a small passerine, the blue tit (*Cyanistes caeruleus*), and compare these

78   observations with a larger, partly published dataset on the closely related great tit (*Parus*

79   *major*) in the same study area (van Overveld et al. 2011). Both blue and great tits occur

80   sympatrically throughout most parts of Europe and breed during the same period in similar

81   habitat type, and with largely overlapping foraging niche (Cramp and Perrins 1993,

82   Matthysen et al. 2011). However, the two species also differ in a number of respects such as

83   body size (10-12g for blue tits compared to 16-20g for great tits), mating system (Dhondt

84   1987), non-breeding territoriality (Cramp and Perrins 1993), foraging style (Gibb 1954,

85   Mackenzie et al. 2014, Török and Toth 1999), and dispersal distance (Matthysen et al. 2001).

86   In previous work in a highly fragmented study area, we showed that a substantial proportion

87   of great tit families make excursions outside their breeding territory, with some families

88   moving up to 1.5 kilometer away (van Overveld et al. 2011). Post-fledging family movements

89   in blue tits have so far been described in one study only, and in continuous habitat, with

90 limited movements (mean distance 134m for great and blue tits combined, Slagsvold et al.

91 2013). Our aims in this paper are two-fold. First, we provide basic data on the temporal and

92 spatial scale of post-fledging movement behaviour of blue tits in a fragmented landscape.

93 Second, by comparing the post-fledging movements of two closely related species, we also

94 aim to gain insights into the potential mechanisms responsible for post-fledging movement

95 behaviour.

96

97 **Material & Methods**

98

99 **Study population**

100 Blue tit data were collected in 2009 in a landscape with scattered woodland fragments called

101 'the Boshoek' in northern Belgium (51.13°N - 4.52°E). This area of approximately 10 km²

102 consists of 17 woodlots of mature forest ranging in size from 1 to 12 ha. Neighbouring

103 woodlots are 100 to 600 m apart and separated by small residential areas and agricultural

104 land. Since 1993 all forest woodlots are equipped with standard nestboxes (height 1.5 m

105 above ground, dimensions 23 x 9 x 12 cm) at a high density of nine boxes per hectare (six

106 large-entrance boxes (used by great and blue tits) and three small-entrance boxes (accessible

107 by blue tits only). These boxes contain virtually the entire breeding populations inside the

108 woodlots (for more details see Matthysen 2002).

109

110 **Post-fledging space use of families**

111 The procedures used to determine space use by blue tit families were identical to the study on

112 great tits (van Overveld et al. 2011). When nestlings were about 15 days old, we captured

113 parents with nestbox traps or mistnets and fitted the male with a radio-tag. The radio-tags (16

114   x 6 x 4 mm, antenna: 7 cm) weighed 0.5 g, 4.6 % of the average body mass of the tagged

115   individuals (10.8 g ± 0.4 SD, n = 15). Radio-tags were attached to the birds using a backpack

116   harness from stretch cord of ca. 40 mm (for more details see Naef-Daenzer 2007). The tags

117   lasted for 17–24 days (Model 1035, Advanced Telemetry Systems, Isanti, USA). Families

118   were located 2-3 times per day (range 1-6) by TVO and KS (between 7:00 and 21:00 h,

119   average time interval 2.5 hours, range 1-8 hours). Nestlings of focal broods were provided

120   with brood-specific combinations of colour rings at day 15 to visually confirm whether the

121   fledglings were present after families were located. When families were high in the canopy

122   the presence of fledglings was determined by auditory cues (i.e. begging or parental alarm

123   calls). Once a week we located the roosting sites of all focal males. In case families made

124   excursions (defined as a clear shift in home range towards areas outside the breeding woodlot

125   reflected by core areas and/or total home ranges showing a multimodal distribution, see van

126   Overveld et al. 2011), we performed additional checks to determine whether males/families

127   changed their roosting site or not. We were able to collect data on range use for 12 families (3

128   males were predated within 6 days after tagging), which we were able to track on average 14

129   days after fledging (range 11-17, fledgling age = 21/22 days). However, for none of the

130   families the duration of tracking was long enough to cover the time until family break-up.

131   Based on the average duration of 17 days of post-fledging care of great tits in the same year

132   and breeding in two similar woodlots (range 15-21, n = 9), we expect that our data

133   nevertheless captured a major portion of the post-fledging dependency period, assuming these

134   are similar between the species (Slagsvold et al. 2013).

135

136   **Data Analysis**

137   Post-fledging space use by family groups was quantified using kernel density estimators,

138   calculated in R using the "adehabitatHR" package (Calenge 2014), using a fixed Href of 50m

139   (Naef-Daenzer and Grüebler 2008, van Overveld et al. 2011). For estimations of core areas

140   we used the contours of 50% of the location distribution with the highest use density (50%

141   KDE) and total home range was estimated by the contours of 95% of the total location

142   distribution (95% KDE). We used the furthest distance travelled from the breeding nestbox as

143   a proxy to describe the overall spatial extent of family movements (referred to as maximum

144   distance travelled (m), for more details see van Overveld et al. 2011)

145

146   Space use of blue tit families was compared with pooled data on great tit families collected in

147   2007-2009 (van Overveld et al. 2011, N =32) and 2012-2013 (unpublished data collected by

148   MV and LA, N = 90). Both data sets were quantified in an identical manner, as described

149   above. We calculated three additional characteristics to compare family movements between

150   both species: (1) 'first excursion day': days from fledging until the first excursion was made,

151   (2) 'roost-site selection': roosting in the breeding territory (yes or no), using a radius of 30m

152   around the breeding nestbox based on a breeding density of 3-4 per ha) (no data for 2013)

153   and, (3) 'habitat use': the percentage of observations within woodlots, per family, used to

154   quantify general patterns of habitat selection, i.e., the use of woodlots (mature oak stand) vs.

155   surrounding matrix (gardens, small tree patches, young deciduous shrub).

156

157   Species differences in the family space use (50%KDE, 95%KDE, Maximum distance

158   travelled (all log (x) transformed)) were analysed using linear mixed models based on type III

159   sum of squares using the *lme4* and *car* package in R (Fox and Weisberg 2011). Timing of

160   excursions and habitat use were analysed using Poisson regression models for count and rate

161   data respectively. To test for species differences in excursion behaviour, we included species

162   identity and excursion (yes or no), and the interaction thereof, in all models. To test for

163   seasonal effects on ranging behaviour and habitat use, we included fledging date (relative to

164   the annual average per woodlot using the average weighing date of 15-day old fledglings as a

165   reference). We performed an additional test to examine whether excursion probability

166   increased over the course of the season using a binomial logistic regression. Woodlot was

167   included as a random variable to account for the spatial structure of the population (van

168   Noordwijk 1984) as well as year.

169   **Results**

170

171   **Blue tit family movements**

172   Mean maximum distance travelled by blue tit family groups was 646 ± 187m (range 87-

173   2374m). The most striking differences among families were the frequency and extent of

174   excursions outside the breeding woodlot (Table 1), which were observed in 6 out of 12

175   families (maximum distance: mean ± SE: 1100m ± 265, range: 643-2374, Figure 1). The

176   second largest distance travelled (family a, 1121m) may have been underestimated because

177   the family moved into an inaccessible area, outside the study site. Blue tits undertook their

178   first excursion on average at day 5 after fledging (range 2-8 days). Average time spent outside

179   the breeding woodlot was 3 days (range 2 -5 consecutive days, Figure 1, family a, c-e).

180   Families b and f never returned to their breeding woodlot during the tracking period.

181

182   **Blue tit vs. great tit**

183

184   The proportion of families with foraging excursions was very similar in blue and great tits

185   (50% and 52% respectively, see Table 1 for number of families with excursions for each

186   species). There were no differences between blue and great tit family groups in 50%KDE

187   (p=0.49; mean ± SE: 1.22 ha ± 0.19 and 1.53 ha ± 0.08) and 95% KDE (p=0.25; mean ± SE:

188   5.90 ha ± 0.82 and 7.48 ha ± 0.34), nor did range use differ between families, with or without

189   excursions included as predictor variable (interaction species * excursion: 50% KDE, p=0.34

190   and 95% KDE, p=0.28). However, during foraging excursions blue tit families travelled on

191   average over larger distances than did great tits (interaction species* excursion: p=0.004, β=-

192   0.29, Table 1, Figure 2A). In contrast, when only considering families that remained in their

193   breeding woodlot, maximum distances travelled did not differ between species (p=0.16).

194   Fledging date did not have an effect on family space use in any of the models (p>0.2, all

195   interactions p>0.1).

196

197   In both species, excursion probability only slightly increased with fledging date (p=0.09,

198   interaction species*fledging date: p=0.5). However, the number of days until the first

199   excursion strongly decreased with fledging date in great tits (p<0.001, β=-0.06), although not

200   in blue tits (interaction species*excursion days: p=0.055, β=-0.34), indicating that even

201   (relatively) early broods may eventually decide to make excursions. Blue tit families started

202   their excursion on average 5 days earlier than great tits (Table 1), but taking into account

203   effects of fledging date, this difference was non-significant (p=0.09).

204

205   Overall, blue tit families spent more time within woodlots than great tits (88% and 62% of all

206   locations, p<.001, β=1.51, Figure 2B, Table 1). This differences was mainly due to great tits

207   expanding their habitat range more to areas outside woodlots during excursions than blue tits

208   (76% and 36% of excursion days respectively, interaction species*excursion: p=0.009, β=-

209   1.09). Time spent outside woodlots strongly increased with fledging date for late breeding

210   great tits with excursions (p<0.001, β=0.03; interaction excursion*fledging date: p=0.001).

211   Note that one blue tit family moved to a small wetland area 2.4 km away (Figure 1, family f).

212

213 All blue tit families remained to roost at the site where they had foraged in the day during

214 excursions, even if they returned to their breeding woodlot to forage the following day. In

215 contrast, most great tit families returned to roost in their breeding territory (23 out 30 families

216 (77% , 10 unknown).

217

218 **Discussion**

219 The range of distances travelled varied greatly between different blue tit families, with some

220 frequently leaving their breeding woodlot, similar to great tits studied in the same area (van

221 Overveld et al. 2011). In both species, maximum distances travelled were four times longer

222 than those observed in a continuous forest in Norway by Slagsvold et al. (2013). Despite the

223 small number of tracked families, we showed that distances travelled by blue tit families were

224 significantly longer than in great tits. In addition, we observed significant differences in

225 habitat preferences and roosting behaviour between the two species.

226

227 The similar occurrence of excursions in blue and great tits is most likely explained by their

228 shared dependency on the seasonal peak in caterpillar availability for feeding their young

229 (Naef-Daenzer and Keller 1999) with fledging of young in both species typically occurring

230 shortly after this peak in caterpillar abundance (Matthysen et al. 2011, van Noordwijk et al.

231 1995). The finding that in great tits excursions started at an earlier age in late-fledging

232 families, and that late families spent more time outside woodlots, further suggest that this

233 seasonal change in general food availability may force parents to leave the proximity of their

234 breeding territory to search for other food resources (Slagsvold et al. 2013, Naef-Daenzer and

235 Grüebler 2008). The observation of a blue tit family group moving up to 2 km away from

236 their breeding territory to forage in willow and reed habitat of a small wetland area provides a

237 striking, albeit anecdotal, example of a switch to alternative food resources. Incidentally, reed

238   beds have been documented as important winter foraging habitat for blue tits, but not great tits

239   (Tscharntke 1992). We are currently not aware of other examples in the literature reporting a

240   similar extreme scale of family movements in a small songbird.

241

242   Although food availability in oak habitat may radically change over the course of the season,

243   a substantial portion of parents seem capable of adapting to these changed food conditions by

244   increasing their overall foraging range to find (alternative) food, but without switching to

245   distant foraging areas. Since some oak trees may support large caterpillar populations until

246   quite late into the season (Fischbacher et al. 1998, see also Slagsvold et al. 2013), it is

247   possible that these parents may specifically search for some of these rare spots still rich in

248   caterpillars. Furthermore, foraging excursions by great tits in our population are more

249   frequently observed in families with inexperienced parents and/or parents occupying low

250   quality territories (van Overveld et al. 2011), suggesting family movements to be linked to

251   aspects of parental quality. Unfortunately, our limited sample size does not allow generalizing

252   the above results to blue tits.

253

254   Despite the overall similarity in post-fledging dynamics between blue and great tits, we noted

255   significant species difference in habitat use and the spatial extent of excursions. In contrast to

256   great tits, which seem to expand their range into the surrounding matrix during excursions,

257   including gardens, small tree patches, and young deciduous shrub, blue tits rather seem to

258   target specific habitat patches (other mature woodlots scattered in this matrix or in one case a

259   reed bed). The difference in habitat selectivity between the two species suggest that, when

260   food becomes more scarce late in the season, great tits switch to a more generalist foraging

261   strategy than blue tits. Differences in foraging preferences between both species have also

262   been reported in a recent study on habitat selection in an urban environment, which showed

263   that great tits were less selective in their choice of tree species (Mackenzie et al. 2014). The

264   observed species differences in spatial extent of foraging excursion in our study may therefore

265   be due to foraging specialisations and spatial habitat heterogeneity, rather than differences in

266   mobility *per se*.

267

268   Besides difference in habitat use, we also noted a significant species difference in roosting

269   behaviour. Whereas blue tit families, when moving away from the breeding woodlot, always

270   roosted in the vicinity of their current foraging site, great tit families usually returned in the

271   evening to roost in their breeding territory and/or woodlot. Nonetheless, parents in both

272   species show similarly high breeding site fidelity between seasons (Pampus et al. 2005,

273   Paradis et al. 1998; EM, unpubl. data). Also in our study three blue tit males with large-scale

274   excursions (figure 1, family c, d and f) that survived to the next year were recaptured near or

275   even in the very same breeding nestbox. We hypothesize that differences in roosting

276   behaviour may be linked with an overall lower degree of territory fidelity in blue tits,

277   although direct evidence for this is lacking. While in winter great tits live in flocks, they

278   maintain some degree of territoriality throughout the year, expressed through site-related

279   dominance and defence of roosting sites (Drent 1983, Dhondt and Eyckerman 1980). Juvenile

280   males in their first summer already exhibit strong roost-site fidelity (TVO, unpubl. data). Blue

281   tits roost much less frequently in boxes, at least partly due to competitive exclusion by great

282   tits, and their winter social organization remains largely unstudied (Matthysen 1990).

283

284   An alternative explanation can be sought in the difference in reproductive strategies between

285   the two species. For example, great tits in our population regularly produce second broods

286   (though this has strongly decreased over time; Matthysen et al. 2011), whereas this is much

287   rarer in blue tits (Visser and et al. 2003). It can be hypothesized that by returning to their

288 breeding woodlot and/or territory, female great tits may keep track of local breeding

289 conditions, and we have earlier shown that female rather than male characteristics explain

290 variation in great tit excursions (van Overveld et al. 2011).

291

292 To conclude, our results revealed highly similar temporal and spatial variability in the post-

293 fledging dynamics of blue and great tits. The similar occurrence of large-scale foraging

294 excursions in both species most likely reflects a response to seasonal changes in the

295 availability of their main food resource. Despite strong similarities, we noted significant

296 species differences in movement distances, habitat use and roosting behaviour, for which we

297 offer some possible explanations that deserve further testing.

298

299 **Acknowledgements**

303

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396 **Table 1**. Summary of space use characteristics by blue and great tit families remaining in

397 their breeding woodlot (no excursions) and families making foraging excursions outside the

398 breeding woodlot (excursions). 'First excursions day' refers to the number of days between

399 fledging and the first excursion.

	Blue tit			Great tit		
	Mean ± SE	range	N	Mean ± SE	range	N
No excursions:						
Core Area (ha)	0.77 ± 0.15	0.35 - 1.38	6	1.08 ± 0.06	0.45 - 2.45	58
Home range (ha)	3.75 ± 0.56	1.79 - 5.96	6	5.27 ± 0.25	2.24 - 9.60	58
Max. distance (m)	193 ± 28.2	86 - 251	6	235 ± 10.1	75 - 406	58
Within woodlots (%)	96 ± 2.45	84.6-100	6	74.3 ± 3.92	0 - 100	58
Excursions:						
Core Area (ha)	1.67 ± 0.23	1.21 - 2.73	6	1.94 ± 0.13	0.62 - 6.63	64
Home range (ha)	8.04 ± 0.92	5.16 - 11.44	6	9.50 ± 0.50	3.47 - 26.9	64
Max. distance (m)	1100 ± 265	642 - 2374	6	666 ± 42	245.4 - 1898	64
First excursion day	5.2 ± 0.77	2-8	6	10.0 ± 0.83	0 -27	64
Within woodlots (%)	79.6 ± 7.80	46.6 - 100	6	49.9 ± 3.48	0 - 100	64

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402 **Figure captions**

403 **Figure 1.** Foraging excursions of blue tit families that left their breeding woodlot. Flags

404 indicate the presence of the breeding nestbox. Only families e and f moved to a habitat

405 differing from the oak habitat in their breeding territory/woodlot (e = garden with some oak

406 trees, f = wetland). The largest distance was travelled by family f, which initially moved to

407 another woodlot 1134 m away, followed by another 'jump' of 1240 m towards a small

408 wetland (2 days later), thereby crossing open spaces of up to 100 m.

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411 **Figure 2.** Frequency distributions of (A) maximum distance travelled during the post-fledging

412 period and (B) percentage of locations within woodlots per family. Note that blue tits leaving

413 their breeding woodlot (n = 6) moved over larger distances than great tits, but in only two

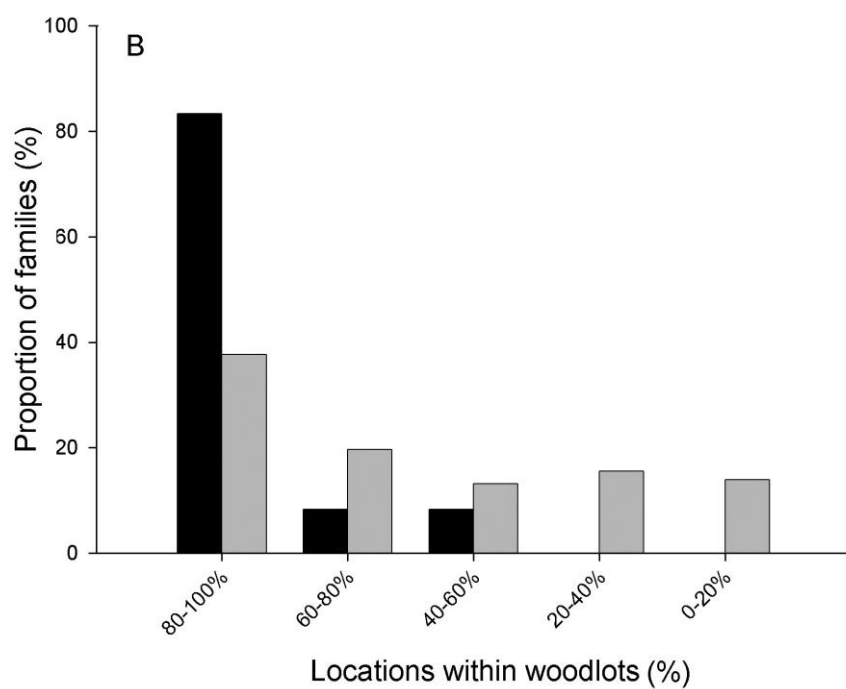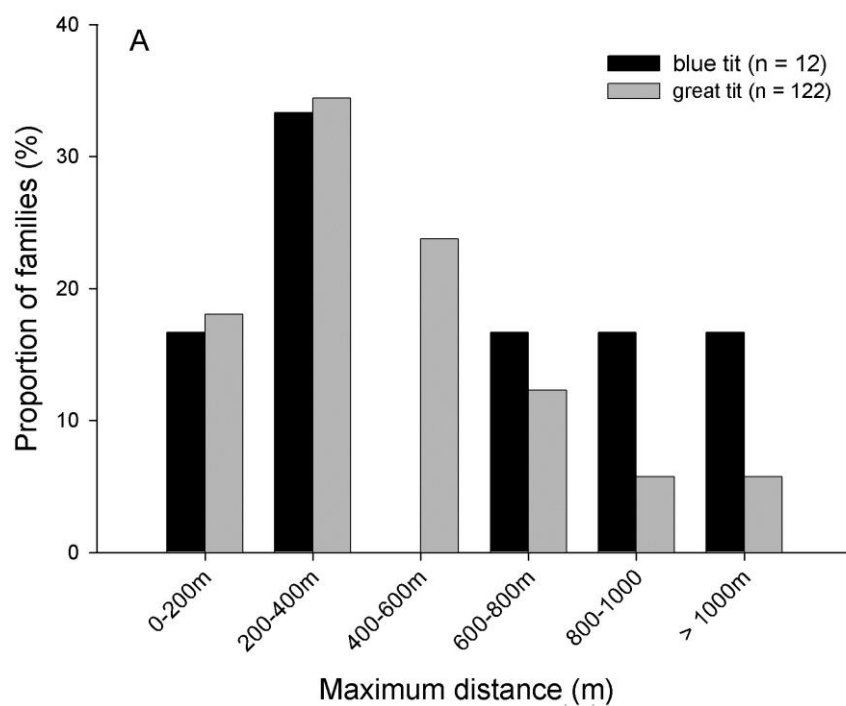414 occasions families switched to different foraging habitat (garden and wetland).

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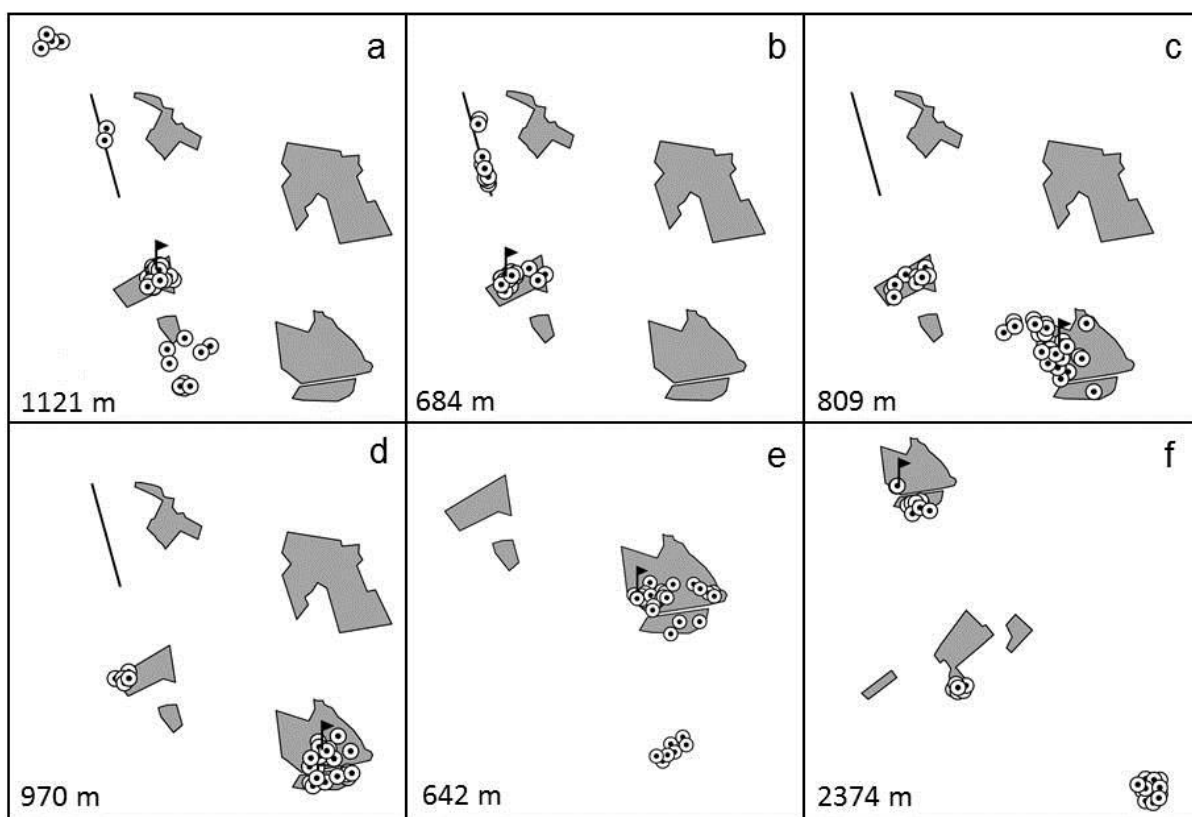
Fig. 1 van Overveld *et al*. Post-fledging family space use in blue and great tit

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Fig. 2 van Overveld *et al*. Post-fledging family space use in blue and great tit

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